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Fine-scale foraging movements and energetics in penguins

Grace Sutton

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Fine-scale foraging movements and energetics in penguins

by

Grace Sutton

BSc(Zoology) (Hons)

Submitted in fulfilment of the requirements for the degree of
Doctor of Biology

Deakin University (Australia),

In cotutelle with Université de La Rochelle (France) école doctorale Euclide.

15th November, 2021



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Abstract

The effects of environmental changes are often most critically felt in species occupying the upper trophic levels. Through top-down processes, top predators influence ecosystem dynamics. In turn, the immediate prey field (i.e. the abundance and type of prey available) can influence a predator's foraging success. Quantifying predator-prey interactions can be logistically difficult, especially in marine environments which are spatially and temporally dynamic. This information is essential to predict how individuals respond to changes in prey availability, an important factor in assessing the impact of natural and anthropogenic climate change.

Considered sentinels of the marine ecosystem, the at-sea behaviour of breeding seabirds reflects the distribution and availability of resources. In comparison to flying seabirds, penguins (Family: Spheniscidae) experience greater constraints when breeding due to their inability to fly. Combined with the high-energy demands of swimming and regular nest attendance patterns restricting at-sea distribution, this group of seabirds are considered good indicators of proximate ecosystem health as they must effectively utilise local resources.

Recent technological advancements in the miniaturisation of animal-borne video data loggers have now made it possible to observe at-sea behaviour of individuals in response to prey field. Used in combination with other tracking devices, these technologies have opened a window into the lives of animals, providing context for fine-scale foraging decisions and other at-sea behaviours. In the present study, a combination of animal-borne video cameras, accelerometers, dive recorders and GPS were used to determine the factors influencing foraging effort and efficiency in

penguins. These factors were investigated at various temporal scales and in 3 penguin species experiencing contrasting oceanographic regimes and, consequently, exhibiting different foraging modes: 1) little penguin, *Eudyptula minor*; 2) African penguin, *Spheniscus demersus*, 3) Macaroni penguin, *Eudyptes chrysolophus*.

In each species, the immediate prey field dictated the 3-dimensional movement in the water column, which ultimately influenced their foraging effort and efficiency. Foraging effort in little penguins was influenced by the abundance of prey but not prey type. The body acceleration of little penguins was examined as an index of effort and compared to energy expenditure rates obtained using the doubly-labelled water technique. Results indicated a strong positive relationship between energy expenditure and mean body acceleration.

Machine learning algorithms for detection of prey captures were developed using a combination of accelerometry, dive loggers and validated using animal-borne video cameras in African and Macaroni penguins. It was found that African penguins exhibited pelagic dives and a large proportion (> 60%) of successful benthic dives, not previously described in this species. Benthic dives were costlier but more successful than pelagic ones, indicating a trade-off between effort and success. The presence of conspecifics and other marine predators also influenced their efficiency. Macaroni penguins displayed prey-specific diving behaviour, diving deep when foraging on subantarctic krill (*Euphausia vallentini*) and completing shallow dives when targeting small juvenile fish.

This body of work highlights the applicability of novel techniques in determining the foraging effort and efficiency of penguins and the drivers of variability in

foraging behaviour. The nuanced predator-predator and predator-prey interactions played a fundamental role in determining foraging efficiency and success and have the potential to influence the structure and dynamics of ecosystems. A greater understanding of the fine-scale factors influencing foraging success of penguin species is important to project how individuals may respond to future climate and anthropogenic pressures.

Preface

The ethical procedures were conducted in accordance with the guidelines, and approval, of the Deakin University Animal Ethics Committee (B25-2016 01/08/2016) and conducted under Wildlife Research Permits (10008044) of the Department of Environment, Land, Water and Planning (Victoria). All work undertaken in South Africa were approved under the ethical regulations of Nelson Mandela University and field experiments were approved by the South African National Parks (PICL1282). Fieldwork conducted on the Macaroni penguins was authorised by the Comité Ethique Polaire (CEP 13/6/2017). This work was included in the research program “Oiseaux Plongeurs” Prog. No.394, funded and logistically supported by Institut Polaire Français Paul Emile Victor (IPEV). Permission to work on the Macaroni penguins and logistical assistance was provided by Terres australes et antarctiques françaises (TAAF).

This project was supported financially by research grants provided by the Holsworth Wildlife Research Endowment and the Centre for Integrative Ecology, Deakin University. In addition, overseas travel between Australia, South Africa and French overseas territories were provided by Birdlife Australia and the Nicolas Baudin travel grant.

This thesis begins with a General Introduction to the topic in Chapter 1. The core data chapters of this thesis (Chapters 2-5) have been published or submitted for publication in peer-reviewed journals. I am the principal contributor to all chapters of this thesis. I collected and analysed all data and I am and the primary author on all publications arising from this thesis. Professor John Arnould is co-author on all

publications for his contribution to the study design, fieldwork, and editorial advice throughout the project. Dr Lorien Pichegru is co-author on Chapter 4 for her assistance with the study design, fieldwork and editorial advice. Professor Charles-Andre Bost is co-author on Chapters 4 and 5 due to his assistance with the study design and editorial advice. Professor John Speakman is co-author on Chapter 3 for his contribution to data analysis. Jonathan Botha is co-author on chapters 3 and 4 due to his assistance with fieldwork, analysis and editorial advice. Professor Abbas Kouzani, Dr Scott Adams, and Kane Mitchell (Chapter 3 and 4) are all co-authors for their contributions to logistics which enabled the data collection for these chapters. Lastly, Chapter 6 forms the General Discussion and synthesis of the main findings of the study.

Publications arising from thesis

Chapter 2

Sutton G.J. and Arnould J.P.Y. (*in review*). Quantity over quality? Prey field characteristics influence the foraging decisions of little penguins (*Eudyptula minor*). *Royal Society Open Science*.

Chapter 3

Sutton G.J., Botha J.A., Speakman J.R., and Arnould J.P.Y. 2021. Validating accelerometry-derived proxies of energy expenditure using the Doubly-Labelled Water method in the smallest penguin species. *Biology Open*. 1;10(4):bio055475.

Chapter 4

Sutton G.J., Pichegru L, Botha J.A., Kouzani A.Z., Adams S, Bost C.A., and Arnould J.P.Y. 2020. Multi-predator assemblages, dive type, bathymetry and sex influence foraging success and efficiency in African penguins. *PeerJ* 8:e9380. 10.7717/peerj.9380

Chapter 5

Sutton, G.J., Bost, C.A., Kouzani, A.Z., Adams, S.D., Mitchell, K., and Arnould, J.P.Y. 2021. Factors influencing fine-scale foraging effort and efficiency in Macaroni penguins. *Marine Biology*. <https://doi.org/10.1007/s00227-020-03811-w>

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If you are reading this, it means I have completed my thesis! This achievement wouldn't have been possible without the support of so many.

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As a first generation university student, I didn't even know what a PhD was until I entered university. From then on, I had a sneaky dream to have "Dr" in front of my name! To my Mum and Dad, Linda and Robert, who have modelled to me the definition of hard work, thank you for your encouraging me in my passions, believing in me, and for sacrificing so much for my brothers and I. Davey, Saya and Lukka, thank you for your support and listening to my crazy stories around the dinner table. Thank you to Voola, Laura and Lauren for your constant prayers, support and encouragement in everything I do. To my Saffa family: Aubrey, Michelle, Megan, Zander, Lizeldi, Jannie, Zandri, Dawie, and little DJ. From day one, you welcomed me with open arms and I can't wait to see you all again (pandemic permitting)! Mom and Dad, thank you for your constant positivity, love and counsel. It means the world. I won't hold it against you if you just flip through the watercolours I put together these last weeks!

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Finally, and I really mean it this time, penguins are the best. They are silly, loyal and so much fun to work on. I am constantly amazed by their tenacity (bite force) and ability to thrive in such rugged and difficult conditions. Thanks for playing along and, for the most part, returning with your little backpacks and revealing your secrets.

But ask the animals, and they will teach you
or the birds in the sky, and they will tell you
or speak to the earth, and it will teach you
or let the fish in the sea inform you
Which of all these does not know
that the hand of the LORD has done this?
In his hand is the life of every creature
and the breath of all mankind.
Job 12:7-10

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Chapter 1: General Introduction.



Top order predators

Top order predators play an important role in the structure and functioning of ecosystems. Through top down processes, top predators effect trophic levels below them, altering the community composition (Schmitz & Suttle 2001), increasing biodiversity (Hayward & Somers 2009) and can control the dynamics of prey populations (Griffin et al. 2008). Due to a number of life history traits, the effects of natural and anthropogenic change occurring in ecosystems are usually most noticeable in species occupying the top trophic levels (Winder & Schindler 2004). For these reasons, many top order predators are considered sentinels for change (Sergio et al. 2008). Consequently, knowing where, when and how predators use their environment is imperative to predict their response to environmental variability and how it may impact the ecosystem as a whole.

Predator-prey interactions are a major evolutionary driving force, mediating the behaviour of both counterparts (Schmitz 2017). For example, predation leads to the removal of prey from the environment which can have major impacts on the ecological dynamics of prey populations (Heithaus 2004). Likewise, prey availability can regulate predator populations (Belgrad & Griffen 2016; Frederiksen et al. 2006). Understanding the relative importance of top-down and bottom-up effects is critical for predicting how climate-driven changes impact top predators (Frederiksen et al. 2006). While there have been many studies linking prey availability with fitness, survival and reproduction (Borges et al. 2011; Mukherjee & Heithaus 2013), few studies have addressed fine-scale decision making of predators in response to prey characteristics (Benoit-Bird 2004).

The presence of conspecifics and heterospecifics may also influence the foraging success and efficiency outcomes of individuals (Clark & Mangel 1986). For example, predators can work together to increase capture success (Cooper 1991; Rodman 1981) or outcompete when aggregated at a depleting shared resource (Cresswell & Quinn 2011; Ranta et al. 1993). The prey field (i.e. the type and abundance of prey immediately available to a predator) is thought to play an important role in the formation and maintenance of foraging groups (Benoit-Bird 2004). Quantifying how a predator interacts with its prey field, and how other predators influence these interactions, allows for a greater understanding of animal behaviour. Furthermore, understanding predator-prey dynamics may allow for predictions of how individuals may respond to changes in the abundance of prey, an important factor in assessing the impact of natural and anthropogenic climate change (Tablado et al. 2014).

Seabirds and the marine environment

The marine environment is a particularly dynamic system with chemical and physical conditions constantly changing over various spatial and temporal scales (Ehler 2012; Zimmer & Butman 2000). Faced with the problem of finding enough food to survive and reproduce, evolution has produced a vast array of morphological and physiological adaptations that enable marine predators to locate and exploit unpredictable resources (Hazen et al. 2019). Marine predators consume a wide variety of prey including passively swimming organisms such as planktonic crustaceans (e.g. krill), salps and jellyfish, as well as nektonic species such as fish and cephalopods (Schreiber & Burger 2001). However, unlike in terrestrial environments, where predator-prey interactions can be observed, the prey field in

marine environments is rarely quantified due to logistical difficulties in observing both predator and prey (Williams & Yeates 2004).

Instead, measures of abiotic factors such as primary productivity and sea surface temperature (SST) have been used to infer areas of high quality throughout the environment (Pienkowski 1983; Sims 2003; Weise & Costa 2007). However, these broad-scale indices rarely provide the temporal and spatial resolution required to accurately measure prey field characteristics. In addition, spatial mis-matches have been identified between predators and their prey. The temporal lags between broad-scale environmental data used to infer prey availability and predator movements indicate these variables may not be a good predictor of predator-prey interactions (Grémillet et al. 2008). Fine-scale prey field information is therefore, necessary for detecting predator responses and accurately testing foraging theory assumptions.

With an overall consumption of biomass of the same order of magnitude as global fisheries (Cury et al. 2011), seabirds play an important role in the structure and function of marine ecosystems. Occurring across all oceans, from coastal areas to open water systems, seabirds are easier to study than most marine animals as they are conspicuous and must return to land to breed. Furthermore, as they usually breed in dense colonies, it is possible to follow the phenology and behaviour of many individuals at once (Carr et al. 2020). Several studies have shown that seabirds are sensitive to environmental variability and unexpected changes in their numbers, health or breeding success may act as an indicator of local environmental degradation (Piatt et al. 2007; Sydeman et al. 2012). Consequently, knowing where they forage and how individual strategies vary, allows for a better understanding of ecosystem

processes (Taylor & Friesen 2012). While seabirds display a wide range of strategies to find and catch prey, few studies have investigated the fine-scale dynamics of these predator-prey interactions.

From Antarctica to the tropics, penguins (Family: Sphensicidae) rely on regions of high oceanic productivity where their prey is found (Pichegru et al. 2010).

Considered sentinels of the marine environment, they are particularly vulnerable to changes in their environment (Boersma 2008) with 10 of the 17 species identified as vulnerable to extinction (IUCN, 2021). During the breeding season, energy requirements of synchronously breeding adults peak while their foraging range narrows (Ropert-Coudert et al. 2019). Therefore, regions close to breeding colonies are especially important to support large numbers of individuals when a large proportion of time and effort is dedicated to provisioning offspring (Bethge et al. 1997).

Many penguin species display group foraging strategies which may increase their foraging success and/or reduce predation risk (Sutton et al. 2015; Takahashi et al. 2008; Takahashi et al. 2004c; Wilson et al. 1986). While foraging behaviour of most penguin species has been thoroughly investigated, few studies have addressed predator-prey interactions and fine-scale foraging decisions in relation to prey field. By further developing our understanding of *in situ* foraging decisions and the effort which these animals expend when foraging, we are better able to predict how individuals may respond to the threats associated with their changing environment (Ropert-Coudert et al. 2019).

Bio-logging is one approach used to understand predator-prey interactions (Ropert-Coudert & Wilson 2005). This method can integrate biotic (i.e. animal behaviours) and abiotic factors (environmental variables) as well as external and internal factors that are easily translatable from individual animals into populations (Ripperger et al. 2020). Animal-borne data loggers can provide position information of free-ranging animals, however, it rarely provides information at a fine enough to understand fine-scale behaviours such as prey captures. Recently, the use of accelerometers have been gaining in popularity due to the fine-scale resolution they provide (Brown et al. 2013; Rutz & Hays 2009). Accelerometers record information at a resolution not provided from any other bio-telemetry (i.e. 25-50 Hz), allowing for identification of rapid behaviours such as flight/fight responses and prey encounter events.

An important prerequisite to understanding and analysing bio-telemetry data is a sound knowledge of the environment experienced by the tracked individual. Animal-borne video cameras can provide information on a predator's responses in relation to their prey field, heterospecifics and conspecifics in otherwise cryptic environments (Yoda et al. 2011). Technological advancements in the miniaturisation of these devices allow for an integrated approach and the instrumentation of multiple sensors on a single individual. This information is crucial for understanding the factors that influence foraging success in free-ranging predators (Rutz & Hays 2009; Watanabe & Takahashi 2013) and a fundamental "missing-link" in understanding predator foraging ecology.

Research objectives and thesis structure

Over half of the world's penguin populations are threatened or experiencing shifts in their ecosystems leading to reduced food availability (Crawford et al. 1995; Ropert-Coudert et al. 2019). Ecological shifts result in short-term reproductive consequences on individuals, which in the long term may cause cascade-effects on populations (Le Bohec et al. 2008). These changes are thought to be due to a combination of anthropogenic climate change and environmental variability (Forcada & Trathan 2009). However, little is known of the fine-scale foraging decisions individuals make, which, ultimately impacts their fitness. This thesis seeks to validate techniques for determining foraging effort and efficiency of penguins. Providing an evidence base for this may help to better understand their behaviour and help develop management strategies for the conservation and protection of these ecologically significant and threatened species.

Using a combination of animal-borne video cameras, accelerometers, dive recorders and GPS data loggers, this project investigated the factors influencing foraging effort and efficiency in penguins.

The objectives of this study were to determine in penguins:

- 1) The influence of prey field on at-sea movements and foraging behaviour.
- 2) The accuracy of accelerometry as a means of estimating energy expenditure.
- 3) Factors influencing effort and efficiency of foraging penguins.

These were investigated at various temporal scales and in three penguin species experiencing contrasting oceanographic regimes and, consequently, exhibiting different foraging modes: 1) little penguin, *Eudyptula minor*; 2) African penguin,

Spheniscus demersus; 3) Macaroni penguin, *Eudyptes chrysolophus*. This collection of work investigated the relationship between energy use, activity budgets, the influence of prey field and other foraging conspecifics and heterospecifics on foraging effort and efficiency. This thesis is structured with the central chapters reporting specific studies that have been submitted to, or published in peer reviewed journals.

Chapter 2 addressed the study objectives in little penguins which forage in shallow waters in south-eastern Australia. This chapter focused on how individuals alter their foraging effort (patch residency time) in response to changes in prey type and patch abundance.

Due to their small size and regular nest attendance patterns, little penguins were used in Chapter 3 as a model species to investigate the relationship between calculated energy expenditure and a number of commonly used proxies of energy expenditure. By validating accelerometry as a reliable measure of energy expenditure, the use of accelerometers in calculating effort was warranted.

Chapter 4 investigated the influence of dive type (benthic and pelagic), conspecifics and heterospecifics on the foraging effort and diving efficiency of African penguins. The African penguin primarily consumes forage fish and is classified as endangered on the IUCN list. Quantifying this species at-sea behaviour is necessary for understanding how changes in prey availability may influence the foraging strategies, success, overall efficiency.

Chapter 5 investigated the foraging behaviour of the Macaroni penguin, in response to prey type, patch density and conspecifics. The Macaroni penguin is the

most numerous penguin species in the world and specialises in foraging on krill. This species was chosen as it is one of the seabirds with the largest prey biomass consumption in the Southern Ocean (Barbraud et al. 2020). As such, it is important to quantify prey consumption rates, how decisions may change over various spatio-temporal scales (i.e. dive-by-dive and prey patch) and the consequences for foraging effort.

Finally, the General Discussion (Chapter 6), summarises the key findings of chapters 2-5, and discusses the potential for a single prey capture model to determine prey captures in penguins. In addition, this chapter examines the factors influencing foraging behaviour in penguins, which is discussed in a broader conceptual framework with respect to future directions for research and, briefly, how it may inform policy for the conservation of penguin species.

Chapter 2: Quantity over quality? Prey field characteristics influence the foraging decisions of little penguins (*Eudyptula minor*).



A version of this chapter has been submitted for publication as:

Sutton, G.J. and Arnould, J.P.Y. 2021. Quantity over quality? Prey field characteristics influence the foraging decisions of little penguins (*Eudyptula minor*).

Royal Society Open Science.



Abstract

An animal's foraging behaviour is known to be influenced by the prey field (i.e. the type and availability of prey). Therefore, quantifying these characteristics is paramount for testing behaviour, especially with regard to the assumptions of optimal foraging models. However, prey information is often lacking due to logistical constraints, especially in marine environments where direct observation of predator-prey interactions is rarely possible. In the present study, animal-borne video data loggers were used to determine the responses of a central place foraging generalist species, the little penguin (*Eudyptula minor*), to its immediate prey field. In accordance with the marginal value theorem, individuals displayed longer patch residency times (PRT) at prey patches of higher density. However, PRT did not vary between prey types of different energetic contents, deviating from what was expected. The results of the study suggest that little penguins maximise foraging performance and overall fitness in an unpredictable environment when facing foraging constraints by concentrating efforts at larger quantities of prey, irrespective of its quality.



Introduction

Animals adapt their behaviour in response to their immediate environment in order to maximise energy gain and minimise their energy expenditure. Energy acquisition through efficient foraging strategies directly translates into an animal's fitness. Therefore, understanding these behaviours is important for predicting population trends in a changing environment (Boyd & Hoelzel 2002). The marginal value theorem (MVT) offers principles to test foraging decisions in an environment where resources are distributed in discrete patches. It postulates that predators should exploit a patch until the rate of gain diminishes to the average for the environment (Charnov 1976). Therefore, the MVT makes the assumption that foragers have *a priori* knowledge of the overall habitat quality and can judge, at the patch level, when their intake has reached the marginal rate of the environment. To date, the MVT has mostly been investigated in controlled environments where food is found in stable densities and can be actively manipulated by researchers (Charnov 1976; Higginson & Ruxton 2015). However, the MVT is largely untried in predators hunting in a highly dynamic environment.

The marine environment is considered a “patchy” system, where the distribution of pelagic prey is extremely variable over space and time (Fauchald 2009). While there have been attempts to quantify prey presence through the use of meso-scale environmental characteristics (e.g. SST and Chlorophyll-*a*), mis-matches between these variables and the distribution of marine predators suggest that there may be time-lags associated with these data (Grémillet et al. 2008). To better understand predator-prey interactions and foraging decisions, high resolution information is



required to quantify prey field (i.e. the type and density of prey which is immediately available to the forager).

Animal-borne video data loggers can provide insights into the otherwise unobservable at-sea behaviours of not only the instrumented individual but the conspecifics, heterospecifics and prey field as well (Sutton et al. 2020; Takahashi et al. 2008; Takahashi et al. 2004b; Thiebault et al. 2019). While video camera data has previously been used to observe predator-prey interactions, few studies have determined behavioural responses to prey abundance and quality (i.e. the energetic value) (Hazen et al. 2015). It is these direct prey field measurements that allow insight into patch-residency time decision making, enabling *in situ* validation of foraging theory assumptions.

Breeding seabirds employ a central place foraging strategy, returning regularly to the colony to feed their offspring. During this period, they must consume high energy content prey for self-maintenance and offspring provisioning (Boyd et al. 2014) while foraging under spatio-temporal constraints. The little penguin is an important consumer in marine ecosystems of south-eastern Australia, a region of highly variable and rapidly warming waters (Lough & Hobday 2011). Due to its high cost of transport and small size, breeding little penguins restrict their foraging range in order to regularly return to the colony for offspring provisioning. While some studies have suggested negative consequences in breeding success due to changes in pelagic prey availability (Dann et al. 2000), few studies have investigated how the immediate prey field influences little penguin foraging decisions (Sutton et al. 2015). Understanding how individuals maximise their foraging success when faced with changes to prey



density and spatio-temporal constraints during important life-history phases may provide insight into how predicted changes to prey availability may impact population dynamics in this region (Ropert-Coudert et al. 2019).

The aims of this study, therefore, were to determine in little penguins the relationship between patch residency time (PRT) and prey field factors: 1) prey type and 2) patch density. According to the MVT, animals should be able to distinguish between prey types to choose those with the greatest profitability and adjust their foraging time accordingly (Patenaude-Monette et al. 2014; Stephen & Krebs 1986). Therefore, it is hypothesised that individuals will forage longer at prey patches of higher calorific density.

Materials and methods

Study sites and animal handling

In order to increase the likelihood of detecting varying types and densities of prey, the study was conducted at two breeding colonies in south-eastern Australia: London Bridge (LB, 38°62'S, 142° 93'E) and Gabo Island (GI, 37°56'S, 149°91'E). During the 2014–15 (October-January) breeding period, adult penguins rearing small chicks were captured in their nest burrows, weighed in a cloth bag using a spring balance (± 10 g) and measured using Vernier callipers (± 1 mm) to determine sex (Arnould et al. 2004).

Individuals were instrumented with a video data logger (Catnip Technologies Ltd., U.S.A, 30 x 40 x 15 mm, 20 g, 400 x 400 pixels at 30 frames·s⁻¹) programmed to record on a duty cycle of 15 min every hour, and a GPS (Mobile Action Technology, I-gotU, GT-120, 44.5 x 28.5 x 13 mm, 20 g) programmed to sample location every 2



min. The devices were attached along the dorsal midline using Tesa® tape (4651), with the camera facing forward. Together, they weighed < 3% of the average little penguin body mass and was < 1% cross sectional surface area. Devices were removed after a single foraging trip.

Data processing and statistical analyses

All data analyses were conducted in the R Statistical Environment (version 4.0.2) (R Core Team 2018). The GPS location data were filtered to remove erroneous fixes that exceeded the maximum average horizontal travel speed of $7.2 \text{ m}\cdot\text{s}^{-1}$ (Hoskins et al. 2008) and the foraging trip metrics range (km) and total duration (h) were determined using the *trip* package (Sumner et al. 2020).

Species of prey were identified in the video data to the lowest taxonomic level possible with aid of a fish identification guide (Gomon et al. 1994). It was not always possible to determine total patch abundance as the whole prey patch was not always visible. Therefore, an index of prey patch density was calculated for each fish prey patch from a random sample of 10 still images from each dive. A standard rectangle based on 3 body lengths x 2 body lengths of the observed fish was overlaid on the still images and all fish within that rectangle were counted. This was repeated 3 times for each image (Figure 2.1). The physical height and length of each polygon was estimated from the body length of each fish species from literature (Gomon et al. 1994). These values were used to determine the window size and estimates of density (number of prey·m²) which was then standardised to control for the use of different window sizes between prey types using the following equation:

$$D_{scaled} = \frac{x - \overline{PT}_i}{\sigma_{PT_i}}$$



where D_{scaled} is the scaled density value, x is the non-scaled value, the mean (\overline{PT}) and the standard deviation (σ) for each prey type (PT_i).

As an indication of prey quality, energetic content of prey types were estimated from a previous study (Sutton et al. 2015). These estimates (kilojoules, kJ) were multiplied by the scaled densities and used to provide ecological context for foraging decisions. Only video footage of when animals were observed entering and leaving the patch was used with patch residency time (PRT) defined as the beginning of the first dive in which the individual encountered a prey patch to the end of the last dive in a patch. Linear mixed effects (LME) models were used to determine the factors influencing (PRT). Initial comparisons revealed no differences in PRT between sexes or colonies and so data were pooled. The model included prey type and D_{scaled} and an interaction term between prey type and D_{scaled} . To determine if PRT is influenced by energetic quality of a patch, a second LME was performed including prey type and the $\text{kJ} \cdot D_{\text{scaled}}$ and an interaction between these variables. All models included individual as a random factor to account for repeated measures. Model selection was undertaken to determine the most parsimonious combination of predictor variables. The best model was determined as the one with the lowest Akaike Information Criterion, corrected for small sample sizes (AICc) (Brewer et al. 2016). Unless otherwise stated, data are presented as Mean \pm S.E.

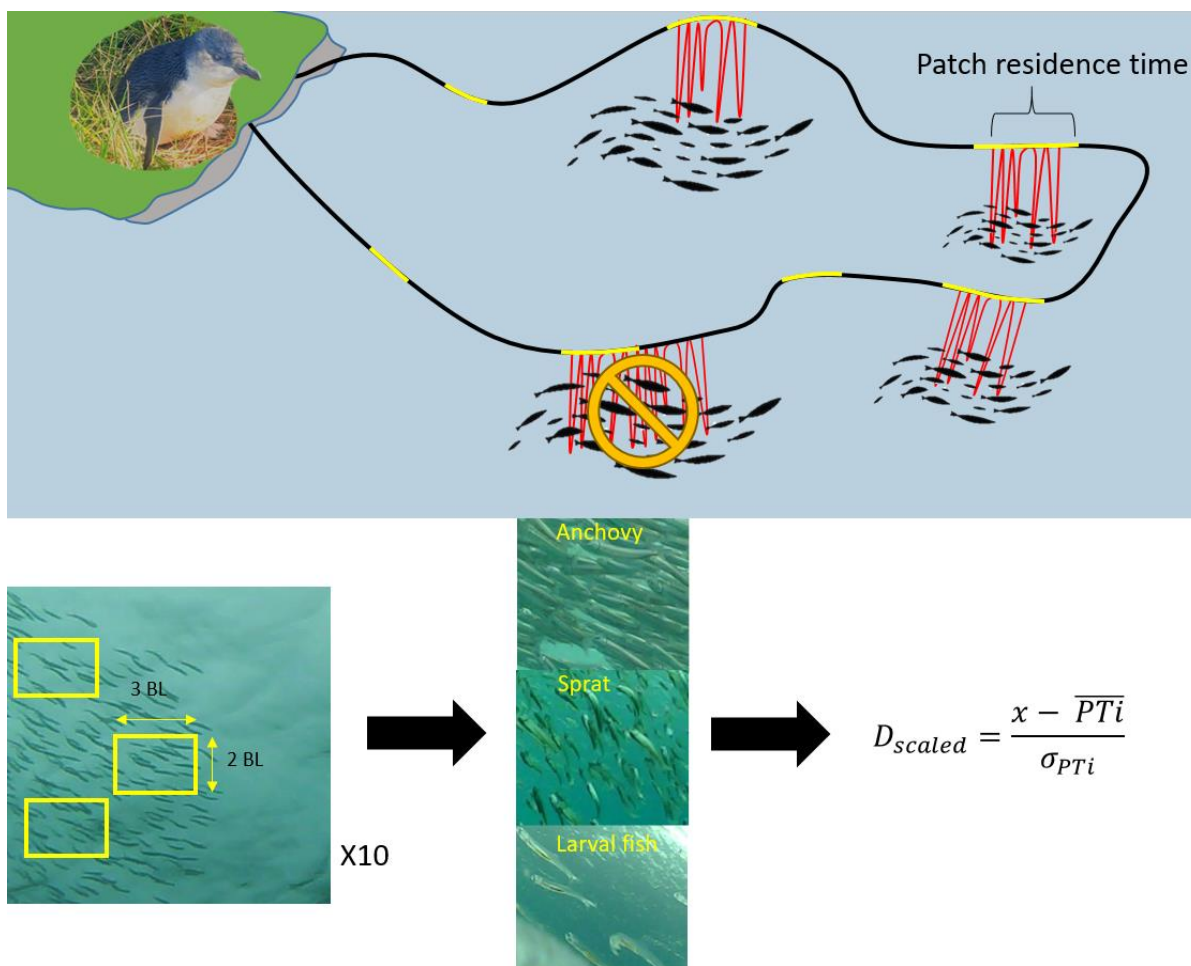


Figure 2.1: Schematic of determining prey abundance and patch residence time from animal-borne video camera data obtained from free-ranging little penguins. Little penguins were tracked with GPS (black line), depth recorder (red lines indicating dives). Video data (yellow lines) was collected over a foraging trip at 15 min every hour. Only prey patches that commenced and concluded during a recording period were used. Number of fish in a window size of 3 x 2 body lengths (BL) was used as an index of abundance for each fish prey type and converted to cm based on average BL values. These values were standardised to obtain a scaled index of patch abundance (D_{scaled}).



Results

A total of 22 little penguins (11 from each colony) were instrumented for a single foraging trip, which lasted on average 15 ± 0.4 h during which individuals travelled a total of 45.06 ± 3.8 km in close proximity to the colony (range: 18.5 ± 1.4 km).

Video data provided on average 4.7 ± 1.1 h of the foraging trip, accounting for approximately 25% of each individual trip. A total of 297 prey patches were identified, during which penguins completed 571 dives (range: 1-16 dives per patch) and consumed a total of 693 prey items. Four main prey species were identified from the video data: southern anchovy, *Engraulis australis*; sandy sprat, *Hyperlophus vittatus*; juvenile Clupeiformes (hence forth referred to as larval fish); and jellyfish, *Cyanea spp* (Figure 2.1).

Numerical and calorific densities were the highest during encounters of anchovy, followed by sprat and larval fish (Table 2.1). The lowest numerical and calorific densities were of jellyfish as they do not school closely together. These were removed from further analyses along with prey captures of solitary prey items and incomplete foraging events ($N = 73$). Individuals consumed on average 5.6 ± 1 fish items per prey patch and spent between 0.5 and 9.3 min foraging at a single patch (mean 1.05 ± 0.2 min). Individuals ceased foraging when the prey patch had dispersed as there were no instances where the prey patch was consumed entirely.

The most parsimonious model explaining PRT included patch density and prey type and an interaction between the 2 variables (Table 2.2). This model accounted for more than 81% of the variation observed in PRT and was the only candidate model



Table 2.1: Summary of prey captures by prey type, range of observed densities and estimated energy content.

| Prey type | Total patches | Total prey captures | Density (m ²) | Energy content (kJ·g ⁻¹) |
|-------------|---------------|---------------------|---------------------------|--------------------------------------|
| Anchovy | 75 | 133 | 0.04-38.4 | 5.2 |
| Sprat | 28 | 52 | 2.6-25.2 | 5 |
| Larval fish | 90 | 180 | 5.5-29.2 | 2.2 |



Table 2.2: Model summary table for patch residency time (PRT) for little penguins.

The predictors: D_{scaled} (scaled density), PT (prey type) and kJ/D (kilojoule per D_{scaled}) were all retained in the most parsimonious model.

| Response Variable | Predictors | Estimates | CI | P |
|-------------------|--|-----------|----------------|------------------|
| PRT | (Intercept) | 71.25 | 26.01 – 116.49 | 0.002 |
| | D_{scaled} | 7.87 | -3.65 – 19.38 | 0.181 |
| | PT(sprat) | 1.78 | -26.00 – 29.57 | 0.9 |
| | PT(larval fish) | -0.85 | -18.52 – 16.81 | 0.925 |
| | $D_{\text{scaled}} * \text{PT(sprat)}$ | 16.15 | -8.05 – 40.35 | 0.191 |
| | $D_{\text{scaled}} * \text{PT(larval fish)}$ | 20.72 | 5.33 – 36.12 | 0.008 |
| PRT | (Intercept) | 71.25 | 26.01 – 116.49 | 0.002 |
| | kJ/D | 0.28 | -0.13 – 0.68 | 0.181 |
| | PT(sprat) | 1.78 | -26.00 – 29.57 | 0.9 |
| | PT(larval fish) | -0.85 | -18.52 – 16.81 | 0.925 |
| | kJ/D * PT(sprat) | 1.57 | -0.11 – 3.26 | 0.067 |
| | kJ/D * PT(larval fish) | 13.85 | 8.86 – 18.84 | <0.001 |



with a $\Delta AICc$ of < 4 . Penguins spent significantly longer at prey patches of higher densities irrespective of its calorific value (Figure 2.2). However, the interaction term indicated that individuals spent more time at higher density patches of sprat and larval fish than anchovy. While prey type was retained in the most parsimonious model, confidence intervals crossed zero indicating that the relationship between PRT and density was not prey-specific (Table 2.2). When accounting for the calorific density of a patch, individuals spent significantly longer at patches of larval fish than at patches of anchovy and sprat which were of similar calorific value.

Discussion

Being visual predators, little penguins are constrained to forage only during daylight hours, with most individuals returning to the colony at sunset to feed their offspring (Klomp & Wooller 1991). Consistent with previous studies (Berlincourt & Arnould 2015; Hoskins et al. 2008), individuals in the present study displayed narrow foraging ranges, further highlighting their spatial and temporal foraging constraints. Subject to these constraints, penguins in the present study made decisions which maximised their capture rate over short periods of foraging and sought to maximise their returns at any opportunity where any prey was present in high densities.

Although considered generalists (Cavallo et al. 2020), it was predicted that little penguins should still differentiate between high and lower quality prey types in order to maintain the necessary time-energy balance and forage in accordance with optimal foraging assumptions. However, in the present study, patch density was an important factor in predicting PRT as individuals spent similar time at patches of higher numerical density irrespective of prey type.

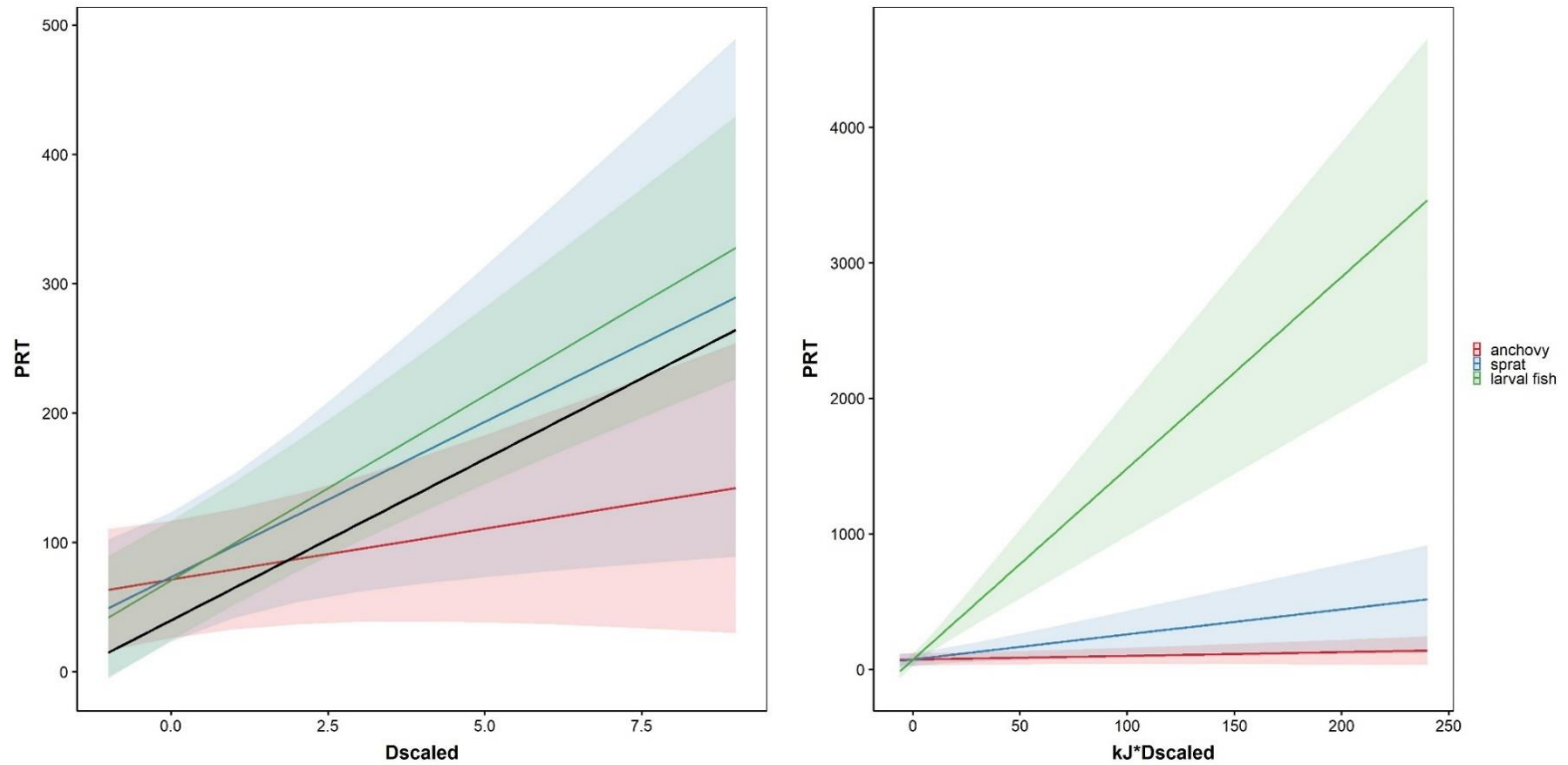


Figure 2.2: Model estimates of patch residency time (PRT) for numerical density (D_{scaled}) of each prey type (left) and calorific density ($kJ \cdot D_{scaled}$; right). Numerical density positively influenced PRT but when accounting for calorific density, individuals spent longer at dense patches of low quality prey. Shaded area represents the 95% confidence interval and black line indicates overall relationship between PRT and D_{scaled} .



Increased time at higher densities of prey, regardless of its calorific value, may also imply that penguins do not have prior knowledge of the habitat quality. Indeed, little penguins display low foraging site fidelity, reflecting the dynamic nature of the marine environment and pelagic prey (Camprasse et al. 2017). As penguins forage in a dynamic environment on prey that is highly mobile, it is likely that individuals in the present study judged the marginal rate of return on a patch-to-patch basis, assuming similar density and calorific quality throughout the environment. Therefore, density, was most important in determining PRT.

When accounting for kJ values in density estimates, individuals spent longer at patches of larval fish than anchovy or sprat. Although larval fish are of lower calorific quality, it is possible penguins may spend a greater time at these patches because fish at this life stage are easier to capture as they are less mobile in comparison to adult fish (Hunter 1972). Indeed, individuals at larval fish patches had a significantly higher capture rate per dive than anchovy, likely reflecting their faster handling/processing times (SI Figure 2.1). As larval fish represented the largest densities in the environment, individuals may have been able to consume greater quantities of these prey as it took longer for the patch to disperse. This could reflect a trade-off between capture effort and energetic gain and also be the reason penguins were observed to consume gelata (Thiebot et al. 2017).

Optimisation models for behaviour must always incorporate constraints. However, without the ability to observe animal behaviour *in situ*, it may be difficult to determine what constraints should be accounted for. The results of the present study suggest a combination of restricted foraging range and lack of prey field knowledge



influence the foraging decisions of little penguins during the breeding season.

Foraging behaviour is often quantified by tracking individuals during the breeding season as they are more easily accessible. However, during these periods they face constraints and, therefore, foraging behaviour during the breeding season may not be representative of their full annual cycle. Indeed, several seabirds have been found to extend their range and utilise alternative strategies outside of the breeding season (Pistorius et al. 2015). Future studies should, therefore, consider investigating the influence of prey field on foraging behaviour during these periods.

In summary, this study presents the fine-scale foraging decisions made by little penguins in relation to their immediate prey field. The results of this study indicated that individuals are influenced by the density of prey at a location rather than its potential calorific value. This likely reflects the spatio-temporal constraints individuals face when foraging under short time periods and in close proximity to the colony. These constraints, with the addition of the dynamic nature of pelagic prey in the marine environment, resulted in individuals choosing prey patch quantity over calorific quality during the breeding season.

Chapter 3: Validating accelerometry-derived proxies of energy expenditure using the Doubly-Labelled Water method in the smallest penguin species.



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Abstract

Understanding energy use is central to understanding an animal's physiological and behavioural ecology. However, directly measuring energy expenditure in free-ranging animals is inherently difficult. The doubly-labelled water (DLW) method is widely used to investigate energy expenditure in a range of taxa. Although reliable, DLW data collection and analysis is both financially costly and time consuming. Dynamic body acceleration (e.g. VeDBA) calculated from animal-borne accelerometers has been used to determine behavioural patterns, and is increasingly being used as a proxy for energy expenditure. Still its performance as a proxy for energy expenditure in free-ranging animals is not well established and requires validation against established methods. In the present study, the relationship between VeDBA and the at-sea metabolic rate calculated from DLW was investigated in little penguins (*Eudyptula minor*) using three approaches. Both in a simple correlation and activity-specific approaches were shown to be good predictors of at-sea metabolic rate. The third approach using activity-specific energy expenditure values obtained from literature did not accurately calculate the energy expended by individuals. However, all three approaches were significantly strengthened by the addition of mean horizontal travel speed. These results provide validation for the use of accelerometry as a proxy for energy expenditure and show how energy expenditure may be influenced by both individual behaviour and environmental conditions.



Introduction

Energy is a finite resource and a central currency in determining the behaviour and physiology of animals (Butler et al. 2004; Speakman & Król 2010). How animals allocate their time and energy critically influences important aspects of their life history, including food acquisition, growth and reproduction (McNamara & Houston 1996). Accurately estimating the energetic costs of these behaviours has long been a central theme in behavioural ecology and is crucial to understanding how animals adapt to environmental variability. However, directly measuring the energy expenditure (DEE) of free-ranging animals is inherently difficult due to various logistical constraints (Speakman & Racey 1988).

Techniques that measure the energy expended by free-ranging animals have centred around three methods. 1) Determining time-activity budgets and assigning energy values to observed activities (Utter & LeFebvre 1973; Weathers & Nagy 1980); 2) estimating energy expenditure from the relationship between heart rate and CO₂ production through implanted heart rate loggers (Arnold et al. 2006; Butler et al. 2004; Green et al. 2001; Halsey et al. 2008) and; 3) the measuring washout rates of injected stable isotopes through the doubly labelled water method (Speakman 1993). Each technique is associated with a suite of drawbacks, namely accuracy (Goldstein 1988), ability to calibrate measurements on captive populations (Goldstein 1988; Morrier & McNeil 1991), invasiveness (Green 2011) and cost of analyses (Butler et al. 2004; Speakman 1997).

Of the aforementioned techniques, the doubly-labelled water (DLW) method requires only blood samples at the beginning and end of the measurement period



(Speakman & Racey 1988). It can thus be more easily applied to free-ranging animals. However, the DLW method only provides a single energy expenditure value over the measurement period and the financial cost of isotopes and their analyses may limit the size and number of animals that can be sampled (Butler et al. 2004; Shaffer 2011). Therefore, it is important to develop and validate techniques to measure energy expenditure over greater temporal periods.

Over the past two decades, there has been widespread deployment of animal-borne accelerometer data loggers (Brown et al. 2013; Vacqu  -Garcia et al. 2015; Yoda et al. 2001). This high resolution data can be used to infer the behavioural states and fine-scale activity budgets of free-ranging individuals (Battaile et al. 2015; Collins et al. 2016). These devices provide whole body acceleration and, with increasing battery life, can provide information over various spatial and temporal scales (Brown et al. 2013; Vacqu  -Garcia et al. 2015; Yoda et al. 2001). With increasing miniaturisation of accelerometer data loggers, it is now possible to obtain this information for relatively small animals (i.e. < 100 g) over extended periods (Brown et al. 2013; Hammond et al. 2016).

In addition to providing information on behavioural activity, accelerometry can be used to quantify energy expenditure (Green et al. 2009; Wilson 2006). By correlating accelerometry-derived estimates of energy expenditure with traditional techniques, the need for such highly-invasive, costly and/or labour-intensive methods of estimating energy expenditure may be by-passed in the future (Halsey et al. 2011b). Simple predictive correlations between Overall and Vectorial dynamic body acceleration (e.g. ODBA and VeDBA, respectively) and energy expenditure



concurrently measured using the DLW method have shown varying degrees of success (Elliott et al. 2013; Hicks et al. 2020; Pagano & Williams 2019). Such relationships have been improved somewhat by separating acceleration into behavioural components (Elliott et al. 2013; Jeanniard-du-Dot et al. 2017). However, studies addressing the relationship between energy expenditure derived from DLW methods and accelerometers have been largely limited to captive or pseudo-captive animals (but see: Elliott et al. 2013; Hicks et al. 2020; Jeanniard-du-Dot et al. 2017).

The little penguin (*Eudyptula minor*), the smallest penguin species, is distributed in colonies around the southern coast of Australia and New Zealand (Chiaradia et al. 2007). The majority of the population is concentrated in south-eastern Australia, a region of rapid oceanic warming (Crossin et al. 2014; Lough & Hobday 2011; Mickelson et al. 1991). The anticipated changes in the marine ecosystem are likely to impact the distribution and abundance of prey for the little penguin (Berlincourt & Arnould 2015; Poloczanska et al. 2007), potentially causing them to work harder (i.e. expend more energy) during foraging. Therefore, an ability to efficiently quantify energy expenditure in free-ranging little penguins is crucial to understanding how an individual's effort may change in response in prey availability (Barbraud et al. 2012; Crossin et al. 2014). While accelerometry is increasingly being used to investigate the foraging behaviour of penguins (Carroll et al. 2016; Kokubun et al. 2011; Van Dam et al. 2002), few have addressed the predictive ability of accelerometers for estimating energy expenditure in free-ranging individuals (Hicks et al. 2020).

Little penguins are diurnal foragers, leaving and returning to the colony at sunrise and sunset, respectively (Klomp & Wooller 1991). Due to their relatively short



foraging trip durations throughout the breeding season (Chiaradia & Kerry 1999) and their small body size (purporting low dosage requirements of DLW), little penguins make an ideal model species for investigating accelerometry-derived estimates of at-sea energy expenditure in aquatic endotherms. The aims of the present study, therefore, were to determine what methods are useful in determining energy expenditure of free-ranging little penguins. The accuracy of three accelerometry-derived estimates of energy expenditure: 1) Vectorial body acceleration (VeDBA); 2) activity-specific body acceleration; and 3) time-activity budgets; were compared to those measured by the DLW method.

Materials and methods

Study sites and animal handling

The study was conducted at two little penguin colonies in Bass Strait, south-eastern Victoria, Australia: Gabo Island (37.56° S, 149.91° E, GI); and London Bridge (38.62° S, 142.93° E, LB). Gabo island, in eastern Bass Strait, which has previously been estimated to host approximately 30-40,000 little penguins (Fullagar et al. 1995) while London Bridge is a small mainland colony in western Bass Strait, which hosted ~100 individuals during the study period. Data collection occurred during November-December 2018, coinciding with post-guard phase of the breeding season where both adults normally forage at sea during the day and return most nights to feed their offspring.

Measurements of daily energy expenditure for adult breeding little penguins were obtained using the DLW method. Individuals were captured at their nest burrow, placed in a cloth bag and weighed using a spring balance (± 10 g, Super Samson,



Salter Brecknall, United Kingdom). An initial blood sample (<1 mL) was collected by venipuncture of a tarsus vein into a heparinised syringe to establish background levels of ^2H and ^{18}O (method D; Speakman and Racey 1987). Individuals were then administered an intramuscular injection (1.01 ± 0.03 g of DLW (64.3% ^{18}O and 34.1% ^2H). Syringes were weighed before and after injection to calculate the mass of DLW injected into each bird (± 0.001 g, FX300i milligram balance, A&D Company Ltd, Japan). Following injections, penguins were returned to their nest burrow for a mean of 3.36 ± 0.09 h, during which time the isotopes equilibrated with the body water pool (Gales 1989).

After the equilibrium period, individuals were removed from the nest and instrumented with 2 devices: a GPS (Mobile Action Technology, I-gotU, GT-120, 44.5 x 28.5 x 13 mm, 20 g) which sampled location at 1 min intervals; and a combined accelerometer/depth recorder (Gulf Coast Data Concepts 76 x 46 x 16 mm, 45g) which sampled depth and acceleration at 1 and 25 Hz, respectively. The devices were securely attached to the feathers along the lower dorsal midline using waterproof tape (Tesa 4651, Beiersdorf, AG, GmbH, Hamburg). A second blood sample was then collected to establish the isotope equilibrium levels and individuals were returned to their nests.

All nests were monitored in the late afternoon of the next day to determine whether individuals had departed to sea on a foraging trip. If an individual was present, it was weighed and a blood sample was collected to obtain a measure of energy expenditure on land. If the individual was absent, the burrow was monitored during the subsequent night and, when the individual returned, it was recaptured after



feeding its chicks, weighed and a blood sample was collected before being released. This process continued for the next 2 days and nights, enabling multiple energy expenditure periods to be sampled in some individuals, before a final blood sample was collected and the data loggers were removed. After the devices were removed, the morphometrics of bill depth, bill length and head length were measured using a Vernier Caliper (± 0.1 mm) and flipper length was measured using a ruler (1 mm). Sex was determined from bill depth following the methods of Arnould et al. (2004).

Data processing and statistical analyses

All blood samples were centrifuged to isolate the plasma from red blood cells within 4 h of collection. Aliquots of plasma were then transferred into flame-sealed capillary tubes (100 μ L) until analyses were performed. Isotope enrichment of blood samples was determined by off-axis integrated cavity output spectroscopy (Berman et al. 2012; Melanson et al. 2018). Total body water was estimated from the ^{18}O dilution space using the plateau method (Speakman 1997). Isotope enrichments were converted into estimates of total energy expenditure (EE_{DLW} kJ) during measurement periods using the two-pool method (Eqn 7.17) (Speakman 1997).

The GPS location data were filtered to remove erroneous fixes that exceeded the maximum average horizontal travel speed of $7.2 \text{ m}\cdot\text{s}^{-1}$ (Hoskins et al. 2008), and dive behaviour data obtained from the depth sensor were corrected for depth drift, using the *diveMove* package (Luque 2007) in the R statistical environment (version 1.1.463) (R Core Team 2018). The filtered GPS track and the dive data were linearly interpolated and merged to the accelerometer data. For each DLW sampling period, the time spent on land and time at sea were calculated from the GPS locations and



accelerometry. The foraging trip metrics: range (km), total duration (h), mean speed ($\text{km}\cdot\text{h}^{-1}$) and total horizontal distance travelled (km), and the dive parameters of mean dive depth (m), total vertical distance travelled (km) were then calculated for each trip using the *trip* and *diveMove* packages, respectively.

At-sea energy expenditure (EE_{DLW-S} kJ) was calculated by subtracting on land energy expenditure (EE_{DLW-L} kJ) from the total energy expenditure over the sampling period (EE_{DLW-T} kJ) using the following equation

$$\text{Eqn 1: } EE_{DLW-S} = EE_{DLW-T} - EE_{DLW-L}$$

Individual estimates of EE_{DLW-L} were determined from the average rate of energy expenditure obtained from individuals sampled while only on land, and adjusted for the proportion of the foraging trip sample duration on land. The EE_{DLW-S} values were then converted to estimates of mass-specific rate of at-sea energy expenditure (DEE_{DLW-S} $\text{kJ}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$) and compared to proxies obtained from the accelerometry data using three methodological approaches:

Approach 1

Accelerometer data for each sampling period were filtered to separate dynamic acceleration (attributed to animal movement) from static acceleration (reflecting animal position with respect to gravity) using a 1 s running mean and, as accelerometers were not attached to the centre of gravity of the animal, Vectorial Dynamic Body Acceleration (VeDBA) was calculated using the following equation:

$$\text{Eqn. 2: } VeDBA = \sqrt{(X_{dyn}^2 + Y_{dyn}^2 + Z_{dyn}^2)}$$

Where X, Y and Z are the dynamic acceleration (*dyn*) of horizontal (surge), vertical (heave) and lateral (sway) movements, respectively.



The sum of VEDBA (area under the curve (Ladds et al. 2017), $VEDBA_{SUM}$) and mean VeDBA ($VeDBA_{MEAN}$), proxies for animal movement, over the study period were calculated for each on-land ($VeDBA_{SUM-L}$, $VeDBA_{MEAN-L}$, respectively) and at-sea sampling period ($VeDBA_{SUM-S}$, $VeDBA_{MEAN-S}$, respectively), as determined from GPS locations at the colony and confirmed by accelerometry (i.e. angle of device indicating individual out of the water).

Approach 2

To determine if activity-specific estimates of energy expenditure provided a better relationship with DEE_{DLW-S} than Approach 1, behavioural categories were identified from the accelerometry and dive data in at-sea periods using *k*-means clustering analysis in the *Ethographer* package in IgorPro (Wavemetrics Inc, Portland OR, USA, version 6.3.7.2) (Sakamoto et al. 2009b). Three behaviour categories were identified: sea-surface resting (e.g. above surface behaviours/grooming on the sea-surface); transiting (horizontal sub-surface movement < 2 m); and diving (sub-surface movement > 2.5 m). The duration of each of the behaviour categories and the mean and total VeDBA was determined for each individual.

Activity-specific energy expenditure was calculated following the methods of Jeanniard-du-Dot et al. (2017). Parameter estimates for each individual were calculated for the behaviour categories based on time spent in each of the behaviour categories. For each individual, the parameter estimates were added to the following equation:

$$\text{Eqn. 3: } EE_{DLW-S} = C_{REST} \times T_{REST} + C_{TRANSIT} \times T_{TRANSIT} + C_{DIVE} \times T_{DIVE}$$



Where EE_{DLW-S} is the total at-sea energy expenditure derived from Eqn. 1, C_i is the parameter estimate for the rate of energy expenditure for each activity and T_i is the time spent (h) in each at-sea behaviour category. The resulting linear equations were used to predict total energy expenditure at-sea, which was converted to an estimate of predicted at-sea mass-specific metabolic rate (DEE_{PRED-S} $\text{kJ}\cdot\text{d}^{-1}\cdot\text{kg}^{-1}$).

Approach 3

To investigate the accuracy of published activity-specific energy values in determining energy expenditure of free-ranging individuals, the time-activity budgets determined above were calculated using the following equation for each individual from published activity-specific energy values using the following equation:

$$\text{Eqn. 4: } EE_{CALC-S} = E_{REST} \times T_{REST} + E_{TRANSIT} \times T_{TRANSIT} + E_{DIVE} \times T_{DIVE}$$

where EE_{CALC-S} is the total calculated at-sea energy expenditure (kJ), T_i is the time spent (h) and E_i is the activity-specific expenditure ($\text{kJ}\cdot\text{h}^{-1}$) for each at-sea behaviour (sea-surface resting, transiting and diving). Published estimates of mass-specific energy expenditure for sea-surface resting and transit behaviour were derived from little penguins. As there was no such information for diving, a proxy was derived from a similar-sized (~1 kg) seabird, the thick-billed murre (*Uria lomvia*), a species which also uses its wings for under-water propulsion (Table 3.1). The EE_{CALC-S}



Table 3.1: Estimates of energy expenditure obtained from literature for sea-surface resting, transiting in little penguins. As there were no species-specific Energy estimates for diving behaviour a proxy was obtained from thick-billed murres (*Uria lomvia*) and mass corrected.

| Activity | Energy value $\text{kJ} \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$ | Reference |
|------------|---|-----------------------|
| Resting | 30.6 | (Bethge et al. 1997) |
| Transiting | 72 | (Bethge et al. 1997) |
| Diving | 87.5 | (Elliott et al. 2013) |



was converted to an estimate of calculated at-sea mass-specific metabolic rate (DEE_{CALC-S} , $\text{kJ}\cdot\text{d}^{-1}\cdot\text{kg}^{-1}$).

The relationships between DEE_{DLW-S} and each metric of daily energy expenditure estimated from accelerometry (i.e. $VeDBA_{MEAN-S}$, DEE_{CALC-S} , DEE_{PRED-S}) were determined using linear regression and the coefficient of determination (r^2) was calculated. To establish whether these relationships could be improved, linear models were constructed to incorporate parameters that were likely to influence energy expenditure. Collinearity of predictor effects were assessed using Pearson's correlation test and parameters with a correlation > 0.70 were removed from further analyses. The retained parameters modelled against DEE_{DLW-S} included: the foraging metrics mean horizontal travel speed ($\text{km}\cdot\text{h}^{-1}$), total vertical distance travelled (km), total horizontal distance travelled (km) and mean dive depth (m); and the morphometrics, flipper length (mm) and bill depth (mm). Model selection was performed using the function *dredge* in the MuMIn package (Barton & Barton 2015). The most parsimonious model was determined as having the lowest Akaike's Information Criterion corrected for small sample sizes (AICc) score and models with $\Delta\text{AIC} < 4$ are presented.

Normality was verified using Shapiro-Wilk tests and *t*-tests were performed to make group comparisons. Unless otherwise stated, results are presented as mean \pm standard error.

Results

A total of 36 individuals were dosed and instrumented for the study (Gabo Island; GI: 15, London Bridge; LB: 21). However, device malfunction resulted in 11



individuals without accelerometer/dive data. In addition, 4 individuals from GI returned from their foraging trip with blood isotopic levels too close to background levels for accurate measures of at-sea energy expenditure to be determined. 12 individuals remained on land following injection of DLW and these individuals were used to determine daily energy expenditure on land (DEE_{DLW-L} , Table 3.2).

Mass specific at-sea metabolic rate (DEE_{DLW-S} $\text{kJ}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$) was obtained over a single foraging trip for 8 individuals and over two foraging trips for one individual with blood samples collected between foraging trips ($N = 10$; Table 3.3). Individual 8 completed two one-day foraging trips, returning in the early hours of the morning before sunrise and leaving again without a blood sample being collected (Table 3.3). As there was only one repeated sampling period at sea, standard linear models were used to determine relationships.

The body mass of individuals at sampling prior to departure on a foraging trip and after returning was 1.14 ± 0.03 kg and 1.10 ± 0.04 kg, respectively. Foraging trips lasted on average 19.3 ± 1.5 h during which individuals covered total horizontal distances of 47 ± 4.2 km. Individuals performed 369 ± 25 dives and covered total vertical distances of 6.3 ± 1.7 km, during 18 ± 2 dives $\cdot\text{h}^{-1}$ to an average depth of 7.5 ± 1.0 m. Body mass differed significantly between the sexes ($t_8 = 3.2$, $P < 0.01$) but there were no sex differences apparent for flipper length, dive depth, foraging range, foraging trip duration and mean or total VeDBA ($P > 0.05$ in all cases).

The DEE_{DLW-L} values ranged 350.3-580.5 $\text{kJ}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$ and there were no statistical differences between the sexes ($t_6 = 0.5$, $P > 0.05$). The calculated rate of daily energy expenditure at sea (DEE_{DLW-S}) was significantly greater (1392.4 ± 119.6 $\text{kJ}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$)



than on land ($429.1 \pm 16.1 \text{ kJ}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$; $t_8 = 10.4$, $P < 0.001$), and did not differ between the sexes ($P > 0.05$ in both cases). These values then provided the relationships between DEE_{DLW-S} and the three accelerometry derived indices of energy expenditure.

Approach 1

Significant differences were evident in the mean VeDBA obtained for when the animals were on land ($VeDBA_{MEAN-L}$; $0.02 \pm 0.01 \text{ g}$) and mean VeDBA for when the animal was at sea ($VeDBA_{MEAN-S}$; $0.2 \pm 0.01 \text{ g}$, $t_8 = 29.8$, $P < 0.001$). While there was a weak relationship ($r^2 < 0.5$) between $VeDBA_{MEAN-L}$ and DEE_{DLW-L} ($r^2 = 0.13$; Figure 3.1), there was a positive significant relationship between DEE_{DLW-S} and $VeDBA_{MEAN-S}$ ($r^2 = 0.83$, $F_{1,8}=32.12$, $P < 0.001$; Figure 3.2a) giving the relationship:

$$\text{Eqn 5.} \quad DEE_{DLW-S} = -877.7 + 10647.7 * VeDBA_{MEAN-S}$$

Model selection after additional predictor variables were added resulted in the most parsimonious model for predicting DEE_{DLW-S} ($\text{kJ}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$) including the predictor variables $VeDBA_{MEAN-S}$ (g) and mean speed (MS , $\text{km}\cdot\text{h}^{-1}$; SI Table 3.1; SI Table 3.3). The addition of MS to the equation provided an improved predictive relationship ($r^2=0.87$; Table 3.4, Figure 3.2b):

$$\text{Eqn 6.} \quad DEE_{DLW-S} = -747.2 + (8046.9 * VeDBA_{MEAN-S}) + (301.0 * MS)$$

Approach 2

Activity budget analysis revealed the highest proportion of time at-sea was spent on performing surface activities ($50.5 \pm 3.6\%$), followed by transiting ($29.4 \pm 2.3\%$; Figure 3.3) and diving behaviour ($17.8 \pm 2.3\%$). Mean VeDBA for sea-surface



Table 3.2: Deployment summary including morphometrics for individuals in DLW experiment at little penguin colonies London Bridge (LB) and Gabo Island (GI), total energy expended calculated from doubly-labelled water (EE_{DLW-T} , kJ). A proxy for rate of energy expenditure ($VeDBA_{MEAN-T}$, g) was calculated for each sampling period (T_{TOTAL} , h) during which individuals were on land only (L) or completed a foraging trip (FT). Letters “a” and “b” indicate where multiple samples were collected from the same individuals.

| ID | Colony | Activity | Sex | Mass start (kg) | Mass end (kg) | Bill Depth | Flipper | $VeDBA_{MEAN-T}$ | T_{TOTAL} | EE_{DLW-T} |
|-----|--------|----------|-----|-----------------|---------------|------------|---------|------------------|-------------|--------------|
| 1 | LB | FT | F | 1.03 | 1 | 12.6 | 112 | 0.18 | 21.1 | 872.5 |
| 2a | LB | FT | F | 1.05 | 0.98 | 13.1 | 122 | 0.20 | 20.9 | 798.1 |
| 2b | LB | FT | F | 1.05 | 0.98 | 13.1 | 122 | 0.19 | 23.4 | 1002.7 |
| 3a | LB | L | M | 1.24 | 1.19 | 14.8 | 121 | 0.01 | 22.7 | 483.0 |
| 3b | LB | FT | M | 1.24 | 1.19 | 14.8 | 121 | 0.23 | 22.3 | 1648.2 |
| 5a | LB | L | F | 1.21 | 1.12 | 12.6 | 119 | 0.02 | 21.6 | 470.7 |
| 5b | LB | FT | F | 1.21 | 1.12 | 12.6 | 119 | 0.19 | 24.8 | 1011.8 |
| 6 | LB | L | M | 1.42 | 1.36 | 14.6 | 120 | 0.02 | 21.8 | 499.7 |
| 7 | LB | FT | M | 1.14 | 1.09 | 15 | 121 | 0.21 | 21.9 | 1240.4 |
| 8 | LB | FT | F | 1.09 | 1.17 | 13.1 | 113 | 0.21 | 45.4 | 2178.2 |
| 9 | LB | FT | M | 1.2 | 1.13 | 15.1 | 113 | 0.17 | 21.9 | 1284.3 |
| 10 | LB | FT | M | 1.24 | 1.37 | 15 | 124 | 0.21 | 23.0 | 1450.3 |
| 11a | LB | L | F | 1.1 | 0.96 | 12.8 | 115 | 0.02 | 23.9 | 436.6 |
| 11b | LB | FT | F | 1.1 | 0.96 | 12.8 | 115 | 0.24 | 25.3 | 1414.2 |
| 12 | LB | L | M | 1.04 | 1 | 14.5 | 118 | 0.03 | 22.2 | 337.7 |
| 13 | LB | L | M | 1.03 | 0.99 | 14.1 | 122 | 0.01 | 22.2 | 443.5 |
| 14 | GI | L | F | 0.97 | 0.93 | 12.1 | 113 | 0.02 | 21.6 | 495.0 |
| 15 | GI | L | M | 1 | 1.11 | 13.4 | 116 | 0.02 | 19.5 | 510.2 |
| 16 | GI | L | M | 1.2 | 1.14 | 13.9 | 121 | 0.02 | 18.7 | 494.9 |
| 17 | GI | L | F | 1.02 | 1.09 | 12.9 | 112 | 0.02 | 18.6 | 528.3 |
| 18 | GI | L | F | 1.08 | 1 | 13.3 | 121 | 0.02 | 17.6 | 511.3 |
| 19 | GI | L | F | 1.23 | 1.41 | 13.2 | 126 | 0.02 | 21.9 | 531.8 |



Table 3.3: Foraging trip parameters for at-sea periods for little penguins including total sampling period (T_{SEA} , foraging trip duration, h^{-1}), and at-sea metabolic rate (DEE_{DLW-S} $kJ \cdot d^{-1} \cdot kg^{-1}$). Time spent on the water's surface, transiting and diving ($T_{SURFACE}$, $T_{TRANSITING}$ and T_{DIVE} , respectively) was calculated by k-means clustering and an estimated rate of energy expenditure, DEE_{CALC} ($kJ \cdot d^{-1} \cdot kg^{-1}$) was calculated using activity-specific energy values obtained from literature.

Mean VeDBA ($VeDBA_{MEAN-S}$) and total VeDBA ($VeDBA_{TOTAL-S}$) are provided are for at-sea periods.

| ID | T_{SEA} | DEE_{DLW-S} | Total distance | Mean speed | Depth (m) | $T_{SURFACE}$ | $T_{TRANSITING}$ | T_{DIVE} | DEE_{CALC} | $VeDBA_{MEAN-S}$ | $VeDBA_{TOTAL-S}$ |
|-----|-----------|---------------|----------------|------------|----------------|---------------|------------------|------------|--------------|------------------|-------------------|
| 1 | 16.8 | 1088.0 | 39.7 | 1.9 | 0.9 ± 0.02 | 11.27 | 4.59 | 0.91 | 1071.08 | 0.18 | 10867.67 |
| 2a | 16.9 | 1145.1 | 41.2 | 2.0 | 9.4 ± 0.37 | 7.35 | 7.61 | 1.95 | 1234.74 | 0.20 | 12105.04 |
| 2b | 16.3 | 1039.4 | 34.0 | 1.5 | 8.5 ± 0.19 | 8.81 | 4.50 | 3.03 | 1323.97 | 0.19 | 10996.48 |
| 3b | 17.1 | 1561.7 | 52.5 | 2.4 | 1.7 ± 0.09 | 6.93 | 5.74 | 4.39 | 1411.15 | 0.22 | 13799.60 |
| 5b | 16.7 | 1027.7 | 32.6 | 1.3 | 8.4 ± 0.15 | 9.75 | 4.13 | 2.84 | 1309.92 | 0.19 | 11625.93 |
| 7 | 17.0 | 1394.6 | 46.3 | 2.1 | 9.3 ± 0.24 | 7.99 | 4.86 | 4.10 | 1352.57 | 0.20 | 12454.84 |
| 8 | 34.0 | 1386.6 | 72.0 | 1.6 | 8.9 ± 0.15 | 15.65 | 10.52 | 7.84 | 1365.63 | 0.20 | 24764.39 |
| 9 | 16.6 | 988.4 | 33.3 | 1.5 | 6.0 ± 0.22 | 11.78 | 2.67 | 2.12 | 1160.33 | 0.16 | 9713.61 |
| 10 | 16.8 | 1454.4 | 46.5 | 2.1 | 3.1 ± 0.07 | 10.16 | 4.65 | 1.99 | 1216.88 | 0.20 | 12327.12 |
| 11b | 19.0 | 1701.8 | 54.8 | 2.2 | 7.4 ± 0.16 | 7.48 | 6.19 | 5.37 | 1443.19 | 0.24 | 16355.30 |

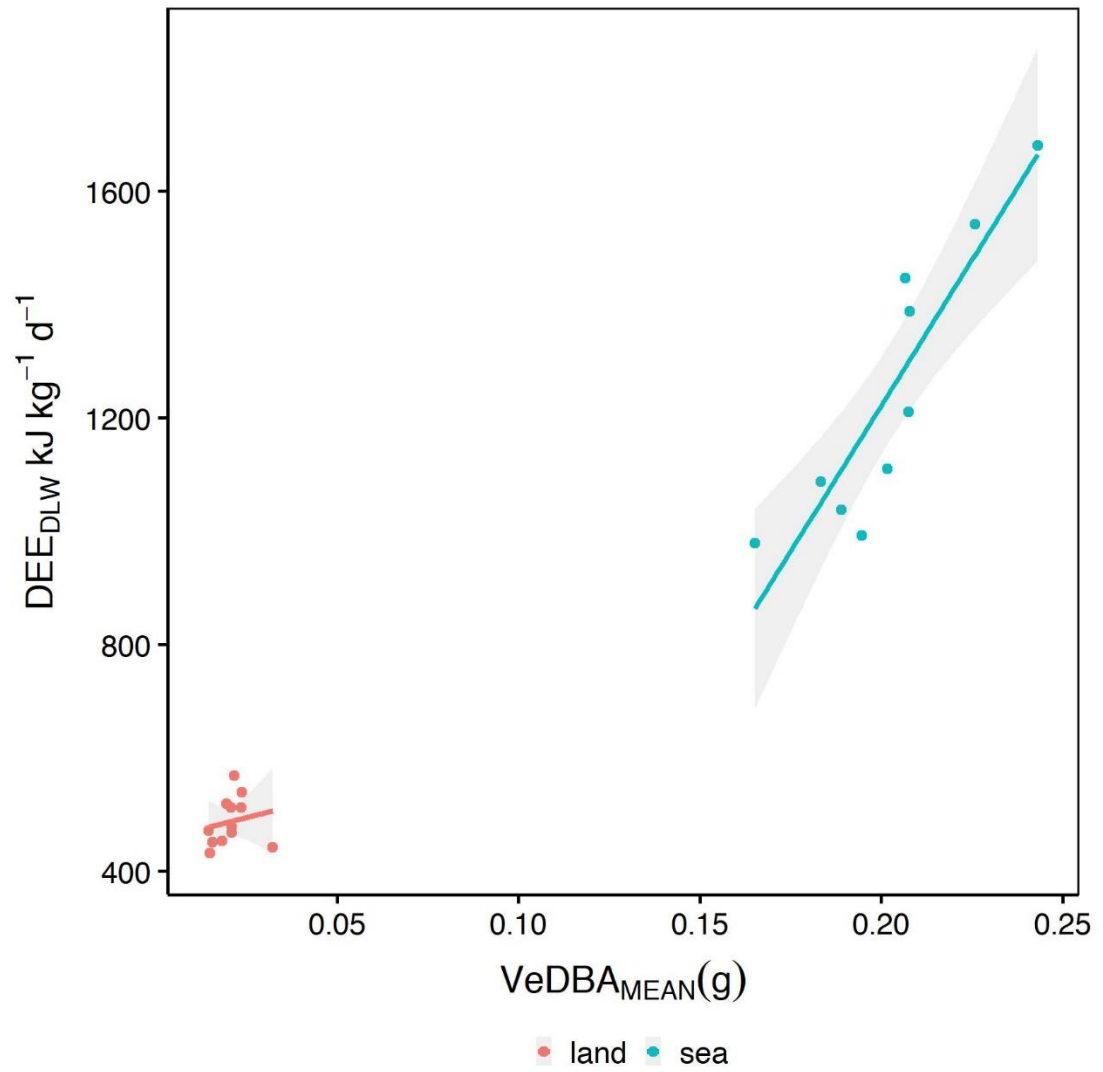


Figure 3.1: Relationships between rate of energy expenditure derived from doubly labelled water DEE_{DLW} ($\text{kJ}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$) and mean VeDBA ($VeDBA_{MEAN}$ g) calculated for periods on land and at sea.

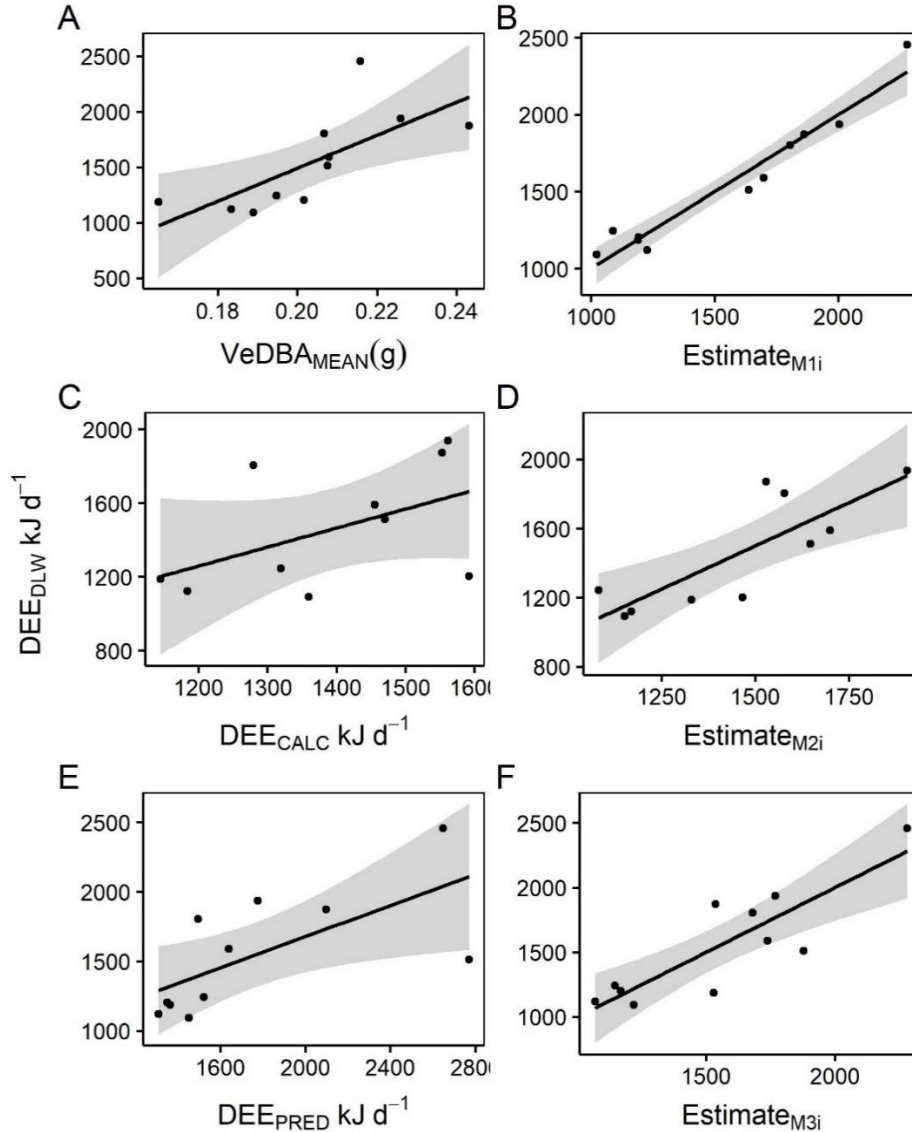


Figure 3.2: Correlations between mass-specific at-sea daily energy expenditure (DEE_{DLW}) derived from Doubly-labelled water method and three approaches of estimating energy expenditure: Approach 1) mean VeDBA ($VeDBA_{MEAN-S}$; A; $DEE_{DLW-S} = -877.7 + (10647.7 * VeDBA_{MEAN-S})$; $r^2 = 0.83$); Approach 2) activity specific VeDBA (DEE_{PRED-S} ; C; $DEE_{DLW-S} = 340.3 + (0.6 * DEE_{PRED-S})$; $r^2 = 0.78$) and; Approach 3) application of energy estimates derived from previous studies (DEE_{CALC-S} ; E; $DEE_{DLW-S} = -424.7 + (1.3 * DEE_{CALC-S})$; $r^2 = 0.28$) and the estimates (M1a, M2a and M3a) derived from the most parsimonious models identified through model selection (B, $DEE_{DLW-S} = -747.2 + (8046.9 * VeDBA_{MEAN-S}) + (301.0 * MS)$; $r^2 = 0.87$; D, $DEE_{DLW-S} = 96.0 + (0.5 * DEE_{PRED-S}) + (313.0 * MS)$, $r^2 = 0.92$ and F, $DEE_{DLW-S} = -549.9 + (0.9 * DEE_{CALC-S}) + (530.3 * MS)$, $r^2 = 0.85$).



Table 3.4: Model results for relationships between at-sea daily energy expenditure (DEE_{DLW-S} $\text{kJ}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$) and three approaches of estimating at-sea energy expenditure rates: Approach 1) mean VeDBA ($VeDBA_{MEAN-S}$); Approach 2) activity specific VeDBA (DEE_{PRED-S}) and; Approach 3) application of energy estimates derived from previous studies (DEE_{CALC-S}). Models denoted with “a” are the most parsimonious model averaged coefficients calculated for each relationship.

| Model | Response variable | Predictor Variables | Estimate | S.E | Statistic | <i>P</i> | CI | <i>r</i> ² |
|-------|-------------------|---------------------|----------|--------|-----------|----------|-----------------|-----------------------|
| 1 | DEE_{DLW-S} | Intercept | -877.7 | 328.4 | -2.0 | <0.05 | -1635, -120.2 | 0.83 |
| | | $VeDBA_{MEAN-S}$ | 10647.7 | 1613.4 | 6.6 | <0.001 | 6927.3, 14368.1 | |
| 1a | DEE_{DLW-S} | Intercept | -747.2 | 314.2 | 2.0 | <0.01 | -1477.3,-17.0 | 0.87 |
| | | $VeDBA_{MEAN-S}$ | 8046.9 | 2417.6 | 3.0 | <0.001 | 2769.5, 13324.2 | |
| | | Mean speed | 301.0 | 109.6 | 2.3 | <0.001 | 41.8, 560.2 | |
| 2 | DEE_{DLW-S} | Intercept | 340.3 | 160.1 | 2.1 | 0.06 | -29.0, -709.6 | 0.78 |
| | | DEE_{PRED-S} | 0.6 | 0.1 | 5.8 | <0.001 | 0.4, 0.9 | |
| 2a | DEE_{DLW-S} | Intercept | 96.0 | 168.0 | 0.5 | 0.6 | -279.3, 471.2 | 0.92 |
| | | DEE_{PRED-S} | 0.5 | 0.1 | 3.4 | <0.01 | 0.2, 0.7 | |
| | | Mean speed | 313.0 | 92.2 | 2.8 | <0.001 | 95.0, 531.0 | |
| 3 | DEE_{DLW-S} | Intercept | -424.7 | 778.8 | -0.5 | 0.6 | -0.01, 1372.2 | 0.28 |
| | | DEE_{CALC-S} | 1.3 | 0.6 | 2.1 | 0.06 | -0.01, 2.7 | |
| 3a | DEE_{DLW-S} | Intercept | -549.9 | 567.9 | -0.9 | 0.37 | -1477.3,- | 0.85 |
| | | DEE_{CALC-S} | 0.9 | 0.3 | 2.4 | <0.01 | 0.4, 1.0 | |
| | | Mean speed | 530.3 | 113.4 | 4.0 | <0.001 | 449.6,641.9 | |

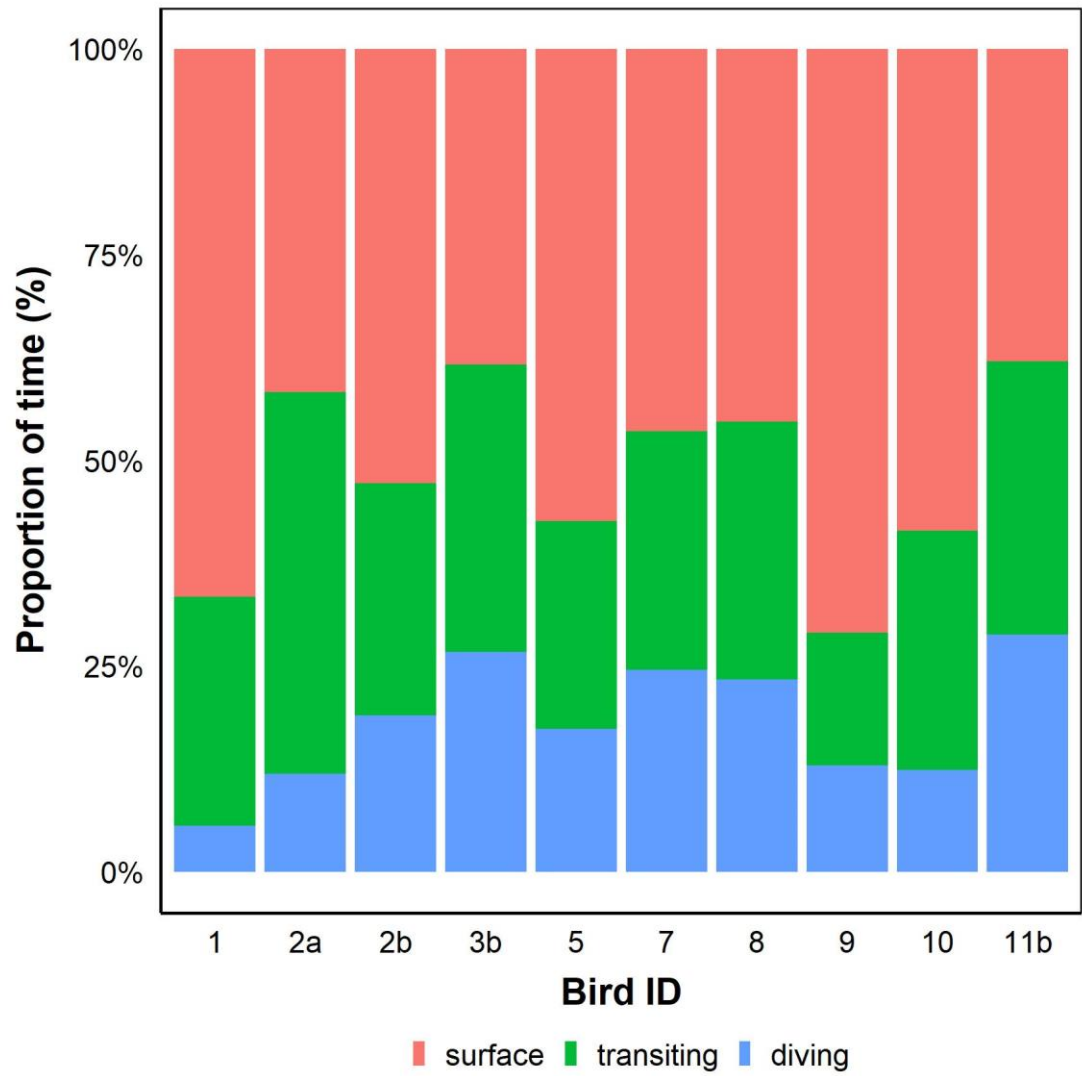


Figure 3.3: Proportion of time spent diving, transiting and resting on the sea surface for little penguins.



resting was the lowest (0.15 ± 0.01 g) while transiting and diving were similar (0.24 ± 0.01 g and 0.23 ± 0.01 g, respectively). Activity-specific VeDBA values were compared with the activity estimates determined from Eqn 8. Correlations between total VeDBA and total predicted energy expended were found for sea-surface resting ($r^2 = 0.91$, $F_{1,8} = 89.3$, $P < 0.001$) and diving ($r^2 = 0.96$, $F_{1,8} = 207.4$, $P < 0.001$; Figure 3.4). There was no significant relationship found for transiting which was of low predictive accuracy ($r^2 = 0.03$, $F_{1,8} = 0.3$, $P > 0.05$).

Linear modelling of DEE_{DLW-S} and the derived mass-specific predicted rate of energy expenditure (DEE_{PRED-S} , $\text{kJ}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$) revealed a strong positive relationship ($r^2 = 0.78$, Figure 3.2c):

$$\text{Eqn 7. } DEE_{DLW-S} = 340.3 + (0.6 * DEE_{PRED-S})$$

Model selection to determine the most parsimonious model resulted in the addition of Mean Speed (MS, $\text{km}\cdot\text{h}^{-1}$; SI Table 3.1; SI Table 3.3). The inclusion of MS further improved the predictive relationship ($r^2 = 0.92$, Figure 3.2d; Table 3.4):

$$\text{Eqn 8. } DEE_{DLW-S} = 96.0 + (0.5 * DEE_{PRED-S}) + (313.0 * MS)$$

Approach 3

The calculated average at-sea energy expenditure rate (DEE_{CALC-S}) determined from activity specific energy values obtained from literature and applied to time-activity budgets was 1270.2 ± 42.2 $\text{kJ}\cdot\text{d}^{-1}\cdot\text{kg}^{-1}$. Linear modelling of DEE_{DLW-S} and DEE_{CALC-S} revealed a weak positive relationship ($P=0.06$, $r^2=0.28$) (Figure 3.4e) with the confidence intervals of DEE_{CALC-S} crossing zero (Table 3.4), indicating this parameter is not a good explanatory variable. Model selection after additional predictor variables were added resulted in the most parsimonious model ($r^2 = 0.85$

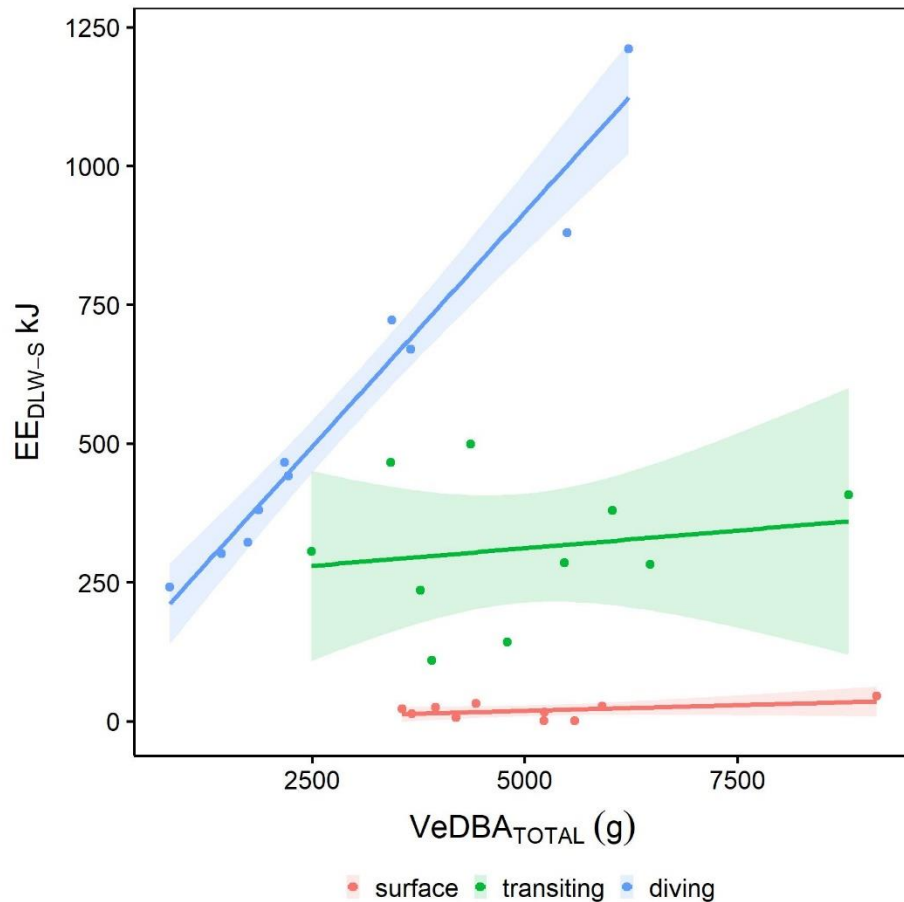


Figure 3.4: Estimates of activity-specific energy expenditure for diving, transiting and sea-surface resting. Plot shows the predicted model linear regression (solid line) and 95% confidence interval (shaded area) for each activity. Regression equations and r^2 statistics for sea-surface resting, transiting and diving are $EE_{DLW-S-SURFACE} = 0.005 * VeDBA_{SURFACE} + 5.7$, $r^2 = 0.91$; $EE_{DLW-S-TRANSIT} = 0.01 * VeDBA_{TRANSIT} + 248.2$, $r^2 = 0.03$; and $EE_{DLW-S-DIVE} = 0.17 * VeDBA_{DIVE} + 72.6$, $r^2 = 0.93$, respectively.



Table 3.4) for predicting DEE_{DLW-S} including MS ($\text{km}\cdot\text{h}^{-1}$, SI Table 3.1; Table 3.3; Figure 3.2f):

$$\text{Eqn 9. } DEE_{DLW-S} = -549.9 + (0.9 * DEE_{CALC-S}) + (530.3 * MS)$$

Discussion

Developing and validating techniques for measuring the metabolic rate of free-ranging animals is central to understanding an animals physiological, behavioural and evolutionary ecology (Butler et al. 2004; McNamara & Houston 1996).

Accelerometry and dynamic body acceleration has been used to determine behavioural patterns in a range of taxa, and is increasingly used as a proxy for energy expenditure (Barwick et al. 2018; Hinchcliff et al. 1997; Noda et al. 2014). In the present study, indices of movement (i.e. VeDBA), both in the simple correlation and activity-specific approaches, was shown to be a good predictor of the mass-specific at-sea metabolic rate derived from DLW. The approach using activity-specific energy expenditure values obtained from literature did not accurately reflect the energy expended by individuals in the present study. However, all three approaches were significantly strengthened by the addition of mean horizontal travel speed. These results suggest that proxies of energy expenditure may be influenced by both individual behaviour and environmental conditions.

Energy expenditure and VeDBA

The estimates of on-land metabolic rate observed in the present study (mean: $429.1 \text{ kJ}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$) are within range of the standard metabolic rate (SMR) for captive little penguins and the fasting metabolic rate of free-ranging individuals ($426.0 \text{ kJ}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$ and $560 \text{ kJ}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$, respectively) (Costa et al. 1986; Stahel & Nicol 1982). On-



land periods for little penguins may include energetically expensive activities such as walking, preening, territorial defence and feeding chicks, all which predominantly occur at night. However, the on-land sampling periods in the present study were comprised mainly of daylight hours, where individuals remain in their nest burrows. Hence, the on-land energy expenditure recorded in the present study is likely to be representative of the physiological processes associated with fasting.

Little movement activity was recorded in the accelerometry values for individuals who remained in their burrows over the sampling period. As accelerometry measures body acceleration and movement (Wilson 2006), it is not surprising that there was a weak relationship between $VeDBA_{MEAN-L}$ and DEE_{DLW-L} . The range of on-land energy expenditure values derived from DLW was narrow in comparison to the at-sea values as little penguins who stayed ashore during the day remained in their nest burrows to avoid predators (Colombelli-Négrel & Tomo 2017). This suggests that the variation observed in the on-land metabolic rate of individuals may be attributed to variation in physiological processing such as digestion, thermoregulation and cellular processes not measured by accelerometers.

The average at-sea metabolic rate observed in the present study ($1278.8 \text{ kJ}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$) was within the range of that reported in previous metabolic studies of free-ranging little penguins ($1124\text{-}1500 \text{ kJ}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$) (Bethge et al. 1997; Costa et al. 1986). The variation observed in the range of daily energy expenditure in the present study may be attributed to a combination of at-sea activity budgets and offspring provisioning. Indeed, little penguins attending to late-stage chicks had maximum daily energy expenditure rates of $2532 \text{ kJ}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$ (Gales & Green 1990), as measured by DLW



method, indicating that energetic requirements may increase with chick age. In the present study, it was not possible to sample individuals based on chick age and breeding adults were provisioning chicks at various stages of chick rearing.

Therefore, a proportion of the variability in at-sea metabolic rate may be influenced by differences in the energetic demands of resource provisioning.

At-sea variation in daily metabolic rates could also be associated with physiological processes such as food digestion and thermoregulation in water. Energy utilised for the digestion of prey is estimated to be equivalent to 13-15% of the available energy content of the prey in little penguins (Green et al. 2006). Therefore, the at-sea energy expenditure of an individual may be influenced by the amount of prey consumed. While thermoregulation in water is thought to influence the energy expended by little penguins (Stahel & Nicol 1982), individuals in the present study were sampled over the same periods. As such, the water temperatures experienced by all individuals was assumed to be similar and, therefore, would have had a negligible effect on the individual variations in measured energy expenditure. While it is possible that these factors may influence at-sea energy expenditure, $VeDBA_{MEAN-S}$ was strongly correlated to DEE_{DLW-S} , accounting for more than 80% of the variation observed. This suggests that individuals have high locomotive costs, with the costs associated with physiological processes not measured by accelerometry being comparatively small.

In the present study, the relationship between DEE_{DLW-S} and $VeDBA_{MEAN-S}$ was substantially improved by the addition of mean speed as a predictor. Mean speed varied substantially between individuals, with those that travelled at a faster speed



having higher rates of energy expenditure. In addition to active movement through the physical medium of water, measurement of mean speed also encompasses passive transport which may be influenced by currents, sea-state and wind conditions which could account for variation in energy expenditure not be adequately captured by accelerometry. Indeed, mean speed alone was significantly correlated with DEE_{DLW-S} ($r^2 = 0.68$; Table S2) and, as a predictor variable, improved the models in every investigated approach.

Activity-specific metabolic rates

Previous studies have attributed weak correlations between body acceleration and energy expenditure measured by DLW to variability in activity levels (Jeanniard-du-Dot et al. 2017). To overcome this, time-activity budgets can be modelled to obtain activity-specific energetic values which seem to improve these relationships. Over short sampling durations, strong relationships between the rate of energy expenditure and body acceleration in free-ranging marine predators has been reported for individuals performing high-energy activities (Elliott et al. 2013; Stothart et al. 2016). Similarly, in the present study, most individuals undertook foraging trips < 24 h and spent more considerable proportions of that time undertaking high-energy activities (i.e. diving and transiting). Hence, the simple correlative and activity-specific approaches were of similar predictive capacity.

Surface activities were less energetically costly than transiting and diving activities, but overall more expensive than the on-land energy expenditure. This could be because surface activities encompass post-dive resting as well as other behaviours such as preening which could be associated with higher costs (Goldstein



1988; Wooley & Owen 1978). Diving behaviour was the most expensive at-sea activity for individuals in the present study, at 7.6 times the SMR calculated by Bethge et al. (1997). This is within the range of diving metabolic rates observed in other penguin species (Chappell et al. 1993; Nagy et al. 2001).

Transiting at the surface was less expensive than diving and was equivalent to 1.6 times the SMR (Bethge et al. 1997). Transiting marine vertebrates usually swim at depths 3 times their body widths which is thought to reduce drag forces and the cost of transportation (Boyd & Hoelzel 2002; Hindle et al. 2010). Transiting can vary in speed, and may be attributed various behaviours such as prey capture behaviour, commuting to and from the colony or between foraging patches (Sutton et al. 2020). The fine-scale sea state variation may also influence the energy expended during transiting. Thus, the low correlation between VeDBA and the estimated energy expended during transiting could indicate a combination of energetic variation in this behavioural mode and external factors influencing the energy expended during this activity.

The summation of activity-specific acceleration should be a better predictor of energy expenditure when there is a large difference in energetic costs between different behaviours (Elliott et al. 2013; Laich et al. 2011). The observed at-sea behaviour categories were found to be associated with different VeDBA values resulting in different activity-specific estimates. Consequently, VeDBA was considered a good predictor of energy expenditure using Approach 2. While the mean travelling speed improved the predictive capacity of Approach 2, comparisons of modelling approaches 1 and 2 indicate that they are of similar predictive capacity.



However, Approach 2, is more labour intensive with regard to data processing and determining activity budgets than the simple correlative approach (i.e. Approach 1).

In the present study, Approach 3 was unsurprisingly found to be the least effective method for predicting at-sea metabolic rate. This is likely due to the accuracy of activity-specific energy expenditure estimate for this species. Using previously determined estimates of activity-specific energy expenditure may be problematic as individuals in captive environments may be less motivated to perform behaviours similar to those of their free-ranging counterparts. For example, the energetic values for transiting in water recorded for little penguins in laboratory conditions was found to be considerably slower than what was recorded in free-ranging individuals (Bethge et al. 1997). This raises questions with regards to the validity of applying such values to activity budgets of free-ranging individuals.

Numerous studies using activity-budgets (derived from accelerometry or other methods) to estimate energy expenditure in free-ranging animals have been performed using estimates obtained from controlled conditions or from phylogenetically distant species moving in similar locomotory modes and in similar environments (Collins et al. 2016; Goldstein 1988; Ladds et al. 2018; Shaffer et al. 2004). The poor predictive capacity of Approach 3 in the present study highlights the potential inaccuracy of such studies and the need for accurate species-specific and activity-specific energy expenditure values. Ultimately, without validation, the accuracy and applicability of these methods for use on free-ranging animals remains unknown.



In summary, accelerometry-derived proxies provided an accurate estimation of at-sea energy expenditure measured by the DLW method in little penguins. Activity-specific energy expenditure predicted from a modelling approach was slightly more accurate than a simple correlation approach. However, both relationships were improved with the addition of mean speed as a predictor, indicating that the transport medium may impact both DLW and acceleration measurements. The results of the present study further support the use of accelerometry as a means to estimate energy expenditure in free-ranging animals but emphasises the need for more validation studies. Confirming the strong predictive relationship between energy expenditure and accelerometry may provide greater understanding of how animals respond to shifts in their environment such as the predicted changes habitat and prey availability resultant from warming ocean temperatures in population hot spots.

Chapter 4: Multi-predator assemblages, dive type, bathymetry and sex influence foraging success and efficiency in African penguins.



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Abstract

Marine predators adapt their hunting techniques to locate and capture prey in response to their surrounding environment. However, little is known about how certain strategies influence foraging success and efficiency. Due to the miniaturisation of animal tracking technologies, a single individual can be equipped with multiple data loggers to obtain multi-scale tracking information. With the addition of animal-borne video data loggers, it is possible to provide context-specific information for movement data obtained over the video recording periods. Through a combination of video data loggers, accelerometers, GPS and depth recorders, this study investigated the influence of habitat, sex and the presence of other predators on the foraging success and efficiency of the endangered African penguin, *Spheniscus demersus*, from two colonies in Algoa Bay, South Africa. Due to limitations in the battery life of video data loggers, a machine learning model was developed to detect prey captures across full foraging trips. The model was validated using prey capture signals detected in concurrently recording accelerometers and animal-borne cameras and was then applied to detect prey captures throughout the full foraging trip of each individual. Using GPS and bathymetry information to inform the position of dives, individuals were observed to perform both pelagic and benthic diving behaviour. Females were generally more successful on pelagic dives than males, suggesting a trade-off between manoeuvrability and physiological diving capacity. By contrast, males were more successful in benthic dives, at least for Bird Island (BI) birds, possibly due to their larger size compared to females, allowing them to exploit habitat deeper and for longer durations. Both males at BI and both sexes at St Croix



(SC) exhibited similar benthic success rates. This may be due to the comparatively shallower seafloor around SC, which could increase the likelihood of females capturing prey on benthic dives. Observation of camera data indicated individuals regularly foraged with a range of other predators including other penguins, other seabirds, predatory fish (sharks and tuna) and whales. The presence of other seabirds increased individual foraging success, while predatory fish reduced it, indicating competitive exclusion by larger heterospecifics. This study highlights novel benthic foraging strategies in African penguins and suggests that individuals could buffer the effects of changes to prey availability in response to climate change. Furthermore, although group foraging was prevalent in the present study, its influence on foraging success depends largely on the type of heterospecifics present.



Introduction

Within the marine environment, unpredictable or cyclical changes may cause fluctuations in the availability and distribution of resources (Fauchald 2009; Hoskins et al. 2008). In response, marine predators show spatio-temporal flexibility in their at-sea movements and foraging decisions in order to increase the probability of resource acquisition (Hull 2000; Weimerskirch 2007). Marine predators may target aggregations of predictably abundant prey, arising from physical processes such as upwellings, fronts and eddies (Bost et al. 2009; Dragon et al. 2010). However, the location of these prey can change seasonally and be affected by oceanographic variation, which is thought to affect foraging success (Inchausti et al. 2003).

Knowledge of how marine predators use cues in their environments to find food is fundamental to understanding their influence on prey populations, other predators' populations and ecosystem functioning. Correspondingly, determining the factors that influence the foraging behaviour of marine predators is crucial to predicting their possible responses to environmental variability (Grémillet & Boulinier 2009).

For air breathing marine predators, foraging strategies are also expected to reflect the vertical distribution of their prey. For instance, highly nutritious pelagic prey often occur in spatially and temporally unpredictable distributions, with prey captures by pelagic foragers occurring at a broad range of depths in response to this (Miramontes et al. 2012). In contrast, benthic foragers exhibit “square-shaped” dives which are determined by slope of the ocean floor, with consecutive dives being similar depths and duration (Elliott et al. 2008; Tremblay & Cherel 2000). Benthic diving is often considered more energetically costly and individuals must maximise



the time spent at the bottom of the dive in order to increase foraging success (Costa et al. 2004). However, the benthic diving is thought to be more profitable for some species due to a lack of pelagic prey or difficulties capturing pelagic prey (Arnould & Hindell 2001). Furthermore, the trade-off between physiological diving ability and predictability of prey availability seems to be a motivating factor for the benthic foraging strategies present in some animals.

Group foraging is adopted by many pelagic foraging marine predators due to the patchy distribution of their prey (Pöysä 1992; Silverman et al. 2004; Weimerskirch et al. 2010). In contrast, for benthic foragers, less information is known regarding group foraging behaviour. It is hypothesised that it is less likely due to benthic prey being solitary, more uniformly distributed or not requiring concentration (Casaux & Barrera-Oro 2006). However, aggregations of prey sometime occur in benthic habitats which can cause the assemblage of marine predators to shallow benthic environments (Takahashi et al. 2008; Tremblay & Cherel 2000). Previous studies have highlighted conflicting outcomes of group behaviour on foraging success. For example, where some species may be seen to benefit from group foraging due to information transfer or prey capture facilitation (Thiebault et al. 2014a) others suggest that group foraging is just a response to the spatially aggregated prey, leading to intra-specific competition (Handley et al. 2018; Sutton et al. 2015). While group foraging is thought to benefit some, less is known about how multi-predator feeding associations may influence prey capture success. As the predicted shortage of pelagic prey is thought to increase group size and foraging associations, understanding how the presence of conspecifics and heterospecifics may influence the foraging success



of individuals is crucial to identifying shifts in behaviour in response to a changing environment.

The development and miniaturisation of behaviour data loggers has enabled insights into the distribution and foraging behaviour of air-breathing marine predators (McIntyre 2014; Wakefield et al. 2009). Animal-borne video cameras used in conjunction with these behavioural data loggers can provide context-specific information for cryptic at-sea behaviours (Thiebault et al. 2014a; Watanabe & Takahashi 2013). In particular, they may reveal the complex relationships between individuals, conspecifics and heterospecifics during foraging and how changes in the abundance and distribution of prey may result in different behavioural responses (Sutton et al. 2015; Takahashi et al. 2003). However, very little is known how group behaviour influences individual foraging effort, success and efficiency. Such information is crucial for predicting how changes in prey availability due to environmental variability may influence the foraging decisions of predators.

African penguins (*Spheniscus demersus*) are endemic to Africa and classified as ‘Endangered’ due to a recent rapid population decline (Crawford et al. 2011; IUCN 2019). Typically thought to be pelagic foragers, their survival and breeding success has been considered intrinsically tied to the availability of pelagic shoaling fish species such as anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*) within their foraging range (Crawford 1998; McInnes et al. 2017b). During the breeding season, their foraging range is reduced to <30 km from the colony in due to the need to return regularly to feed their offspring (Pichegru et al. 2009).



Consequently, the presence of pelagic fish in proximity to the colony is of high importance.

Individuals on the west and south-west coast of South Africa are influenced by the productive waters of the Benguela upwelling region (Pichegru et al. 2009). Group foraging in these animals has been shown to positively influence foraging success (McInnes et al. 2017a). In contrast, there is less information regarding the factors influencing African penguins breeding on the south-east coast of South Africa in waters of lower productivity (van Eeden et al. 2016). Furthermore, the prevalence of group foraging behaviour, and its consequences, on the south-east coast African penguin population is not known. Group foraging is suspected to be common, although recent decreases in population size of colonies on the south-east of South Africa raises concerns about Allee effect on foraging success (Ryan et al. 2012). Knowledge of the foraging strategies employed by individuals in a region of comparatively low productivity could provide insights into how the species may respond to changes in prey availability. This is especially important given that over half of the African penguin population resides on islands in this region, an area known for its high degree of environmental variability (van Eeden et al. 2016).

The aims of the present study were to, through use of a video cameras and accelerometry, classify prey captures in African penguins and determine 1) the possible use of the benthic environment and 2) the factors influencing prey capture success, foraging effort and diving efficiency.



Materials and methods

Study site and data collection

This study was approved by South African National Parks (SANParks) (PICL1282), the Department of Environmental Affairs (DEA, Res2017-76) and Nelson Mandela University (NMMU-A15-SCI-ZOO-008). Fieldwork was conducted during April-June 2017 at two African penguin colonies in Algoa Bay, St Croix (SC, 33°48' S, 25°46' E) and Bird Island (BI, 33°50' S, 26°17' E; Figure 4.1). These islands are the eastern-most breeding colonies for the species, hosting approximately half of the global population (Crawford et al. 2011). BI is the eastern-most colony of African penguins and supports approximately 2,500 individuals (DEA unpubl. data). SC is a small (12ha), rocky island and the world largest African Penguin colony, supporting 7,200 breeding pairs in 2017 (DEA unpubl. data).

Data collection occurred during the guard stage when breeding partners alternate between foraging trips to sea and guarding their chicks on land. Following a change-over, the partner departing to sea was captured at the nest and weighed using a digital scale (± 10 g). Individuals were then instrumented with three devices for a single foraging trip: a GPS (Mobile Action Technology, I-gotU, GT-120, 44.5 x 28.5 x 13 mm, 20g) which sampled at 1 min intervals and was packaged in heat shrink tubing for waterproofing; a combined tri-axial accelerometer and depth recorder (Technosmart, Axy-Depth, 12 x 31 x 11mm, 7.5g) which sampled acceleration and depth at 25 Hz and 1 Hz, respectively; and a video data logger (Catnip Technologies, Bird Cam, 25 x 45 x 15mm, 30 frames per second, 24g including housing), housed in

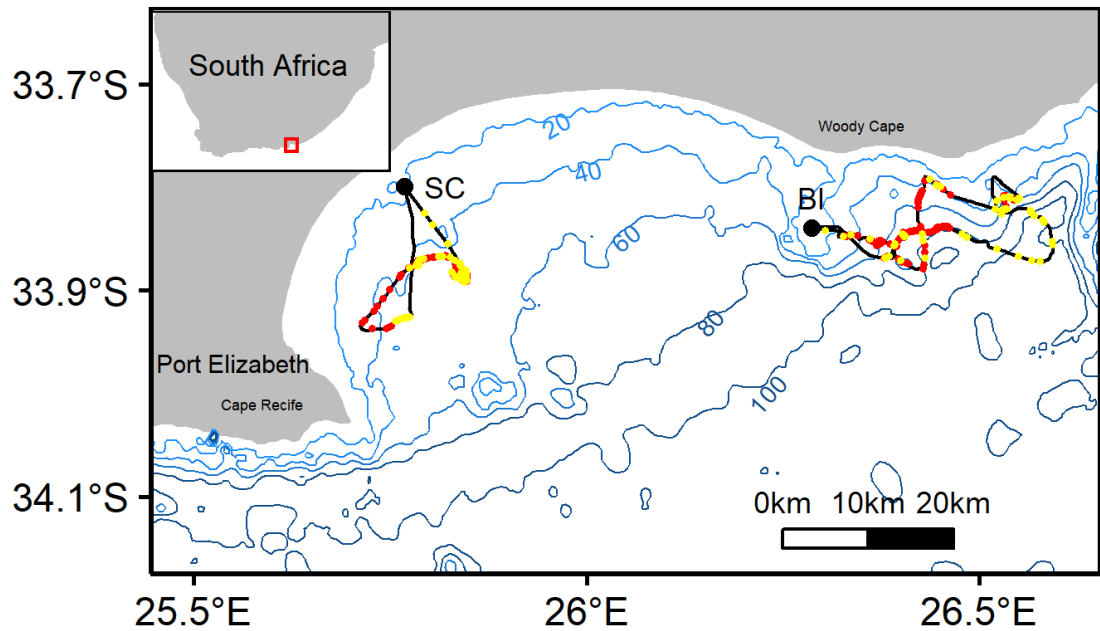


Figure 4.1: Representative tracks from African penguin study colonies St. Croix (SC) and Bird Island (BI). Red and yellow dots along the track indicate benthic and pelagic prey captures, respectively. Bathymetry provided in 20 m isobaths. Red box on inset map indicates the location of Algoa bay along the south-eastern coast of South Africa.



a custom made 3-D printed plastic case, which recorded on a 30 min on, 30 min off schedule.

Devices were deployed before sunset with the cameras programmed with a start delay of 12 hours to avoid recording on land, at night or during periods close to the colony. The devices were attached to feathers along the dorsal mid-line using waterproof tape (Tesa 4651, Beiersdorf, AG, GmbH, Hamburg) with the camera placed in front of the other devices so as to streamline the package and minimise logger effects on diving behaviour. Together, the package was <3% body mass (average body mass = 3127 ± 63 g) and <0.3% cross-sectional surface area (average cross sectional surface area = 152 ± 20 mm²). Efforts were made to minimise disturbance and reduce animal handling time with all procedures lasting <10 min. After deployment, the individual was released back to its nest where it remained until voluntarily departing for a foraging trip.

Individuals were recaptured after a single foraging trip and the devices were removed. Mass was recorded again and morphometric measurements were taken with Vernier callipers (bill length, bill depth, bill width; ± 0.1 mm) and a metal ruler (flipper length; ± 1 mm). Sex of each individual was determined by discriminant function analysis (Pichegru et al. 2013).

Data processing and statistical analyses

Unless otherwise stated, all data processing and statistical analyses were performed in the R statistical environment, version 3.5.2 (R Core Team 2018). The GPS tracks were filtered by removing points located on land and those that exceeded their mean maximum speed of 12.4 km h⁻¹, (Wilson 1985). Retained GPS locations



accounted for > 97% of the filtered foraging trip and the average location distance between consecutive points along a track was 43.4 ± 4.8 m (max 8940.5 m). To account for the irregularity of GPS locations, all tracks were interpolated to 1 min intervals using the package *adehabitatLT* (Calenge 2011). Dive data obtained from depth recorders were corrected for depth drift using *diveMove* package (Luque & Fried 2011) and the following dive parameters were calculated for each dive: beginning and end of a dive; dive duration; dive depth; duration of descent; bottom time; ascent duration; and post-dive interval. Total vertical distance travelled (maximum depth multiplied by two) and dive rate (number of dives divided by foraging trip duration) was estimated for each individual trip.

Data with a depth of < 1.5 m were removed in order to remove surface or transiting periods. For each dive, depth profiles were categorised as either benthic or pelagic following a two-step criterion. Benthic dives were first identified by calculating the ratio between the recorded maximum dive depth divided by the bathymetric depth (bathymetry obtained from GEBCO 15-arc second dataset at a resolution of 0.05°) at the approximate location of the dive (Baylis et al. 2015). Secondly, the depth of each dive was compared to the depth of the previous and following dive. All dives within 10% of either the previous or following dive and with a bathymetric depth ratio of > 0.8 were classified as a benthic dive while the remaining dives were classified as pelagic (Baylis et al. 2015). Benthic dives in shallow waters (i.e. < 15 m) or close to the colony were removed from further analysis as the resolution of bathymetry is not accurate in these conditions. In addition, visual inspection in IgorPro using Ethographer (Wavemetrics Inc, Portland



OR, USA, version 6.3.7.2) was conducted and benthic dives could be characterised as trapezoid shape with a steady descent, horizontal bottom phase and a steady ascent (Tremblay & Cherel 2000).

In order to calculate foraging effort per dive, the tri-axial acceleration data were filtered using a 1 s running mean to separate static acceleration (due to the animal position in space in respect to gravity) from dynamic acceleration (accounting for animal movement). Vectorial Dynamic Body Acceleration (VeDBA), a proxy for whole body activity (Qasem et al. 2012), was calculated for each dive using the equation:

$$VeDBA = \sqrt{(X_{dyn}^2 + Y_{dyn}^2 + Z_{dyn}^2)}.$$

where X, Y and Z are the dynamic acceleration (*dyn*) of horizontal (surge), vertical (heave) and lateral (sway) movements, respectively. The total and mean VeDBA were calculated for each dive and used as an index of energy expenditure.

Video data were viewed frame-by-frame and coded using a custom video annotation sheet created in Solomon Coder (Budapest, Hungary, Version 16.06.26). Video camera data was used to determine prey type, prey capture events and whether they occurred in the presence of other foraging predators. Position in the water column (diving or resting on the surface) was also recorded and used to align the camera data to the accelerometer, depth and GPS data in IgorPro (Wavemetrics Inc, Portland OR, USA, version 6.3.7.2) using Ethographer (Sakamoto et al. 2009a).

In order to evaluate prey captures over the full foraging trip, a two-class Support Vector Machine (SVM) (Meyer & Wien 2015), a type of pattern classifier, was used to detect potential prey captures from swimming periods. This was developed using



positive prey capture signatures detected in accelerometer data and confirmed by video camera footage. A total of 1,648 prey capture events were identified from the video data and a sample of data at a ratio of 5:1 swim:prey capture was taken to train the model. This was done in order to reduce computing time for R software but maintain variation so as to retain the predictive power of the dataset and enable the accurate detection of prey captures across all individuals (Lee & Mangasarian 2001). As in previous studies (e.g. Carroll et al. 2014; Chessa et al. 2017), statistics were extracted using a rolling window of 8 data points (corresponding to approximately 0.32 Hz) and were used to train the model. Where previous studies used ODBA as a proxy for energy expenditure, the current study used VeDBA as it may be a better proxy due to the slightly lower placement of the accelerometer in relation to the bird's centre of gravity (Qasem et al. 2012). The model was developed using a 10-fold cross validation where data were randomly split 70:30 (training:testing) and the range of parameters which showed the highest overall accuracy were retained (Table 4.1; see SI Text 4.1 for further information).

For the prey captures over the full foraging trip as determined using the SVM, a Generalised Linear Mixed Models (GLMM) using a binomial error distribution with a logistic link function were employed to determine the factors influencing the likelihood of a successful foraging dive. Initial inspection of data indicated probability of success could be both colony- and sex-linked. As such, a Bernoulli response variable represented dives resulting in prey capture(s) (1) or no prey capture (0). This was fitted against the predictor variables: dive type (benthic or pelagic), sex



Table 4.1: Results of cross validated SVM model used to detect swimming behaviour vs. prey captures events in African penguins. Model utilized a radial kernel and was 89% accurate in correctly identifying between swim and prey capture events with a false 11% positive rate.

| Metric | Mean \pm S.E. (%) |
|---------------------|---------------------------------------|
| Accuracy | 89 \pm 0.07 |
| Recall | 75 \pm 0.07 |
| False Positive Rate | 11 \pm 0.3 |



and a three-way interaction between colony, dive type and sex.

While tri-axial accelerometers have been used to measure energy expenditure during foraging in numerous species (Grémillet et al. 2018; Jeanniard-du-Dot et al. 2017; Qasem et al. 2012), validation of such a relationship in African penguins has yet to be determined. Therefore, to investigate the factors influencing foraging effort, the following 2 metrics were used per dive: Foraging Efficiency Index (FEI, prey captures/total VeDBA); and Dive Efficiency (DE, prey capture/dive duration). Linear Mixed Effects Models (LME) were fitted using the *lme4* package (Bates et al. 2014). The FEI and DE were log transformed in both models in order to normalise positively skewed data. Predictor variables included in the model were dive type (benthic or pelagic), colony and dive depth.

Separate LMEs were also performed for foraging behaviour periods with concurrent video data in order to investigate the influence of other predators on the FEI and DE. FEI and DE were modelled against the three class factor presence of other predators (solitary, seabirds and multi-heterospecifics) with individual bird as a random factor.

For each model, model selection was undertaken using Akaike Information Criterion scores corrected for small sample sizes (AICc), calculated for all combinations of the predictor effects using the dredge function in the package *MuMIn* (Barton & Barton 2013). A subset of the most parsimonious models was identified as those with a Δ AIC of less than or equal to 4 and used to generate model averaged coefficient estimates. Mann-Whitney U test was performed to compare foraging trip parameters between sexes or colonies and LMEs were used to compare



diving metrics between colonies and between sexes. Individual bird ID was used as a random factor to account for repeated measures in all models presented.

Unless otherwise stated, results are expressed as Mean \pm SE.

Results

Video, accelerometer, diving and GPS data loggers were deployed on a total of 18 breeding African penguins, 9 from SC and 9 from BI. However, due to water damage, video data were obtained from 14 individuals and GPS, accelerometer and dive recorder data was obtained for 17 individuals (Table 4.2). The average foraging trip lasted 23.09 ± 1.83 h during which individuals completed 576.41 ± 2.13 dives. On average, individuals spent 7.73 ± 1.01 h diving with depths averaging 14.46 ± 0.19 m, with a maximum of 90.56 m) and travelled total horizontal distances of 53.8 ± 5.1 km at a speed of 2.33 ± 0.07 km·h⁻¹, covering total vertical distances of 17.28 ± 2.87 km. There was no significant difference in horizontal distances travelled ($W = 23$, $P = 0.24$), vertical distances travelled ($W = 33$, $P = 0.81$) or trip duration ($W = 34$, $P = 0.88$) between colonies in this study.

Fine-scale diving behaviour and foraging success

A total of 10029 dives were recorded, however by removing dives < 1.5 m and those close to the colony (representing transiting periods), 6775 foraging dives remained, comprising of 3097 from BI and 3678 from SC (Table 4.2). Analysis of dive profiles in relation to bathymetry revealed penguins completed both pelagic and benthic dives. All individuals completed benthic and pelagic dives and the proportion of benthic dives for was slightly higher at SC with 31.4% of dives classified as

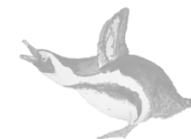


Table 4.2: Dive and foraging efficiency indices for female and male African penguins rearing chicks on Bird Island (BI) and St Croix Island (SC). Parameters for benthic (B) and pelagic (P) dives are provided where applicable.

| | BI | | | | SC | | | |
|------------------------------------|--------------|-------------|-------------|-------------|-------------|-------------|-------------|------------|
| | Female | | Male | | Female | | Male | |
| | N=4 | | N=4 | | N=4 | | N=5 | |
| Adult mass (kg) | 2.85 ± 0.06 | | 3.26 ± 0.14 | | 3.06 ± 0.13 | | 3.30 ± 0.06 | |
| Vertical travelled distance (km) | 15.5 ± 4.0 | | 22.5 ± 6.8 | | 13.2 ± 4.1 | | 16.9 ± 1.2 | |
| Dive rate (dive/h ⁻¹) | 22.7 ± 3.9 | | 27.4 ± 5.1 | | 25.2 ± 8.2 | | 29.8 ± 6.4 | |
| Dive type | B | P | B | P | B | P | B | P |
| Dives (n) | 170 | 1366 | 454 | 1132 | 392 | 1169 | 680 | 1412 |
| Total captured prey | 159 | 655 | 595 | 381 | 482 | 466 | 992 | 428 |
| Successful dives (%) | 45.3 | 27.5 | 61.5 | 23.2 | 66.7 | 23.6 | 62.9 | 18.8 |
| Mean capture depth (m) | 46.0 ± 2.0 | 20.0 ± 0.6 | 57.5 ± 1.0 | 17.1 ± 1.0 | 28.4 ± 0.9 | 7.3 ± 0.4 | 38.0 ± 0.5 | 9.1 ± 0.5 |
| Mean bottom time (s) | 8.7 ± 1.2 | 10.3 ± 0.3 | 16.5 ± 1.0 | 14.8 ± 1.2 | 15.0 ± 0.9 | 8.4 ± 0.2 | 24.7 ± 1.6 | 7.9 ± 0.2 |
| Prey capture rate (captures/dives) | 1.02 ± 0.1 | 0.35 ± 0.1 | 1.41 ± 0.1 | 0.25 ± 0.1 | 1.25 ± 0.1 | 0.35 ± 0.1 | 1.61 ± 0.1 | 0.24 ± 0.1 |
| Mean VeDBA | 0.19 ± 0.1 | 0.20 ± 0.1 | 0.17 ± 0.1 | 0.24 ± 0.1 | 0.16 ± 0.1 | 0.24 ± 0.1 | 0.17 ± 0.1 | 0.27 ± 0.1 |
| Total VeDBA | 392.4 ± 10.0 | 158.3 ± 3.0 | 493.7 ± 8.1 | 138.8 ± 3.4 | 329.3 ± 4.2 | 101.6 ± 2.1 | 415.6 ± 3.1 | 87.0 ± 1.7 |



benthic compared to 20.6% at BI (Table 4.2, SI Figure 4.3). Application of the SVM to the entire foraging trip identified capture signals throughout the water column on pelagic dives and during the bottom phase of benthic dives (Figure 4.2). A total of 2,264 and 2000 prey captures were recorded during benthic dives and pelagic dives, respectively, equating to a mean of 10 ± 14.5 prey·h⁻¹. Interestingly, 60% of total benthic dives were successful whereas only 23% of all pelagic dives were successful (Table 4.2). Prey capture rate for benthic dives was 1.2 ± 0.1 prey·dive⁻¹ compared to 0.4 ± 0.1 prey·dive⁻¹ for pelagic dives.

For benthic dives, individuals dived to a maximum depth of 91.5 m (mean 53.0 ± 0.9 m) at BI and 60.6 m (mean 40.3 ± 0.3 m) at SC. The most common mean maximum depth on benthic dives was 41.7 ± 1.7 m for females and 58.8 ± 1.0 m for males at BI, while females and males at SC dived to 36.8 ± 0.6 m and 43.22 ± 0.2 m, respectively. Males performed significantly longer benthic dives than females (Figure 4.3; LME: $F = 4.7$, $P < 0.05$), and spent almost twice as long on the bottom phase (LME: $F = 8.2$, $P < 0.5$; Table 4.2). On benthic dives, there was a strong positive correlation of 0.91 between capture depth and maximum dive depth (SI Figure 4.1) indicating that individuals captured on the bottom phase of the dive. Only 11.3% benthic dives were of incidences where individuals captured prey in the pelagic zone after performing a benthic dive.

For pelagic dives, individuals at BI dived significantly deeper (16.6 ± 0.2 m; max: 79.7 m) than individuals at SC (8.2 ± 0.1 m, max: 40.2 m; LME: $F = 9.0$, $P < 0.5$). On successful dives prey capture rate was 1.6 ± 0.02 . Irrespective of dive mode, males completed longer duration dives than females (male: 55.7 ± 0.9 s female: 37.7 ± 0.5

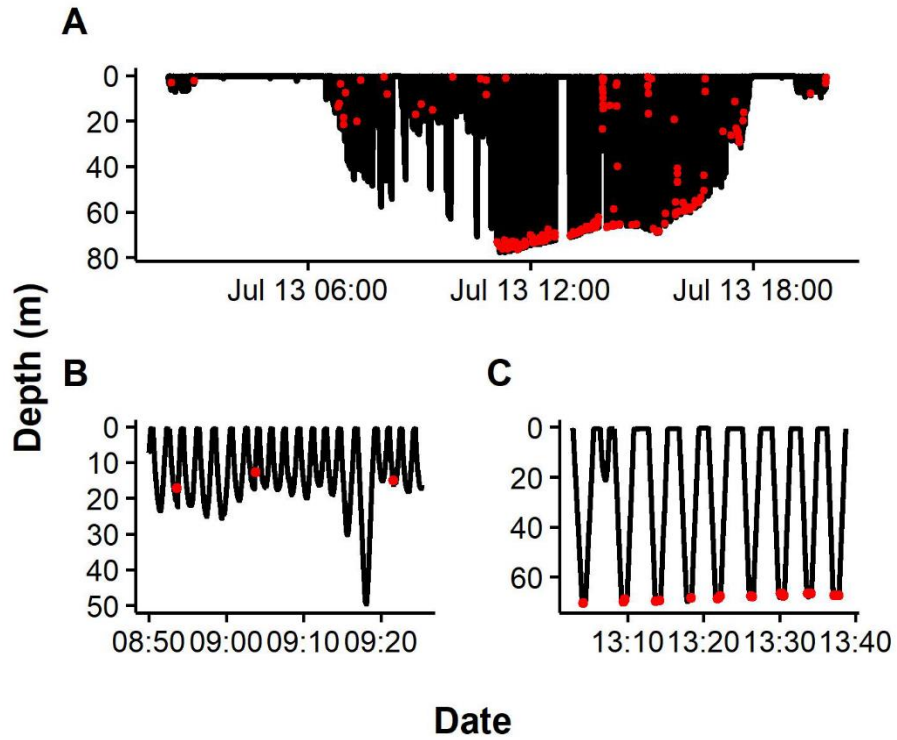


Figure 4.2: Representative dive profiles of African penguins from Algoa Bay. Red dots indicate prey capture events predicted by Support Vector Machine (SVM). Insets indicating pelagic (B) and benthic dives (C).

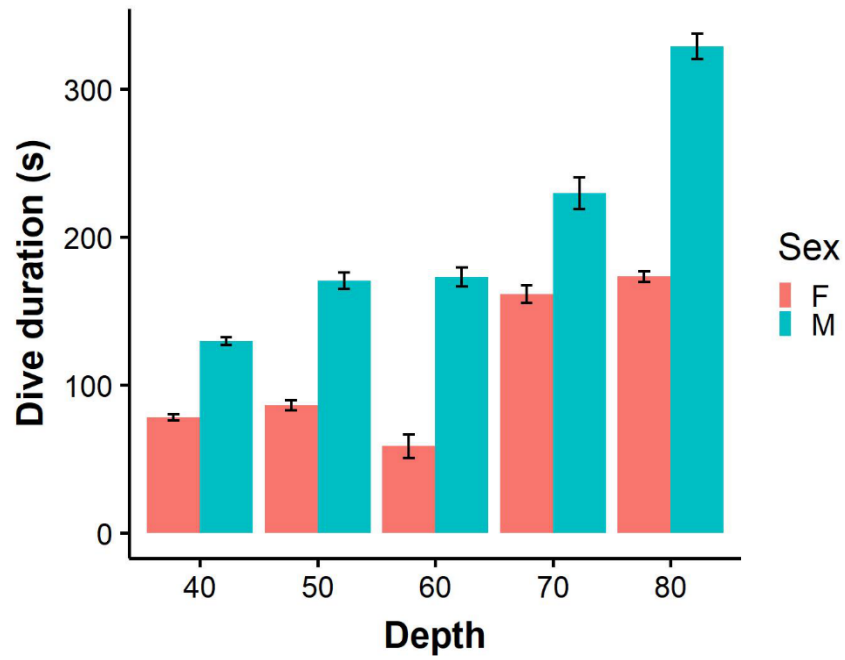


Figure 4.3: Dive durations of benthic dives (binned into 10 m intervals) performed by male (N = 9) and female (N = 7). Error bars represent standard error (S.E.) from the mean.



s). Contrary to previous studies (Pichegru et al. 2013), males had a slightly higher dive rate of 28.7 ± 4.0 dives \cdot h $^{-1}$ compared to females, 23.9 ± 4.2 dives \cdot h $^{-1}$. However, this difference was not significant ($P > 0.05$).

Candidate subsets explaining the probability of prey capture success comprised a total of ten models (SI Table 4.1). The most likely set of models retained the predictor effects sex, dive type, colony and an interaction terms between all predictors (Table 4.3). The probability of success was lower on pelagic dives compared to benthic dives. However, this relationship was stronger at SC than at BI. While sex-specific differences in foraging success were evident, they appeared to be dependent on colony and dive type. Males from both colonies performed equally well at benthic dives. Similarly, females from both BI and SC showed similar success rates for and pelagic dives. Males at BI were more likely to be successful on pelagic dives than males at SC, while females at SC were more likely to be successful at benthic dives than females at BI (Figure 4.4). While model averaging retained sex, colony dive type and all possible interaction terms in the most parsimonious model, confidence intervals crossed zero for all parameters except dive type and an interaction between colony and dive type indicating that these two variables alone were good predictors of probability of success.

Indices of energy expenditure, total and mean VeDBA, were significantly higher during prey capture dives (339.3 ± 3.6 and 0.20 ± 0.01 , respectively) than non-prey capture dives (120.6 ± 1.4 and 0.16 ± 0.01 , respectively; LME: $F = 4777.4$, $p < 0.001$, LME: $F = 1095.2$, $P < 0.001$, respectively).



Table 4.3: Model summary tables for probability of prey capture success, Foraging Efficiency Index (FEI) and Dive Efficiency (DE) as predicted by Support Vector Machine (SVM) and as observed on camera. The abbreviations SC (St Croix), P (pelagic), F (female) and the symbol “:”, indicating an interaction between explanatory variables. “Seabirds” and “multi” indicate where seabirds or seabird, fish and sharks were present during feeding events, respectively.

| Response Variable | Explanatory Variables | Estimate | S.E. | Z/t value | P value | CI (upper, lower) |
|------------------------|------------------------------|----------|------|-----------|------------------|-------------------|
| Probability of Success | Intercept | 0.45 | 0.15 | 2.93 | <0.01 | 0.15, 0.74 |
| | Colony (SC) | 0.18 | 0.20 | 0.92 | 0.36 | -0.2, 0.56 |
| | Sex (F) | -0.14 | 0.23 | 0.61 | 0.54 | -0.59, 0.31 |
| | Type(P) | -1.56 | 0.14 | 11.14 | <0.001 | -1.83, -1.28 |
| | Colony (SC):Sex (F) | 0.39 | 0.28 | 1.38 | 0.17 | -0.16, 0.94 |
| | Colony (SC) :Type (P) | -0.35 | 0.14 | 2.47 | <0.01 | -0.62, -0.07 |
| | Sex (F):Type (P) | 0.27 | 0.17 | 1.56 | 0.12 | -0.07, 0.61 |
| | Colony (SC):Sex (F):Type (P) | -0.37 | 0.20 | 1.88 | 0.06 | -0.75, 0.02 |
| FEI (SVM) | Intercept | -5.7 | 0.07 | -78.7 | <0.001 | -5.9, -5.6 |
| | Type (P) | 0.48 | 0.03 | 18.17 | <0.001 | 0.4, 0.5 |
| | Colony (SC) | 0.40 | 0.10 | 4.1 | <0.001 | 0.2, 0.6 |
| DE (SVM) | Intercept | -4.2 | 0.21 | -20.0 | <0.001 | -4.6, -3.8 |
| | Type (P) | 0.77 | 0.03 | 23.4 | <0.001 | 0.7, 0.8 |
| | Colony (SC) | 0.20 | 0.29 | 0.7 | 0.48 | -0.4, 0.7 |
| FEI (camera) | Intercept | -5.16 | 0.08 | -62.91 | <0.001 | -5.33, -5.0 |
| | Present predators (seabirds) | 0.08 | 0.05 | 1.56 | 0.1 | -0.02, 0.18 |
| | Present predators (multi) | -0.08 | 0.05 | -1.79 | 0.07 | -0.17, 0.001 |
| DE (camera) | Intercept | -3.31 | 0.22 | -15.49 | <0.001 | -3.78, -2.91 |
| | Present predators (seabirds) | 0.17 | 0.06 | 2.68 | <0.01 | 0.05, 0.30 |
| | Present predators (multi) | -0.19 | 0.06 | -3.21 | <0.01 | -0.30, -0.07 |

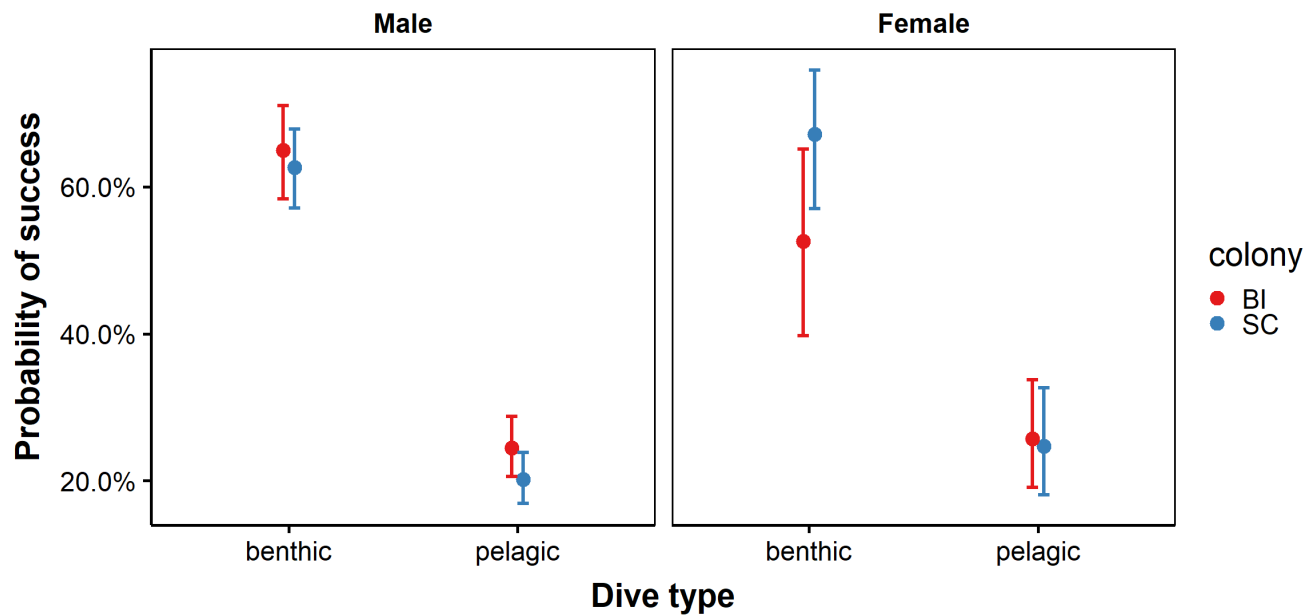
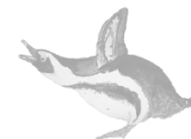


Figure 4.4: Probability of success for benthic and pelagic dives performed by male and female African penguins at Bird Island (BI) and St Croix (SC) colonies. Error bars represent standard error (S.E.) from the coefficient.



The most parsimonious model for FEI (prey captured/total VeDBA) included both dive type (benthic or pelagic) and colony, with FEI being higher for SC birds and generally higher during pelagic dives than benthic dives regardless of the colonies (Table 3). For DE (diving efficiency; prey captures/dive duration) only dive type was retained in the most parsimonious model. While there were some differences between individual total VeDBA, sex did not appear to be a significant factor in predicting FEI. For both FEI and DE models, a single candidate model was retained and model averaging was not deemed necessary.

Prey types and interactions with other predators

The video camera programming schedule provided sampling at regular intervals throughout the entire foraging trips. A total of 5511 dives were observed in the video data obtained from 14 African penguins, representing 56.2% of all dives recorded. Individuals captured clupeoid fish (anchovy, sardine and red-eye round herring *Etrumeus whiteheadi*) and pipe fish (*Syngnathus* spp.) on pelagic dives. Jellyfish (phylum Cnidaria) were also present, but unlike in other penguin species (Thiebot et al. 2017) there were no capture attempts made by African penguins. Due to low light levels at depths > 30 m, it was not possible to determine prey type during benthic dives however the video cameras could pick up the sound of chase and capture, similar to when the animals were on the surface. This, in conjunction with the high precision SVM was evidence enough to suggest that prey captures occurred close to, or along the sea floor.

Penguins were observed in multi-species feeding groups (in 30% of dives) with other seabirds such as Cape gannets (*Morus capensis*) and Cape cormorants



(*Phalacrocorax capensis*), shearwaters (*Puffinus* spp.), terns (*Thalasseus* spp.) and conspecifics (Table 4.4; Figure 4.5). Incidences of competition with other foraging seabirds (Cape gannet and Cape cormorant) were observed in which the penguin was unsuccessful in capturing prey in both events. Individuals also foraged in association with tuna (*Thunnus* spp.) and sharks (*Carcharhinus* spp.) on 11% of dives. The presence of sharks did not seem to influence the penguins' behaviour, as individuals were observed moving between them and capturing fish escaping the bait ball. Bryde's whales (*Balaenoptera brydei*) were observed on some video footage (N=3 events) but, in these cases, the bait ball was quickly consumed and individuals were observed consuming only a single clupeoid fish on these occasions.

To investigate the influence of heterospecifics on foraging efficiency, foraging groups were separated into 3 levels: "none", when individuals were foraging alone; "seabirds" when individuals were foraging in groups of other seabirds (including African penguins) and "multi-heterospecific" when individuals foraged in the presence of sharks and tuna, other seabirds were also present in these events. It was not possible to further separate the seabird group as penguins were rarely observed foraging in conspecific-only groups. Individuals in the presence of other predators exerted significantly more effort on successful prey capture events, than when alone (Table 4.4). Post-hoc tests indicated that there was a significant difference in mean VeDBA when individuals foraged alone, compared to foraging with other predators. However, there was no relationship between VeDBA and the type of predator present, with values similar for individuals foraging in seabird and multi-heterospecific groups ($P > 0.05$). Modelling indicated that neither the presence of

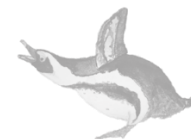


Table 4.4: Total dives, number of prey captures, proportion of successful dives and average rate of activity (Mean VeDBA, g) for African penguins (N=14) equipped with video cameras when foraging alone or in the presence of other predators.

| Predator presence | Total dives (% total dives) | Total prey caught | Proportion successful dives (%) | Mean VeDBA (g) |
|----------------------|-----------------------------|-------------------|---------------------------------|----------------|
| None | 3274 (59) | 657 | 11.6 | 0.15 ± 0.01 |
| Seabird | 1648 (30) | 1373 | 44.2 | 0.20 ± 0.01 |
| Multi-heterospecific | 589 (11) | 451 | 41.1 | 0.19 ± 0.01 |

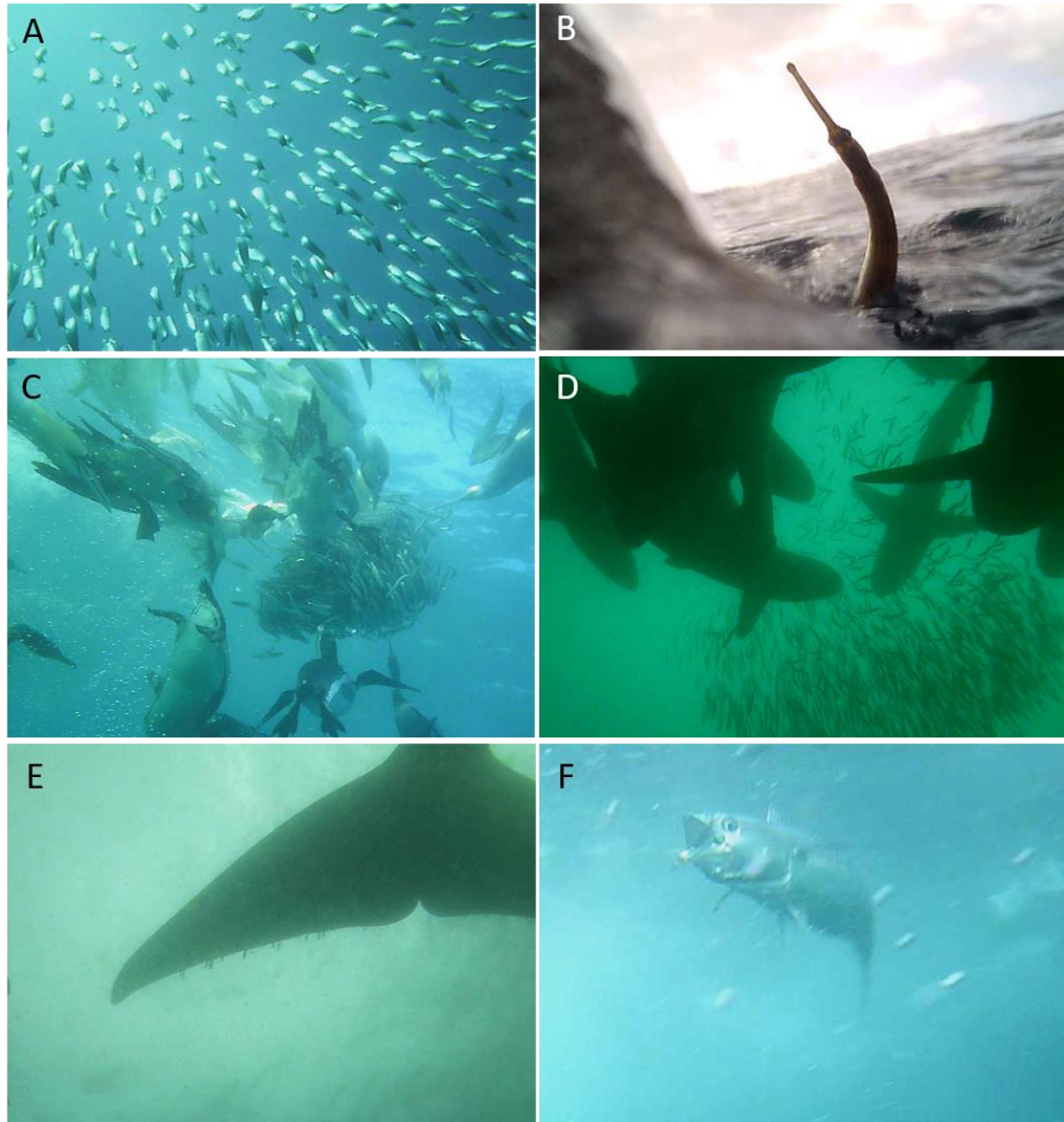


Figure 4.5: Representative still images of video data obtained from foraging African penguins. Bait fish (A); African penguin consuming a pipefish (B); Conspecifics and seabird heterospecifics (i.e., Cape Gannets *Morus capensis*) foraging on bait ball (C); Sharks (D); Whale (E) and Tuna (F).



seabirds nor multi-heterospecifics had a significant effect on FEI (Table 4.3). In contrast, DE was significantly affected both by the presence of seabirds and multi-heterospecifics. There was a significant increase in DE in the presence of seabirds and a decrease in the presence of multi-heterospecific groups.

Discussion

Accurately determining where and when animals find and capture prey is integral to the study of foraging ecology. For diving marine predators, accurately detecting the location and depth of feeding events in the marine environment may provide information about the distribution of prey resources and the strategies by which animals obtain them (Viviant et al. 2010; Wakefield et al. 2009). In the present study, a unique combination of animal-borne video cameras, GPS, depth recorders and tri-axial accelerometers revealed new insights into the foraging behaviour and efficiency of an endangered marine predator, the African penguin. It was found that, while individuals performed both pelagic and benthic foraging dives, benthic diving was more successful in terms of the probability of prey captures, but successful pelagic dives were more energetically efficient. Modelling indicated success rates for pelagic dives were higher for females while males were more successful at capturing prey on benthic dives. However, differences in foraging success between colonies were observed, possibly due to the bathymetry surrounding each colony. Interestingly, camera footage revealed that African penguins' diving efficiency increased with the presence of other seabirds but decreased in the presence of larger non-flying predators (sharks, whales, predatory fishes).



Diving behaviour and foraging success

Linking diving behaviour and prey capture success is important for understanding the foraging behaviour of some marine predators. Accelerometry has been used in a range of studies to detect patterns of movement through unsupervised models because of the logistical difficulties of verifying datasets. In the current study, a supervised machine learning approach identified feeding events at sea from observations of African penguins wearing cameras and accelerometers. The model was developed from prey captures observed on pelagic dives as observing benthic prey captures was difficult due to low light conditions. However, studies that have used signals in accelerometry to detect prey captures suggest that prey capture signals remain the same, irrespective of depth or dive type (Volpov et al. 2015) but signals may change in duration or intensity with regard to prey type (Watanabe & Takahashi 2013). The high accuracy of the SVM model for predicting potential prey captures highlights the beneficial use of accelerometers to calculate prey captures where cameras may be limited by battery capacity, or reduced light conditions during deep dives.

Diving behaviour varies within a species and may be dependent on habitat and prey availability, as well as sex or individual body size. In the present study, benthic foraging was more successful for males than females at BI only, which is likely due to a combination of differences in physiological diving capacities (as a result of sexual size dimorphism) and in exploited habitats. Indeed, male African penguins are generally larger than females which is thought to contribute to differences in foraging behaviour (Pichegru et al. 2013). Consequently, individuals with larger body sizes



should have larger oxygen stores and, therefore, be able to dive for longer durations and reach greater depths (Lewis et al. 2005; Weise & Costa 2007). The benthic environment surrounding BI is comprised of relatively steep sloping sea floor with depths exceeding 80 m, as such males may be more capable of exploiting these deeper benthic environments than females. In comparison, the seafloor surrounding SC Island is shallower, which may explain the similar success rates of females and males during benthic dives.

By contrast, females at both colonies showed similar probability of capture success during pelagic dives. Female success may be due to their overall smaller size, as smaller predators have shorter turning angles which may make them more manoeuvrable (Fish et al. 2003) and may enable more efficient movement through the water while capturing highly mobile prey (Lovvorn et al. 2001). This may explain why males, who were highly successful benthic divers, also consumed pelagic prey when available, even though their capture success was lower than females.

Low prey capture rates on pelagic dives in this study may be due to the inclusion of shallower dives up to 1.5 m, which may be considered transiting dives. Previous studies in Algoa Bay have used a dive threshold of three metres in an attempt to remove transiting dives from analyses (McInnes & Pistorius 2019). However, in the present study, 204 prey captures were observed within the first three metres of the water column which would have been omitted if a threshold of 3 m was used, accounting for just over 10% of the prey captures detected during pelagic dives. By setting the dive threshold too high, it is possible to miss prey captures, however setting the dive threshold lower, it may include travelling dives as foraging dives,



thereby reducing pelagic dive success rate. Even though some prey captures were detected close to the surface of the water, the dive threshold of 1.5 m was selected in order to remove most transiting periods. However, increasing the dive threshold to 3 m only improved the proportion of successful pelagic dives from an average of 23.2 to 26.9%.

Benthic diving has been documented in several penguin species including Gentoo, *Pygoscelis papua* (Kokubun et al. 2010; Robinson & Hindell 1996), Yellow-Eyed, *Megadyptes antipodes* (Mattern et al. 2007), Emperor, *Aptenodytes forsteri* (Rodary et al. 2000), Adelie, *Pygoscelis adeliae* (Ropert-Coudert et al. 2002), Chinstrap, *Pygoscelis antarcticus* (Takahashi et al. 2003) and macaroni penguins, *Eudyptes chrysolophus* (Tremblay & Cherel 2000). However, no such diving behaviour has been previously reported for African penguins. Throughout their range African penguins appear to be entirely reliant on pelagic prey (Crawford et al. 2006; McInnes et al. 2017b; Petersen et al. 2006), even in areas of low prey quality and abundance (Ludynia et al. 2010). Although prey capture events could be identified on benthic dives, it was not possible to identify the prey type being consumed due to low visibility. A single study, reported Beaked sandfish (*Gonorhynchus gonorhynchus*) and Barred fingerfin (*Cheilodactylus pixi*), two benthic fish species, commonly presented in 9.6 and 4.2% of African penguin diet samples in individuals at SC and BI (Randall & Randall 1986). Although it is probable that penguins are consuming some benthic species during benthic dives, pelagic prey have been known to occupy depths > 70 m (Beckley & Van der Lingen 1999; Roel & Armstrong 1991), deeper than many parts of Algoa Bay. Hence, penguins foraging at these depths could be



consuming pelagic species on benthic dives. Indeed, similar behaviour was observed in Cape cormorants foraging on the west and south western coast of South Africa who performed benthic dives, while diet samples indicated they foraged exclusively on pelagic prey items (Cook et al. 2012).

As females may be less successful on benthic dives, they may have a higher reliance on pelagic prey compared to males, thereby possibly being more sensitive to reduced pelagic prey availability. A male-bias in the adult sex ratio of African penguins exists due to a combination of male-biased chick production and female mortality (Spelt & Pichegru 2017). The higher rates of female mortality (Pichegru et al. 2013) could be partially explained by their extra sensitivity to the recent decrease in small pelagic prey in South Africa (Pichegru et al. 2012). Similarly, in Magellanic penguins (*Spheniscus magellanicus*), mortality rate is higher for females when conditions are unfavourable, resulting in a male-skewed adult sex ratio and population decline in this species (Gownaris & Boersma 2019). Certainly, this could be the case for African penguins, however due to low sample sizes in the present study, further assessments of sex-specific diving behaviour, particularly in years of low prey availability are needed to better understand how females may adapt to changing conditions.

Foraging efficiency and implications

Sea-floor depth has been shown to influence prey availability and foraging efficiency in marine predators (Christophe et al. 2001; Yen et al. 2004). For instance, in little penguins (*Eudyptula minor*), individuals from colonies with shallower waters show lower diving effort (total diving duration per hour) compared to individuals



from colonies with deeper waters (Meyer et al. 2017). In African penguins, indices of foraging effort in this study (mean and total VeDBA) were higher on benthic dives than pelagic dives, suggesting that individuals from colonies surrounded by steeper bathymetry may put in more effort to capture prey.

Individuals at the SC colony were more efficient in both pelagic and benthic strategies than individuals at BI possibly due to the shallower bathymetry associated with SC. For example, as the bathymetry was shallower, the energy expenditure from benthic dives was lower, hence overall energy efficiency was higher for individuals at SC. Furthermore, pelagic foraging efficiency was higher at SC and may suggest higher prey availability in the waters around this colony during the time of our study, or that individuals were more efficient at capturing prey. This is consistent with the prediction that colonies with shallow waters are more favourable to diving seabirds compared to deeper waters as prey is presumably less dispersed and, therefore, easier to catch (Meyer et al. 2017).

Environmental variability has led to divergent foraging behaviours in many marine predators (Arthur et al. 2016; Castillo-Guerrero et al. 2016; Waugh & Weimerskirch 2003). The south and south-east region of South Africa is characterised by warmer and less productive waters compared to the west and south-west coast which are enriched by the productive Benguela upwelling (Kirkman et al. 2016). African penguins breeding in Algoa bay experience highly variable changes in ocean temperatures which is thought to influence the availability of prey (Goschen et al. 2012; Schumann et al. 1995).



Collectively, the islands and surrounding waters of Algoa bay support a large biomass of marine predators, including half of the global African penguin population, two thirds of the global Cape gannet population, several tern, cormorant and gull colonies (Crawford et al. 2009), as well as a variety of other resident (Kirkman et al. 2007) and migratory marine mammals (Melly et al. 2018; Reisinger & Karczmarski 2010) all which forage within the bay. The fact that African penguins display benthic diving in the current study, but that no such diving behaviour is evident in individuals from the West coast, could indicate the ability to adapt foraging behaviour to buffer against the effects of reduced pelagic prey availability. Indeed, a breeding African penguin is estimated to require 213 kg of anchovy per year in order to successfully raise 2 chicks (Steinfurth & Underhill 2011). The large number of other predators and the high degree of environmental variability in the region may reduce success and, therefore, drive the development of competition avoidance foraging strategies.

In periods of low productivity, individuals with a higher degree of flexibility in their foraging strategies are predicted to have a greater chance of surviving (Montevecchi et al. 2009; Quillfeldt et al. 2011). While pelagic prey surveys (Pichegru, unpublished data) and trip durations during the study year were similar to previous years, benthic diving may indicate degree of plasticity in the foraging behaviour of African penguins. This may be useful in buffering the negative effects in years of low pelagic prey availability. However, more information is needed over multiple seasons to address this.



Prey type and at-sea predator interactions

Recent deployments of miniaturised animal-borne video cameras on African penguins revealed that conspecifics group foraging behaviour increase individual foraging success by aggregating and pushing prey towards the surface (McInnes et al. 2017a). Other seabirds such as shearwaters and Cape cormorants have been shown to also benefit from African penguins driving aggregated prey towards the surface within their reach (McInnes & Pistorius 2019). It was not known, however, whether African penguins themselves also benefit from the presence of such heterospecifics during pelagic foraging. In the present study, African penguins foraged in the presence of at least four species of seabirds. These intra-specific aggregations increased the diving efficiency of instrumented individuals. Mixed species feeding flocks may indicate prey location (Thiebault et al. 2014b), work as a predator avoidance strategy (Sutton et al. 2015) and assist in aggregating large bait balls (McInnes & Pistorius 2019; McInnes et al. 2017a; Ryan et al. 2012) which facilitates efficient capture.

While mixed feeding flocks of seabirds have been observed during at-sea surveys (Ryan et al. 2012), the consequences of African penguins foraging in the presence of sharks has not been previously documented. Competitive exclusion may occur when larger individuals/species outcompete and exclude smaller individuals/species for the same resources (Wilson 1975). Although sharks did not appear to deter African penguins from attempting to capture prey, the presence of larger predators may act as a physical barrier to the bait ball by forcing penguins to target prey escaping the school and preventing penguins corralling prey closer to the surface. As such, diving



efficiency was lower as individuals could not gain access to the bait ball.

Furthermore, lower efficiency observed in the presence of large apex predators may also reflect predator avoidance. Indeed, African penguins have been observed coming ashore with bites from larger predators (Johnson et al. 2006). Both competitive exclusion and predation avoidance could be composite factors in reduced foraging efficiency for African penguins when feeding in the presence of larger top order predators.

In summary, African penguins breeding in Algoa Bay, South Africa, were observed to display sex--specific diving behaviours and foraging efficiency related to the bathymetry around their colonies. Individuals exploiting shallower sea-floor habitats may have a greater chance of capturing benthic prey. In addition, benthic foraging behaviour might buffer the effects of changes in pelagic prey availability, however this may come at a greater cost due to higher energy costs of benthic dives, especially for females which smaller size reduces their resilience. This study confirms the positive role conspecifics and other seabirds may have on African penguin individual foraging behaviour and efficiency. However, we revealed that the presence of larger predators decreased prey capture rates of African penguins, likely due to a combination of competitive exclusion and/or predation risk.

Chapter 5: Fine-scale foraging effort and efficiency of Macaroni penguins is influenced by prey type, patch density and temporal dynamics.



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Abstract

Difficulties quantifying *in situ* prey patch quality have limited our understanding of how marine predators respond to variation within and between patches, and throughout their foraging range. In the present study, animal-borne video, GPS, accelerometer and dive behaviour data loggers were used to investigate the fine-scale foraging behaviour of Macaroni penguins (*Eudyptes chrysolophus*) in response to prey type, patch density and temporal variation in diving behaviour. Individuals mainly dived during the day and utilised two strategies, targeting different prey types. Subantarctic krill (*Euphausia vallentini*) were consumed during deep dives while small soft-bodied fish were captured on shallow dives or during the ascent phase of deep dives. Despite breeding in large colonies individuals seemed to be solitary foragers and did not engage with conspecifics in coordinated behaviour as seen in other group foraging penguin species. This potentially reflects the high abundance and low manoeuvrability of krill. Video data were used to validate prey capture signals in accelerometer data and a Support Vector Machine learning algorithm was developed to identify prey captures that occurred throughout the entire foraging trip. Prey capture rates indicated that Macaroni penguins continued to forage beyond the optimal give up time. However, bout-scale analysis revealed individuals terminated diving behaviour for reasons other than patch quality. These findings indicate that individuals make complex foraging decisions in relation to their proximate environment over multiple spatio-temporal scales.



Introduction

Optimising foraging efficiency is paramount to maximising reproductive success, especially for animals that are restricted in their foraging range during offspring provisioning (Baylis et al. 2015; Cook et al. 2012; Doniol-Valcroze et al. 2011; Hart et al. 2010). The availability and type of prey plays a central role in foraging efficiency and patterns of energy flow within an ecosystem (Brose et al. 2008). For example, a predator's decisions of where and when to search for food, and how much energy to expend in doing so, are greatly influenced by the abundance and distribution of prey in the environment (Higginson & Ruxton 2015). The challenge for predators is to locate and exploit prey aggregations in a way that best limits the overall energetic cost of foraging, while prey should seek out locations of low predator densities (Fauchald 2009). Previous studies have provided insight into how predators utilise the experience of other foragers to locate prey (Clark & Mangel 1986; Thiebault et al. 2014b), adjust their search trajectories in response to prey (Higginson & Ruxton 2015; Lescroël et al. 2004; Weimerskirch et al. 2007) and move between prey patches in response to changing quality (Mori & Boyd 2004a). However, without direct observation of the prey field (i.e. prey type and abundance), understanding predator-prey interactions remains limited.

In the marine environment, prey is distributed across a wide range of spatial and temporal scales (Fauchald 2009). Due to the often cryptic nature of marine species, prey abundance and distribution has long been inferred from mesoscale oceanographic features (e.g. eddies, fronts and upwellings) and quantified using proxies of primary productivity (e.g. sea surface temperature and Chlorophyll-*a*



concentration) (Grecian et al. 2016). However, these may not necessarily be associated with prey availability (Grémillet et al. 2008). Furthermore, remotely sensed Chlorophyll-*a* and SST information are often obtained at coarse resolutions, which limit their applicability to fine-scale foraging data.

Linkages between prey and predator foraging behaviour have been revealed through the use of animal-borne data loggers (Bon et al. 2015; Bost et al. 2009; Goulet et al. 2019; Humphries 2015). Air-breathing marine predators, such as seals and diving seabirds, may increase their prey encounter rate by spending more time at depth (Mori 1998; Mori & Boyd 2004a). However, due to physiological constraints of diving, the depth at which prey are encountered may also influence the efficiency of patch exploitation (Doniol-Valcroze et al. 2011). Animal-borne video data loggers have allowed greater insight into the foraging behaviour of some marine predators. However, information on factors influencing foraging success over various temporal scales (i.e. dive-by-dive or patch-by-patch) still remains limited. Determining these, and the strategies individuals use to increase foraging success can provide valuable information about how they adapt to changes in prey abundance and distribution (Boyd et al. 2017).

The Macaroni penguin (*Eudyptes chrysolophus*) is the most abundant of the Spheniscidae family. While this species is thought to predominately consume krill (*Euphausia* spp.), myctophid fish and amphipods commonly occur in their diet during later stages of chick rearing (Deagle et al. 2007). However, it is not known how changes in prey type may influence the foraging strategies of this species. Macaroni penguins are thought to adjust their dive depth in relation to the vertical



diel migration of krill (Hart et al. 2010). However, behavioural responses to prey fields are inherently difficult to measure and have not yet been quantified at finer scales (i.e. dive-by-dive, patch-to-patch). According to the marginal value theorem (MVT), prey patch quality and the travel time between foraging patches should influence how long a forager remains at a patch (Charnov 1976; McNair 1982). Therefore, Macaroni penguins are expected to increase their patch residency times when encountering patches of high quality in accordance with the MVT.

In penguins, group foraging has been shown to have both positive and negative consequences depending on the prey targeted and heterospecifics present (Sutton et al. 2020; Sutton et al. 2015). Individuals may benefit from the presence of others by concentrating schools of fast moving prey, thereby making it easier to catch. While the majority of group foraging studies in penguins have investigated its consequences in fish-eating species, less information is available for species that predominately consume krill. As Macaroni penguins breed in densely populated colonies (Deagle et al. 2007; Sato et al. 2004; Woehler 1993), it is likely that individuals may encounter one another at sea, especially when commuting or foraging close to the colony. However, as krill is less mobile than schooling fish and may not require concentrating, individuals may not display the coordinated at-sea behaviour observed in fish-hunting penguin species. While a recent study with limited video footage (7 dives) indicated Macaroni penguins dived in the presence of conspecifics (Thiebault et al. 2019), information on how close to the colony this occurred, or whether the presence of conspecifics influenced foraging success was lacking. Such knowledge is necessary for understanding how changes in prey distribution and abundance may



influence foraging behaviour and energy expenditure. A greater understanding of Macaroni penguin foraging behaviour is vital for predicting how the population may respond to environmental variability as a consequence of climate change and/or increased human exploitation of marine resources.

The aims of the present study, therefore, were to: 1) investigate the fine-scale foraging effort and efficiency of Macaroni penguins in relation to prey type and patch quality; 2) assess temporal variability in foraging effort and efficiency and; 3) determine the potential role of conspecifics in foraging.

Materials and methods

Data collection procedures

The study was conducted at Cape Cotter, located on the northern coast line of Coubert Peninsula, Kerguelen archipelago, in December 2017. Approximately 73,000 pairs of Macaroni penguins breed at this location, which is one of many colonies on the archipelago (Barbraud et al. 2020). Individuals were sampled during early chick rearing period during which time females forage and males guard offspring at the nest. Females were identified from a breeding pair based on their smaller body and bill size in comparison to their male partner (Warham 1975).

Individuals were captured at the nest after feeding their chicks, weighed in a cloth bag on a digital scale (± 10 g) and axillary girth was measured with a flexible tape measure (± 0.5 cm). Individuals were then instrumented with three devices for a single foraging trip: 1) a video data logger (Catnip Technologies, Bird Cam, 25 x 45 x 15mm, 30 frames per second, 24 g), which was housed within a custom made 3-D printed housing and programmed to switch on 20 h after deployment (to avoid



recording on-land or transiting periods) and record on a 30 min on: 30 min off schedule; a combined tri-axial accelerometer and depth recorder (Technosmart, Axy-Depth, 12 x 31 x 11mm, 7.5 g) sampled acceleration and depth at 25 Hz and 1 Hz, respectively; and GPS (Mobile Action Technology, I-gotU, GT-120, 44.5 x 28.5 x 13 mm, 20 g) which sampled at 2 min intervals and was packaged in heat shrink tubing for waterproofing. The devices were attached to feathers along the dorsal mid-line with waterproof tape (Tesa 4651, Beiersdorf, AG, GmbH, Hamburg), with the camera in front of the other devices so as to streamline the package in an effort to minimise hydrodynamic drag (Bannasch et al. 1994; Ludynia et al. 2012). Together, the package was < 3% body mass (average body mass = 3655 ± 77 g) and < 0.3% cross-sectional surface area. Efforts were made to minimise handling time with all procedures lasting < 10 min. Furthermore, a small drawstring hood was used to cover the penguin's head in order to reduce stress (Cockrem et al. 2008) and, after handling, the individual was released back to its nest where it remained with its partner and chicks until voluntarily departing for a foraging trip.

After a single foraging trip, individuals were recaptured and the devices were removed. Body mass and axillary girth were again recorded and additional morphometric measurements were taken with Vernier callipers (bill length, bill depth, bill width; ± 0.1 mm) and metal ruler (flipper length; ± 1 mm). These measurements were used to assess structural size and body condition of individuals.



Data processing and statistical analyses

Video data were initially viewed in media player software and a list of all behaviours, prey types, conspecifics and heterospecifics that individuals encountered were noted. These were included as “buttons” on a custom video annotation sheet created in Solomon Coder (Budapest, Hungary, Version 16.06.26) where videos were coded frame-by-frame. Video camera data were used to determine prey type, prey captures and whether they occurred in the presence or absence of conspecifics or other predators. Coding sheets were aligned with corresponding accelerometer/depth data in IgorPro (Wavemetrics Inc, Portland OR, USA, version 6.3.7.2) using Ethographer (Sakamoto et al. 2009a) and all further analyses were conducted in the R statistical environment (version 3.5.2) (R Core Team 2018).

The tri-axial acceleration data (X: surge; Y: sway; and Z: heave) were filtered using a 1 s running mean to dissociate static acceleration (due to the animal’s position in space in relation to gravity) from dynamic acceleration (accounting for animal movement). Vectorial Dynamic Body Acceleration (VeDBA), an index of energy expenditure (Qasem et al. 2012), was estimated using the equation: $VeDBA = \sqrt{(X_{dyn}^2 + Y_{dyn}^2 + Z_{dyn}^2)}$.

Where X_{dyn} , Y_{dyn} and Z_{dyn} correspond to the dynamic surge, sway and heave accelerometer data. The values were then summed and averaged across each dive and used as proxies for rate and total energy expenditure, respectively.

Video data only accounted for a portion of the foraging trip and low light levels resulted in some unclear footage. As such, a two class Support Vector Machine (SVM) classifier was developed from the aligned camera and accelerometer/depth



data using the package *e1071* (Meyer et al. 2019) in order to detect prey captures across the full foraging trip. Data corresponding to depths shallower than 0.5 m were removed to limit investigation to underwater periods only. Based on the camera data, a known behaviour (swimming or prey capture) was assigned to each data point. A total of 4,166 prey capture events and 659,382 swimming events were identified in the aligned data and a stratified random sample was taken as a dataset to train the model. In accordance with previous studies (Carroll et al. 2014; Chessa et al. 2017; Lara & Labrador 2012), a rolling window of 8 (corresponding to approximately 0.32 s) was used to extract statistics for each accelerometer axis and VeDBA. The best model utilised a radial kernel where tuning parameters gamma and cost were 0.01 and 10, respectively. To ascertain model performance, a 10-fold cross validation was performed. Data were randomly split into 10 groups (folds) and for each fold, the SVM was trained with a data set corresponding to 70% of the fold and tested using the remaining 30%. Model performance was evaluated using the following 3 metrics obtained from each fold, and the mean and standard error (S.E.) were reported: 1) Accuracy - The number of correct predictions made by the model; 2) Recall (or Sensitivity) - The number of positive predictions divided by the total number of positive class values in the test data and 3) False Positive rate - The number of times the model incorrectly identified swimming as a prey capture event (Table 5.1) (Wei & Dunbrack 2013). Only dives > 1.5 m and with a duration > 10 s were retained to further reduce potential erroneous prey captures associated with surface activity, transiting and acceleration during porpoising. These values were chosen as conservative thresholds based on observed successful prey capture dives.



Table 5.1: Results of cross validated SVM model used to detect swimming behaviour vs. potential prey captures events in macaroni penguins. The model was 75% accurate in correctly identifying between swim and prey capture events with a low false positive rate.

| Metric | Mean \pm S.E. (%) |
|---------------------|---------------------------------------|
| Accuracy | 75 \pm 0.07 |
| Recall | 75 \pm 0.07 |
| False Positive Rate | 19 \pm 0.3 |



The GPS data were restricted to locations at sea and a speed filter was applied to the data to removed erroneous fixes greater than $10 \text{ km}\cdot\text{h}^{-1}$ (McConnell et al. 1992). In order to correct for irregular fix frequencies, all tracks were linearly interpolated to 1 min intervals using the *adehabitatLT* package (Calenge 2011). This was merged with the SVM prey capture results in order to provide bout locations and distances between consecutive foraging bouts. The average foraging trip bearing (degrees) was calculated using the *geosphere* package (Hijmans et al. 2019). To determine the relationship between foraging efficiency and distance from the colony, a Spearman rank correlation was calculated between the total number of prey captured divided by total VeDBA and the maximum distal point from the colony (km).

Raw dive data were processed using *diveMove* package (Luque 2007) and zero-offset corrected to account for pressure transducer drift. The following metrics were calculated per dive: maximum depth, dive duration, post dive duration, mean ascent and descent rates. Penguins are known to complete multiple dives at a single prey patch in bouts of foraging. Therefore, each dive was grouped into foraging bouts defined as a dive or series of consecutive dives where surface periods lasted < 2.5 min which was determined through dive bout criterion analysis using the *diveMove* package (Luque & Guinet 2007). Each foraging bout represented patch residency time (PRT) and time between foraging bouts or “inter-bout time” was defined as the duration between the end of the previous bout and the beginning of the next bout.

According to the MVT, the optimal time to leave a prey patch is when the return rate reaches, and begins to drop below, the average return rate (McNair 1982; Watanabe et al. 2014). To determine if individuals followed the MVT, the cumulative



number of prey captures was calculated for dives and foraging bouts. Six mathematical equations were fitted to determine the best fitting trend. These relationships were further categorised into 3 types of prey capture rates: diminishing (sigmoid and decelerating); increasing (logit and accelerating); constant (linear and accelerating-to-linear) following the methods of Watanabe et al. (2014). The most parsimonious regressions, determined by Akaike Information Criterion (AIC), were fitted to the data. Trends were also visually assessed and where there was no clear pattern and regression lines fitted poorly, dives or dive bouts were categorized as “other”. Additionally, to determine if individuals followed the MVT at the bout-scale the cumulative number of prey captures was determined for each dive and cumulated over the bout. The same mathematical equations were fitted to determine the best fitting trend and the proportion of each trend is presented for both dives and bouts. Dives with < 10 prey captures and bouts of < 10 dives were not used to determine prey capture rates curves as the resolution was too low to ascertain relationships.

According to a previous study the diving behaviour of Macaroni penguins may change according to daylight levels (Hart et al. 2010). Therefore, Generalised Additive Mixed Models (GAMMs) were fitted using the *mgcv* package (Wood 2004) to allow for non-linear relationships between time of day (hour) and the response variables dive frequency ($\text{dives}\cdot\text{h}^{-1}$) and mean maximum depth (m). In addition, GAMMs were performed in order to determine the factors influencing mean prey capture depth, rate of effort (mean VeDBA, *g*) and efficiency (total prey captures divided by total VeDBA) per dive. Separate splines for time of day were fitted for each prey type, and the following parametric coefficients were included in these



models: dive-patch quality (number of prey captures/mean VeDBA per dive), prey type (fish or krill), number of prey captures and individual body condition (mass divided by flipper length). Preliminary investigation indicated that individuals altered their diving depth according to prey type. As such, an interaction between prey type and dive depth was also included in the model to examine this further. Morphometric measurements bill depth, bill width, head length and bill length were positively correlated with other parametric coefficients ($r^2 = >0.8$) and therefore, were excluded from further analysis in order to avoid collinearity between predictor variables.

To determine factors influencing patch residency time (PRT, calculated as the total duration of a bout), linear mixed effects (LME) models were fitted using the *lme4* package (Bates et al. 2014). A LME model was selected after initial GAMM modelling determined that there were no temporal relationships present in the data. The predictor variables modelled against patch residency time were mean dive depth for the bout (m), bout-patch quality (total prey captures/total VeDBA per bout), prey type, time between bouts (inter-bout time), and an interaction term between prey type and bout-patch quality. To account for pseudo replication, individual was used as a random factor in all models. In each case, the best fitting models were determined using a stepwise backwards selection of the full model where the coefficient with the largest non-significant P -value was removed (Zuur et al. 2009). This process was repeated until all retained coefficients were statistically significant (at a significance level $P < 0.05$). Unless otherwise stated, results are presented as Mean \pm S.E.



Results

Video, accelerometer and diving behaviour data loggers were deployed on a total of 10 female Macaroni penguins. However, due to device malfunctions, video data were obtained from only 6 individuals for 4.7 ± 0.2 h (range: 4.0 - 5.4 h). As the video data were set to record on a delay start, the data obtained was of daylight periods between the hours of 06:00 and 17:00 (local time) and represented 13% of the average foraging trip duration (Table 5.2). The GPS data loggers failed during the outward commute in two individuals, during the inbound commute to the colony in three individuals and three did not record at all due to water damage. As such, maximum distance from the colony was calculated as the maximum distance reached for birds that were returning to the colony before the GPS failed ($N = 5$) and trip duration was determined from the complete accelerometer-depth records ($N = 7$). Two individuals did not have video camera data due to water damage to devices. However, their accelerometer, depth and GPS data were retained for analysis. Mean dive depth (24.6 ± 0.3 m; max: 119.2 m) and foraging trip duration (35.5 ± 8.2 h) were similar to that previously reported for Macaroni penguins at this breeding site (Sato et al. 2004).

Dive-scale analysis

A total of 961 dives were observed in the video data, 15% of the total 5,942 foraging dives recorded. Individuals were observed resting/preening on the surface in small groups or close to the colony. However, penguins foraged in the presence of



Table 5.2: Deployment summary for Macaroni Penguins at Cape Cotter during the 2017 breeding season. Trip duration

(h) is underestimated for MP6 as both GPS and accelerometer data were incomplete. The following symbols signify

incomplete data: * accelerometer-depth data and + GPS data. No camera data was obtained for MP6 or MP8.

| ID | Mass (g) | Trip duration (h) | Total distance travelled (km) | Average bearing (°) | Mean VeDBA | Prey captures | Mean dive depth (m) | Prey capture depth (m) |
|---------------------|-------------|----------------------|----------------------------------|------------------------|---------------|------------------|------------------------|---------------------------|
| MP1 | 3300 | 19.2 | 415.8 | 40.7 | 0.20 ± 0.0 | 5037 | 24.4 ± 1.1 | 16.1 ± 0.7 |
| MP2 ⁺ | 3600 | 45.7 | 403.9 | 55.8 | 0.24 ± 0.0 | 14145 | 6.0 ± 0.3 | 4.1 ± 0.2 |
| MP3 ⁺ | 3700 | 18.1 | 413.5 | 70.7 | 0.19 ± 0.0 | 3196 | 43.3 ± 2.9 | 28.2 ± 1.9 |
| MP4 | 4150 | 17.0 | 402.9 | 24.0 | 0.23 ± 0.0 | 14262 | 44.7 ± 1.5 | 31.5 ± 1.1 |
| MP5 ⁺ | 3600 | 24.0 | - | - | 0.19 ± 0.0 | 11046 | 14.2 ± 0.7 | 9.9 ± 0.5 |
| MP6 ^{++*} | 3350 | 70.3 | 403.2 | 74.3 | 0.20 ± 0.0 | 19086 | 29.0 ± 0.8 | 20.0 ± 0.6 |
| MP7 ⁺ | 3850 | 21.0 | 393.6 | 93.5 | 0.20 ± 0.0 | 5886 | 58.6 ± 2.1 | 39.0 ± 1.3 |
| MP8 ⁺ | 3550 | 71.2 | 173.4 | 49.1 | 0.20 ± 0.0 | 41020 | 16.1 ± 0.5 | 11.1 ± 0.3 |
| MP9 ^{++*} | 3650 | 5.0 | - | - | 0.19 ± 0.0 | 1017 | 9.2 ± 0.9 | 6.2 ± 0.6 |
| MP10 ^{++*} | 3800 | 6.0 | - | - | 0.19 ± 0.0 | 3128 | 8.2 ± 0.6 | 5.6 ± 0.4 |



conspecifics on only 4 occasions (< 0.1% of dives observed in video data). In addition, a single occurrence of a heterospecific, a Kerguelen shag (*Phalacrocorax verrucosus*), was observed during a single dive. Prions (*Pachyptila* spp.) and storm petrels (*Oceanitidae* spp.) were regularly seen flying overhead but did not appear to influence the direction individuals travelled in.

Dive frequency increased throughout the day, peaking between 17:00-19:00 where individuals completed approximately 200 dives·h⁻¹ (Figure 5.1). These dives reached depths of between 20-30 m and lasted on average 1.35 ± 0.03 min. Dive depth was deepest in the middle of the day (between 09:00-12:00) where mean maximum depth was between 35-40 m, and individuals spent longer durations underwater (1.82 ± 0.03 min). Both dive frequency and mean depth were markedly reduced during twilight and night periods (Figure 5.1).

Within the video-recorded dives, individuals were observed to consume a total of 4,238 subantarctic krill (*Euphausia vallentini*, henceforth referred to as krill) and 318 larval fish (species unknown) in prey-specific foraging strategies. When targeting krill, birds dived > 40 m (mean: 42.9 ± 0.4 m) and were observed to travel through the patch, rapidly capturing large numbers of single prey items (maximum 153 krill within a dive), with individual captures lasting < 0.5 s. During the ascent phase of some dives (i.e. when the bird was no longer in the krill prey patch), individuals travelled passively to the water's surface and opportunistically captured fish as they ascended.

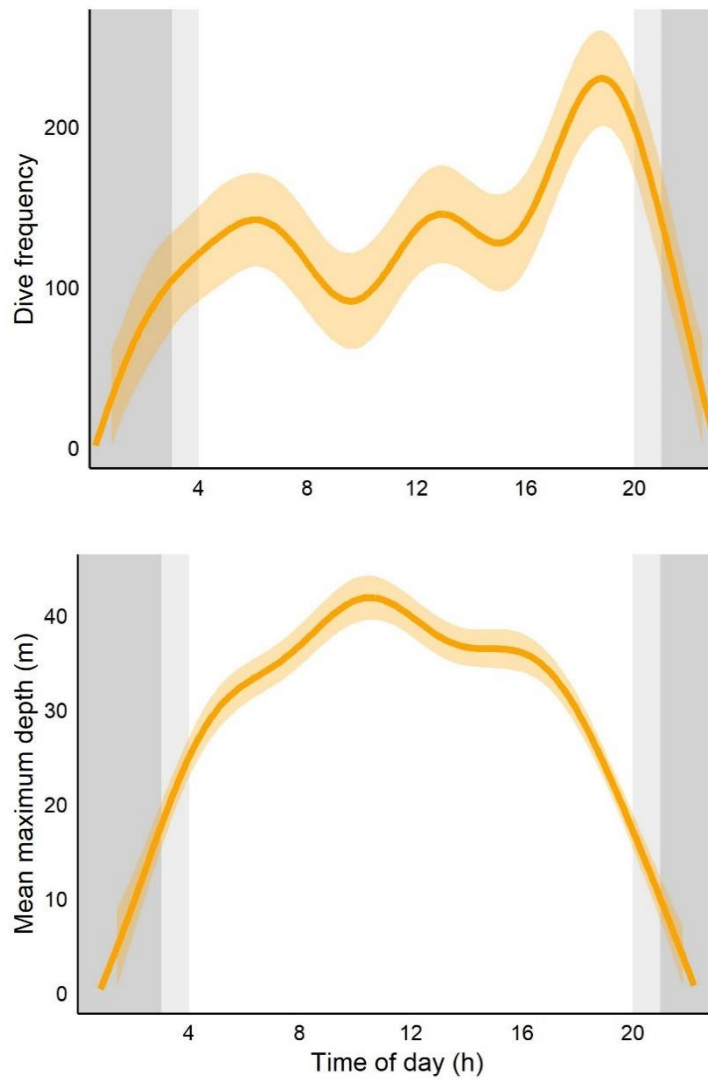


Figure 5.1: Temporal variation for dive frequency and mean maximum depth per hour predicted by generalised additive mixed models (GAMMs). Shaded areas along the curves represent 95% confidence intervals and grey shaded areas represent twilight and night periods.



In contrast, when targeting small fish, birds completed shallow horizontal dives (mean depth: 2.9 ± 0.1 m), searching for prey in the water close to the surface. Once a fish was detected, the individual ascended rapidly to capture it, then descended again to repeat the process, capturing multiple fish in a single shallow dive. Irrespective of prey type, all observed prey capture attempts appeared to be successful.

Applying the SVM to the accelerometer and depth data, a total of 112,609 prey captures were identified. Individuals consumed an average of $14,650 \pm 4,921$ prey items per foraging trip equating to 236 ± 88 prey·h⁻¹ (Table 5.3). Video data revealed that the majority (> 90%) of fish prey captures occurred at depths < 12 m (Figure 5.2). As such, captures identified by the SVM that occurred in waters ≤ 12 m were labelled as fish captures and the remaining, as krill captures.

Prey capture response curves (i.e. temporal pattern of cumulative prey captures within each dive) were determined in 2,974 dives. The majority of dives (80.9%) showed a diminishing curve (i.e. decreasing rate of prey captures). During these dives individuals captured on average 43.1 ± 0.6 prey and dived to an average of 33.0 ± 0.5 m. Individuals continued to forage beyond the optimal give up time according to optimal foraging theory (Charnov 1976; Watanabe et al. 2014) (Figure 5.3a). The second most common prey capture response curve was a constant curve, representing 8.94% of dives. Increasing response curves and dives that displayed irregular capture patterns (categorised as ‘other’) were the least common and accounted for 5.35% and 4.77% of dives, respectively (Figure 5.3).

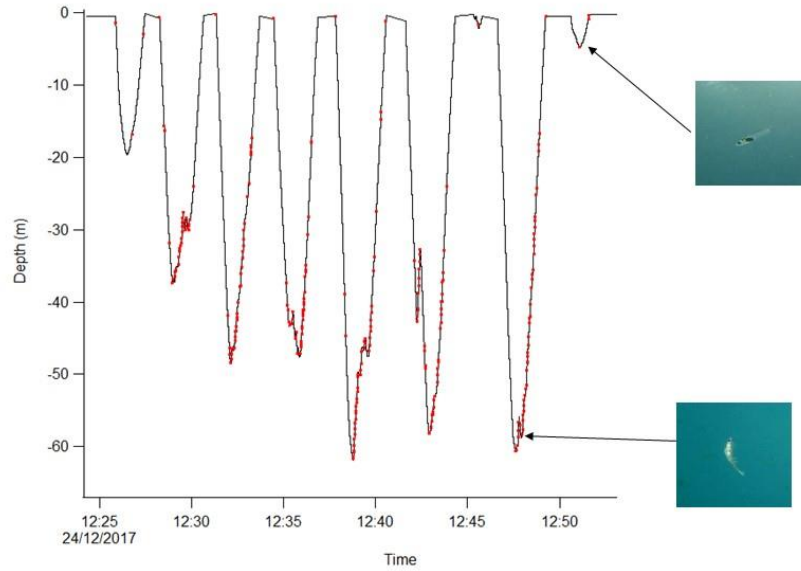


Figure 5.2: Representative dive profile with associated prey captures as estimated by SVM (indicated by red dots). Individuals were observed consuming subantarctic krill (bottom right) on deep dives and small fish (top right) on shallow dives.



Table 5.3: Prey capture summary for Macaroni penguins. Prey captures were determined using a two-class SVM. Prey types were inferred from depth of capture. Means +/- S.E. presented.

| Prey type | Number of dives | Number of prey captures | Prey Captures per dive | Mean Max Dive depth (m) | Depth of prey capture (m) | VeDBA (g) | Ascent rate (m·s ⁻¹) |
|--------------|-----------------|-------------------------------|---------------------------|----------------------------|------------------------------|------------|-------------------------------------|
| Fish | 3 394 | 16 848 | 5.0 ± 0.0 | 2.9 ± 0.1 | 2.13 ± 0.03 | 0.22 ± 0.0 | 0.39 ± 0.0 |
| Krill + Fish | 1 843 | Krill: 85 935 Fish: 10 771 | 26.6 ± 0.3 | 42.9 ± 0.4 | 29.17 ± 0.3 | 0.21 ± 0.0 | 0.84 ± 0.0 |
| No captures | 705 | - | - | 1.5 ± 0.1 | - | 0.23 ± 0.0 | 0.48 ± 0.0 |

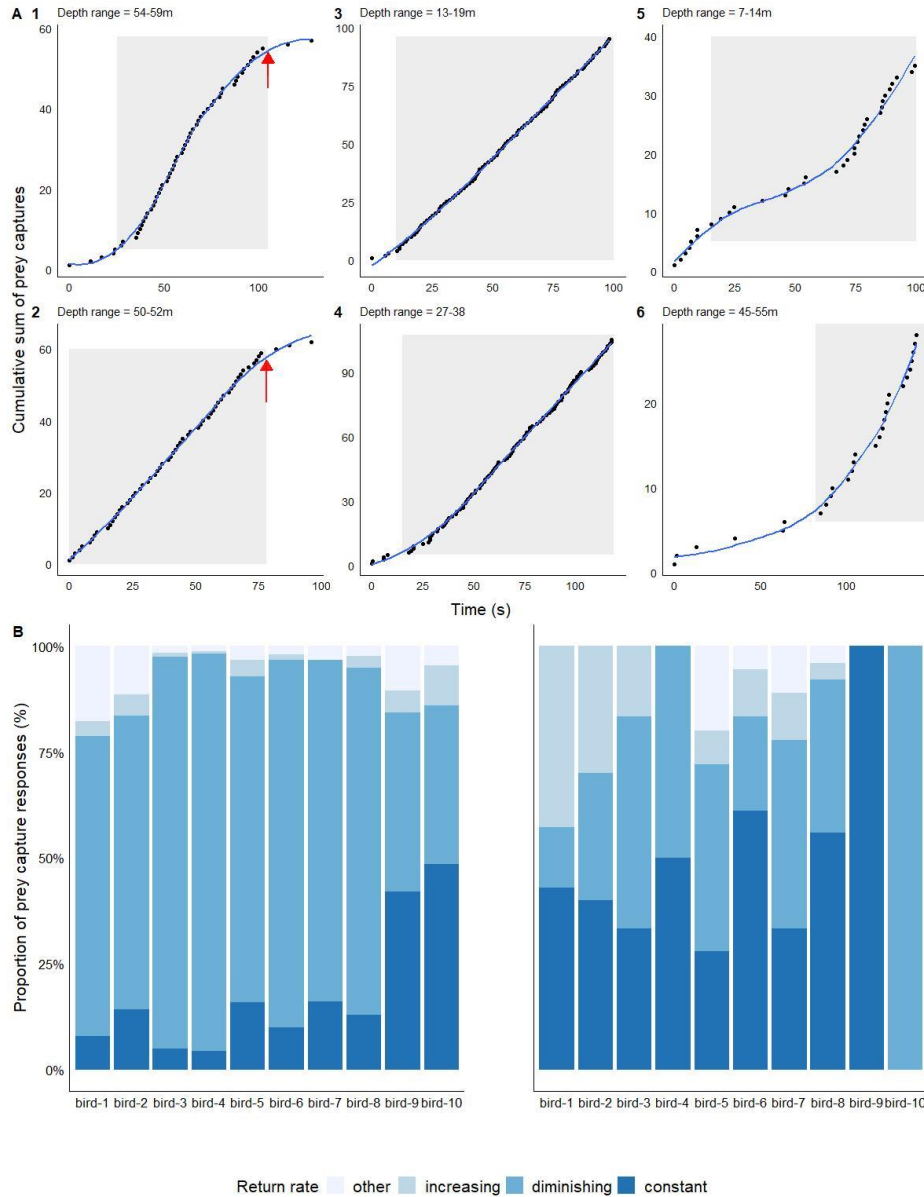


Figure 5.3: Representative examples of prey capture rate shapes (A) for diminishing (A1), sigmoid (A2), accelerating to linear (A3), linear (A4), logit (A5) and accelerating (A6) for Macaroni penguins. Shaded area represents the prey patch and arrow indicates the approximate optimal give up time according to the Marginal Value Theorem (on diminishing and sigmoid curves only). Proportion of prey capture rate curves observed per dive (B, left) and per bout (B, right) for each individual.



Where data for the inbound commute were not available, the maximum distance reached before the GPS failed was used as a proxy for the maximum distance from the colony ($N = 7$). Individuals travelled an average maximum distance of 77.8 ± 14.5 km in a north north-easterly direction (average bearing of 58.3 ± 0.1 degrees, Figure 5.4). There was a strong positive correlation between maximum distance from the colony and total prey consumed (Spearman Rank Correlation: $\rho = 0.86$, $P < 0.05$). In order to determine if distance between foraging patches was an important factor in predicting foraging behaviour, modelling was performed on individuals with GPS data. Results indicated that distance between foraging patches was not retained in any of the most parsimonious models ($P > 0.05$ in all cases) and was excluded from further models, thus enabling the inclusion of data from all individuals ($N = 10$).

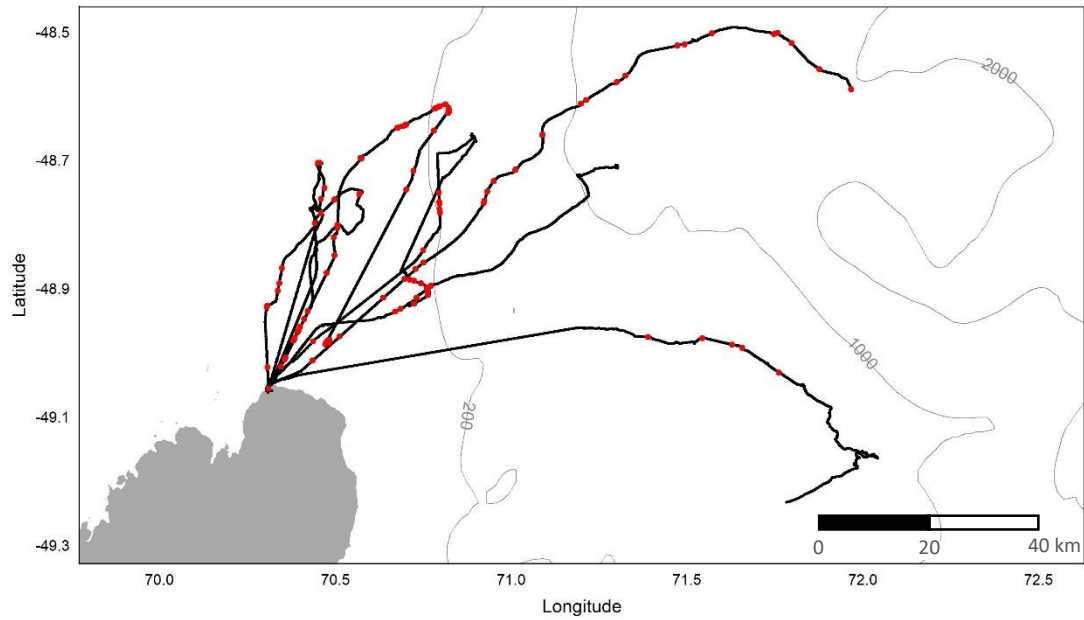
GAMMs revealed significant influence of all predictor effects on prey capture depth, rate of effort (Mean VeDBA values) and efficiency (number of prey captures divided by total VeDBA per dive; Table 5.4; SI Figure 5.1, 5.2, 5.3). Overall, individuals captured more prey per dive when hunting krill compared to when hunting for fish. Capture depth for krill was significantly deeper than for fish. In addition, prey capture depth increased significantly with higher dive-patch quality. Individuals with a higher body condition index captured prey at deeper depths, however, this should be interpreted with caution due to low sample size in the present study.

Foraging effort and efficiency varied significantly between prey types with effort being higher when capturing fish and efficiency being higher when foraging on krill



Figure 5.4: GPS tracks obtained from 7 Macaroni penguins from Kerguelen Islands.

Isobaths represent the 200, 1000 and 2000 m contours. Locations of foraging bouts are indicated by red dots along the foraging track.





(Table 5.4; SI Figure 5.2 and 5.3). Both effort and efficiency decreased significantly with increasing dive depths. However, when accounting for prey type, foraging effort remained relatively constant for krill across the depth range while effort decreased significantly with increased depth when foraging on fish. Conversely, efficiency decreased significantly with depth for individuals foraging on krill, while this trend was less apparent for individuals foraging on fish. The number of prey captures and dive-patch quality had a significant effect on foraging effort and efficiency, respectively with effort increasing in response to the number of prey caught per dive and efficiency increasing at higher patch quality.

Time of day had a significant effect on prey capture depth, effort and efficiency. For krill, the depth of capture and efficiency was greater during daylight hours, whereas this trend was less apparent for effort. In comparison, fish prey captures did not greatly vary in depth, effort or efficiency throughout daylight hours. Across prey types, trends in effort and efficiency diverged during the twilight hours when efficiency on krill captures decreased due to increasing effort, while effort on fish captures decreased and was mirrored by increased efficiency (Figure 5.5).

Bout-scale analysis

A total of 207 foraging bouts were identified throughout the foraging trips. On average, foraging bouts consisted of 28 ± 7 dives and lasted 23.4 ± 4.4 min, during which individuals captured 548 ± 116 prey items during the course of a bout. Prey captures occurring outside of identified bouts accounted for only $1.34 \pm 0.38\%$ of total prey captures. In the majority of bouts, prey capture rates were constant throughout the bout (48.3% of bouts) followed by diminishing rates of capture

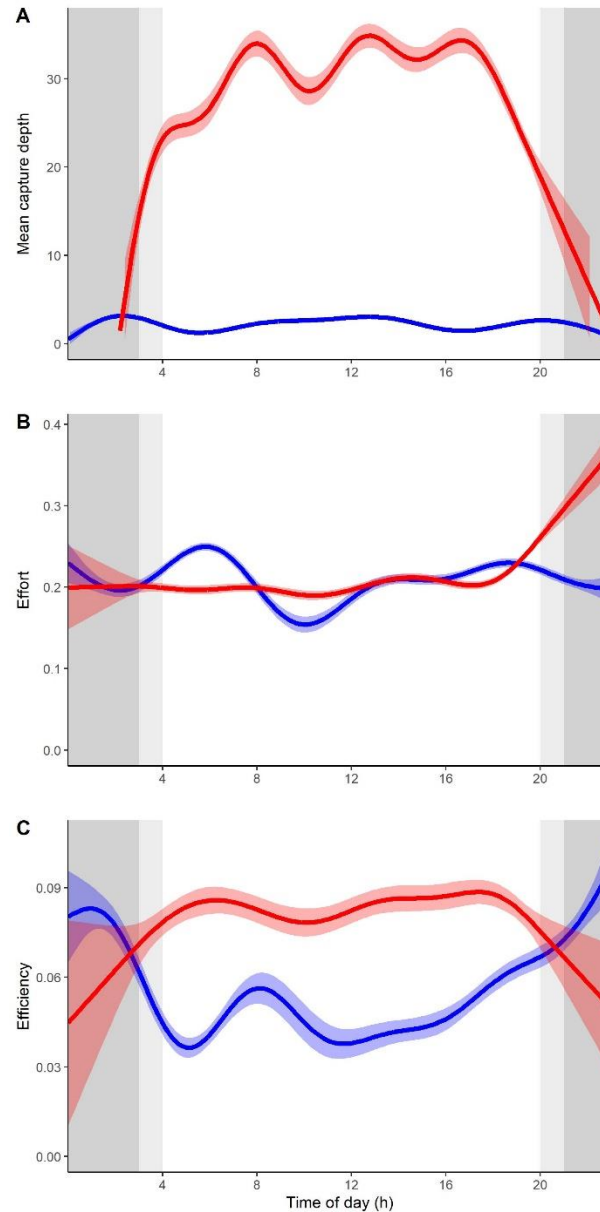


Figure 5.5: Temporal variation for foraging Macaroni penguin capture depth (A), mean VeDBA (B) and efficiency (C) predicted by generalised additive mixed models (GAMMs) calculated on an hourly basis for prey types: krill (red) and fish (blue). Blue and red shaded areas along the curves represent 95% confidence intervals while dark and light grey areas represent twilight and night periods.



Table 5.4 Model estimates for the most parsimonious models predicting capture depth, effort (mean VeDBA, g), efficiency (number of prey captured/total VeDBA) and patch residency time (total duration of foraging bout, min). Bold text indicate those parameters which were significant ($P < 0.05$) and “:” indicates an interaction between terms.

| Response variable | Parametric coefficients | | | | Approx. significance of smoothed terms | | P-value |
|-------------------|-------------------------------------|----------|--------|---------|--|-------|------------------|
| | Variables | Estimate | S.E. | T value | Edf | F | |
| Capture depth | Intercept | -72.4 | 32.1 | -2.3 | | | <0.001 |
| | Prey type(krill) | 17.2 | 0.4 | 38.6 | | | <0.001 |
| | Dive-patch quality | 0.02 | 0.001 | 18.7 | | | <0.001 |
| | Body Condition | 0.4 | 0.2 | 2.4 | | | <0.05 |
| | Hour(fish) | - | - | - | 5.9 | 5.4 | <0.001 |
| | Hour(krill) | - | - | - | 8.7 | 184.4 | <0.001 |
| Effort | Intercept | -0.2 | 0.006 | 33.6 | | | <0.01 |
| | Prey type(krill) | -0.04 | 0.004 | -9.1 | | | <0.001 |
| | Prey captures | 0.001 | 0.0001 | 19.7 | | | <0.001 |
| | Maximum dive depth | -0.004 | 0.0003 | -11.8 | | | <0.001 |
| | Prey type(krill):Maximum Dive depth | 0.004 | 0.0001 | 11.1 | | | <0.001 |
| | Hour(fish) | - | - | - | 8.6 | 23.0 | <0.001 |
| | Hour(krill) | - | - | - | 6.6 | 24.1 | <0.001 |
| Efficiency | Intercept | 0.06 | 0.004 | 14.9 | | | <0.001 |
| | Prey type (krill) | -0.03 | 0.002 | -11.2 | | | <0.001 |
| | Dive-patch quality | 0.002 | 0.0001 | 39.5 | | | <0.001 |
| | Maximum dive depth | -0.003 | 0.0002 | -18.5 | | | <0.001 |
| | Prey type(krill):Maximum Dive depth | 0.003 | 0.0002 | 16.0 | | | <0.001 |
| | Hour(fish) | - | - | - | 8.5 | 68.1 | <0.001 |
| | Hour(krill) | - | - | - | 2.3 | 5.3 | <0.01 |
| Patch residency | Intercept | -6.6 | 3.7 | -1.8 | | | 0.1 |



| | | | | | |
|------|--------------------------------------|------|------|------|------------------|
| time | | | | | |
| | Bout-patch quality | 2.1 | 0.2 | 11.1 | <0.001 |
| | Prey type (krill) | 13.2 | 6.8 | 1.9 | <0.05 |
| | Inter-bout time | 0.3 | 0.03 | 8.8 | <0.001 |
| | Bout-patch quality:Prey type (krill) | 3.6 | 0.8 | 4.2 | <0.001 |



(31.6% of bouts), and increasing rates of capture (7.9 % of bouts). A further 12.3% of bouts showed no clear relationship (Figure 5.3). The GPS data revealed the time between bouts was not always spent commuting to a new patch, with individuals resting on the surface and then foraging again close to the previous patch. To investigate this further, the 207 foraging bouts were further grouped into foraging zones where multiple foraging bouts occurred within consecutive radii of 1 km ($N = 84$). Within these zones, individuals completed an average of 2.5 foraging bouts and travelled on average 423.5 ± 33.9 m during 33 ± 8.2 minutes at the surface between consecutive foraging bouts. All other bouts were punctuated with commuting periods of 70.7 ± 8.3 min during which individuals travelled on average 3.8 ± 0.6 km (Figure 5.4).

The model that best explained PRT included prey type, patch quality, inter-bout time, and an interaction between prey type and patch quality as explanatory variables (Table 5.4; SI Figure 5.4). Overall, individuals spent more time at prey patches of higher quality and when feeding on krill than when individuals were feeding on fish. Mean dive depth did not have a significant effect on patch residency time and was not retained in the final model. There was a strong positive relationship between inter-bout and foraging bout duration indicating that individuals spent more time in a foraging bout when the travel time between the current and the previous patch was longer (Figure 5.6).

Discussion

Macaroni penguins are the most abundant penguin species and are the leading consumer of marine resources among seabirds (de L. Brooke 2004). Therefore, fine-

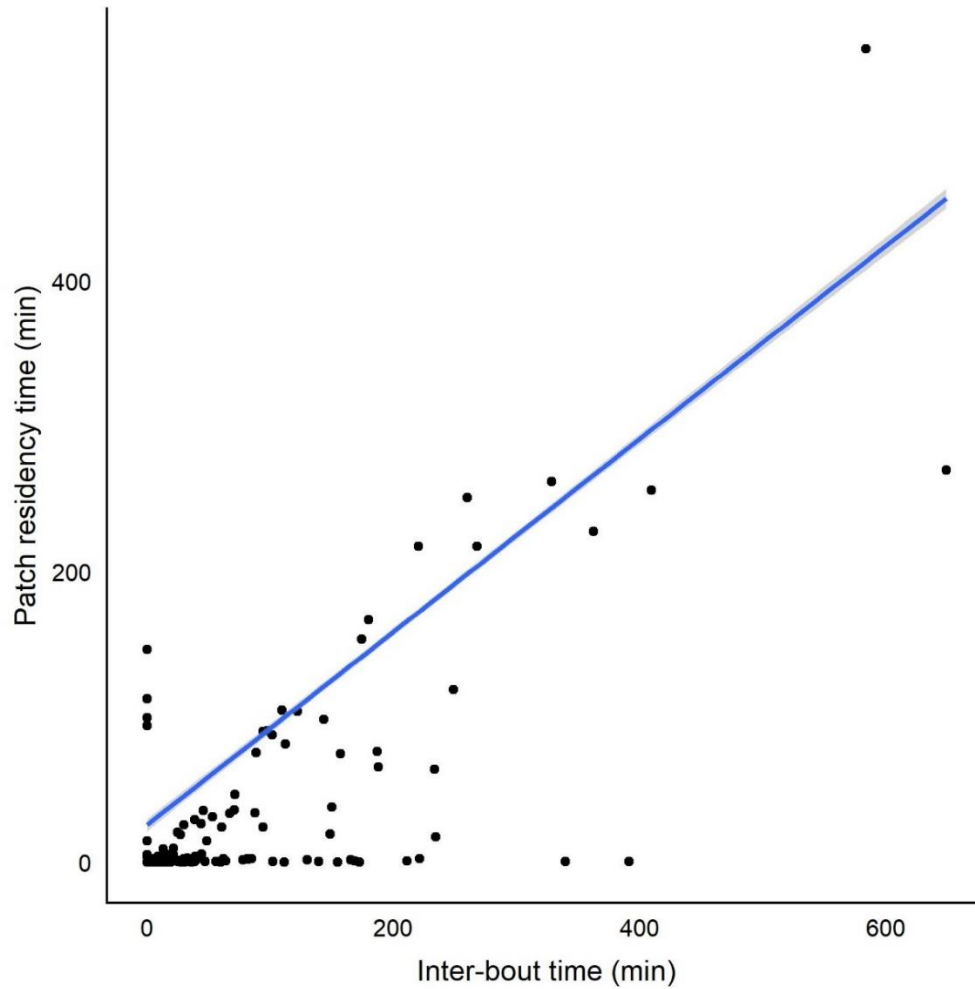


Figure 5.6: Observed values with predicted trend of Patch residency time (total time spent in a foraging bout) against inter-bout time (total time between two consecutive foraging bouts). Grey shaded area around the predicted trend line representing the 95% confidence interval.



scale information on their foraging behaviour is essential to gaining a better understanding of their role in regulating prey availability in the proximity of their breeding colonies (Guinet et al. 1996). The combination of accelerometer, depth recorder, GPS and animal-borne video cameras used in the present study revealed prey-specific foraging strategies, indicating that this species may be a solitary forager and that it adapts its behaviour to exploit various prey types. Temporal differences in diving behaviour, effort and prey captures were evident, suggesting that Macaroni penguins make foraging trip decisions according to their proximate environment in order to maximise intake and efficiency. For the majority of dives, individuals consumed prey past the optimal point of each dive while on a bout-scale, penguins ceased foraging before the optimal give up time. However, inter-bout interval and patch quality was found to influence patch residency time suggesting that, on a bout-scale, the foraging behaviour of Macaroni penguins met the assumptions of the MVT (Charnov 1976). This study highlights the importance of investigating foraging decisions over multiple spatial and temporal scales and in relation to prey type and availability.

Quantifying fine-scale foraging behaviour

For marine predators, dive metrics have been used to infer foraging activity and prey type (Elliott et al. 2008) while GPS and satellite tracking data have been used to identify key oceanographic features which may be important foraging areas (Fauchald 2009; Hindell et al. 2020; Humphries 2015). More recently, the combination of depth recorders and accelerometers have indicated that the dives with increased bottom durations may not always indicate foraging success (Viviant et al.



2010). Recent technological advancements in the miniaturisation of data loggers has enabled the use of animal-borne video cameras to provide greater insight into the foraging behaviour of penguins (Handley et al. 2018; McInnes et al. 2017a; Sutton et al. 2015; Sutton et al. 2017; Takahashi et al. 2008; Takahashi et al. 2004b; Thiebot et al. 2017; Watanabe & Takahashi 2013) and other seabirds (Sakamoto et al. 2009c; Tremblay et al. 2014; Watanuki et al. 2007; Yoda et al. 2011). In conjunction with GPS, accelerometers and depth recorders, animal-borne video cameras in the present study have provided new information about the environment animals experience and how they might adjust their foraging patterns in response to environmental variation.

Macaroni penguins occupy a wide geographic range and inter-colony differences in foraging behaviour have been well documented. For example, during breeding, individuals at Bird Island, South Georgia forage exclusively over the continental shelf in the pelagic zone, exploiting depth ranges of up to 30 meters (Barlow & Croxall 2002; Green et al. 2005; Trathan et al. 2006). In contrast, some individuals from Heard Island undertake short foraging trips, venturing only 5 km from the colony, and conduct benthic diving in the shallow waters surrounding the island (Deagle et al. 2008). In the present study, the average foraging range was significantly broader with most individuals foraging range extending to *ca* 77 km from the colony. In addition, some individuals travelled further, and in a north-easterly direction, past the 200 m isobath, possibly to forage in waters in closer proximity to the highly productive subantarctic front (Bon et al. 2015).

Macaroni penguins forage predominantly on krill (*Euphausiid* spp.), with myctophid fish and amphipods comprising a smaller proportion of their diet (Deagle



et al. 2008; Deagle et al. 2007). In the current study, individuals consumed 2 main prey types and displayed prey-specific foraging strategies. On dives when krill was consumed, individuals travelled down through the water column to the prey layer (approximately 30 m) and captured multiple prey items before ascending to the surface. In contrast, dives where only fish were consumed were significantly shallower and individuals travelled horizontally through the water column searching for prey.

Although it was not possible to identify the fish species consumed on shallow dives, being a small soft-bodied fish, it is likely that they were partially or completely digested before individuals returned to the colony (Jackson & Ryan 1986; Votier et al. 2003). Consequently, these prey items are likely to have not been detected in previous diet analyses. Sato et al. (2004) showed that during the upper periods of ascent phase of dives, individuals stopped beating their flippers and passively floated up to the surface. Results of the present study revealed that individuals were opportunistically consuming fish during this period and were observed angling their bodies in the path of fish with minimal flipper beats. Furthermore, individuals only made a capture attempt if their ascent pathway coincided with prey items, thereby obtaining prey items with little effort involved. Studies often use dive thresholds to remove shallow dives or exclude ascent/descent periods which are assumed to be largely absent of prey (Deagle et al. 2008; Duhamel et al. 2000; Falk et al. 2000; Green et al. 2005; Green et al. 1998; Tremblay et al. 2003). The present study indicates that this is not appropriate for Macaroni penguins as the majority of fish captures in this study occurred on the ascent phase or during shallow dives within the



first few metres of the water column. As such, future studies should consider modifying dive thresholds and take into account that prey captures may occur throughout the entire water column.

Mean and total VeDBA have been found to be positively correlate with the rate and total amount of energy expended in a number of free-ranging species (Gleiss et al. 2011; Laich et al. 2011; Qasem et al. 2012). In the present study, they were used to assess effort and efficiency during the foraging periods of individuals. Individuals used more effort in capturing fish than krill. This may be because fish were consumed close to the surface and, as solitary prey items, more effort is needed to capture the individual prey. These results suggest that individuals do discriminate between prey types and adjust their foraging effort according to the potential returns. This could also indicate that fish may have higher energetic content than krill. However, there is limited information available with regard to energy values or mass estimates for the prey species identified in this study (Schaafsma et al. 2018).

Krill vertically migrate up through the water column in response to low light conditions (Hamame & Antezana 2010). Therefore, it might be expected that individuals feeding on these prey should show increased foraging effort and efficiency as prey are more easily accessible. However, with most penguin species being visual predators (Cannell & Cullen 1998; Poupart et al. 2019), Macaroni penguin diving behaviour and efficiency was markedly reduced in response to low light levels. In the present study, temporal variation in dive frequency and depth was apparent, with individuals diving deepest in the middle of the day. Diving depth was shallower towards the end of the day and dive frequency increased before individuals



rested on the surface overnight. While prey captures of krill did occur during twilight periods, individuals were less efficient. The increase in foraging effort towards the end of the daylight period and during twilight may reflect individuals making a final attempt at consuming prey, before resting on the surface overnight.

Several penguin species have been shown to forage in groups, which is thought to assist with concentrating schooling prey, decreasing search effort or reducing the risk of predation (McInnes et al. 2017a; Sutton et al. 2017; Takahashi et al. 2004a; Takahashi et al. 2008; Takahashi et al. 2004c; Tremblay & Cherel 1999; Wilson et al. 1986). Therefore, it might be expected that Macaroni penguins also forage in groups. However, in the present study conspecifics were observed during foraging activity on only 4 occasions (< 0.1% of dives observed in video data). While the foraging range of Macaroni penguins during the breeding season was estimated to be 150km by Guinet et al. (1996), GPS tracking indicated individuals foraged within a bearing range of 65-356 degrees from the colony and travelled a mean distance of 50.4 km. This corresponds to an approximate foraging area of 2,190 km². Based on a breeding population at the Cape Cotter colony of 75,000 pairs and accounting for individuals at the nest, the number of Macaroni penguins in the area equates to approximately 17 individuals·km⁻². Consequently, it was surprising that even random encounters were not more prevalent in the video data. A potential reason for the lack of foraging associations could be the sheer size of the krill swarms. Alternatively, in comparison to fast-moving schooling prey such as pelagic fish, subantarctic krill are slower and exist in already dense aggregations (Hewitt & Lipsky 2009), which may negate the need for conspecifics to assist in concentrating prey to facilitate capture.



Dive-level prey capture dynamics

While animal-borne video cameras can provide a greater insight into the behaviour of penguins in the presence of prey and other species at sea, limitations on battery life and memory capacity of such devices are still prevalent. Furthermore, ability to detect prey captures are reduced on deeper dives due to poor visibility. Therefore, camera and accelerometer data were utilised in order to develop a machine learning algorithm in order to identify prey captures across the entire at-sea period. Prey capture identification models have been developed for Adélie penguins, *Pygoscelis adeliae* (Watanabe & Takahashi 2013) and little penguins, *Eudyptula minor* (Carroll et al. 2014), with comparable model accuracy. However, the current study's slightly lower accuracy rates could be attributed to the rapid prey capture rate of subantarctic krill in comparison to larger prey items. Similar to Watanabe & Takahashi (2013), it was possible in the current study to separate capture events into 2 prey types based on their occurrence at depth in the water column which was validated using observations from the camera data.

In the present study, the majority of individual prey capture response curves indicated the rate of captures decreased as the dive progressed and that individuals continued foraging beyond the optimal point of the dive. However, the diminishing curve observed over the dive-scale is more likely a reflection of within-patch prey density variation and opportunistic prey captures under physiological constraints. For example, a Macaroni penguin may dive down to a patch and begin to consume prey at the patch edge where density would be lower. They then travel through the patch, consuming prey where density is presumed to be the highest, and continue to capture



prey to the edge of the patch where prey is supposedly less dense and during the ascent phase. Oxygen reserves limit the amount of time individuals can remain at depth, therefore, once out of the prey patch, opportunistic captures of small fish during ascent is beneficial to the individual. Therefore, this behaviour resulted in a disproportionately large number of diminishing prey capture rate curves.

Patch exploitation and residency time

The MVT suggests that, in a resource-rich environment, the value of leaving a depleting patch in search of new patches is higher than staying (Charnov 1976). Hence, when animals cease foraging in a bout, it is generally assumed that they leave the area to search for a new foraging patch or due to physiological constraints. However, in the present study, GPS data revealed that in 59% of foraging bouts individuals rested on the surface after a foraging bout and then completed consecutive foraging bouts within 1 km, potentially utilising the same prey patch. Alternative hypotheses for diving animals giving up foraging and returning to the surface has been related to individuals drawing near or exceeding their Aerobic Dive Limit (ADL), where they require longer periods on the surface to clear the build-up of lactic acid (Ponganis & Kooyman 2000; Schreer et al. 2001). While previous studies have suggested Macaroni penguins may conduct dives exceeding their ADL (Mori & Boyd 2004b), visual inspection of the relationship between post dive duration and dive durations (Ponganis et al. 1993) in the present study revealed no exponential increase in post dive durations. This suggests that individuals in the current study did not exceed their ADL.



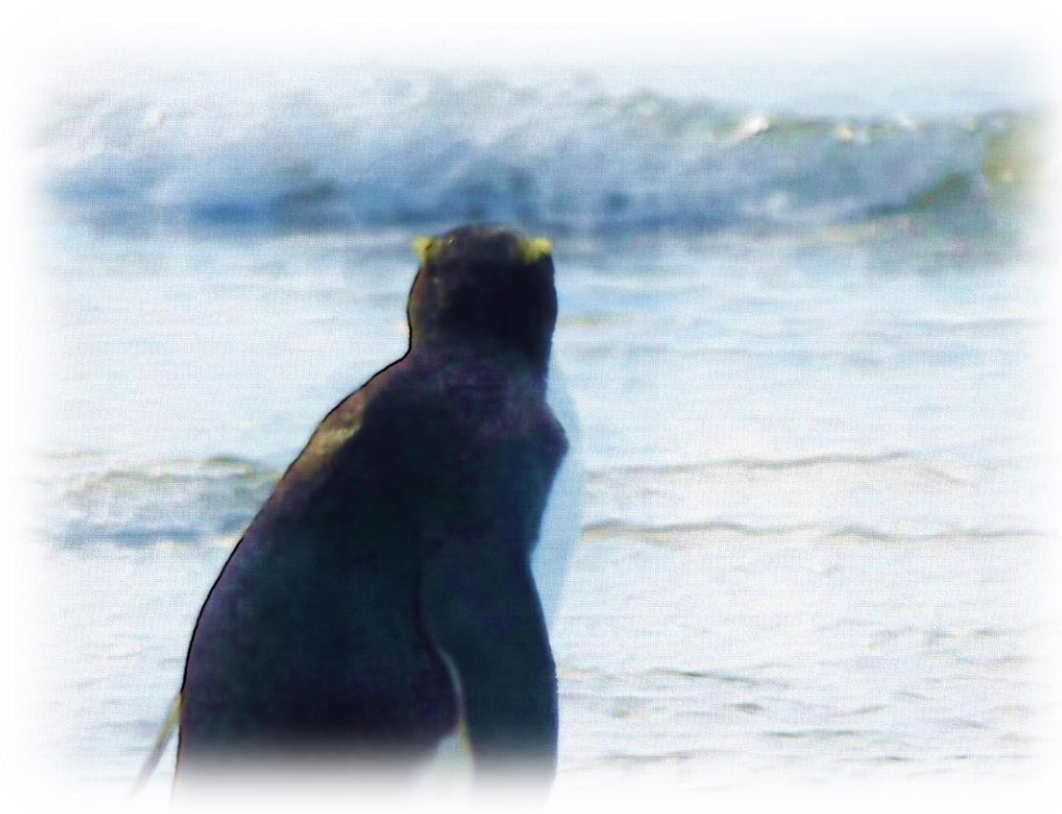
The large proportion of linear response curves observed in bout-scale analysis, indicated that penguins ceased a foraging bout before the theorised optimal give up time. As individuals rested on the surface after a foraging bout and did not exceed their ADL, it is possible that individuals were satiated, requiring time to digest prey before the prey patch was depleted or scattered in response to predator activity. In the present study, no increase in patch quality with distance from the colony could be detected, suggesting that food appeared to be locally abundant. A possible explanation for individuals foraging further afield may be that from past experience, prey is more predictably available or that larger or superior nutritional content prey items can be found further away (Soanes et al. 2014). Indeed, Macaroni penguins have been found to preferentially select larger krill from a prey swarm possibly in an attempt to reduce foraging effort (Hill et al. 1996). However, due to the short sampling period of the camera footage, it was not possible to assess the size of prey items or whether this varied between patches.

In summary, Macaroni penguins breeding at Cape Cotter were observed to adjust their foraging behaviour in response to prey type, prey patch quality and the time between foraging bouts. Patch residency time was influenced by prey type and inter-bout interval, and negatively influenced by patch quality, conforming to the predictions of the MVT. While diminishing prey capture rates were most common for dive-scale analysis, linear returns were the predominant response shape over a foraging bout. This may indicate that penguins leave patches for reasons other than patch depletion such as satiation and the need to return to the colony. This study has provided new insights into the foraging behaviour of Macaroni penguins revealing



low levels of at-sea associations, despite the presence of large numbers of conspecifics at the colony. While it is possible that the frequency group foraging may change in relation to breeding stage and seasonal prey abundance, prey was already found in large concentrated aggregations negating the need for coordinated group behaviour at a prey patch. These findings suggest that individuals make complex foraging decisions in relation to their proximate environment and highlight the need for investigating behaviour in relation to prey field over multiple spatio-temporal scales.

Chapter 6: General Discussion.



Seabirds are currently the world's most threatened avifauna owing to the numerous anthropogenic induced changes in the environment (Sydeman et al. 2012). While many aspects of their biology have been investigated, data gaps still exist for many species. One of the major pre-requisites for understanding the threats to seabirds has been identified as, “*research(ing) the impacts of ecosystem-level changes that alter predator-prey and competitive interactions between species*” (Croxall et al. 2012). Previous studies have attempted to understand this purely in terms of consumptive exchanges (Schmitz 2017), but these interactions are undoubtedly more nuanced. Due to the difficulties in observing predator-prey associations directly, advancements in technology have provided information on animal behaviour with respect to environmental variables as indices of prey availability (Hunt Jr 1990; Pinaud & Weimerskirch 2005; Scheffer et al. 2016). However, characterising the true prey field experienced by a predator is necessary to provide context for understanding animal decisions (Moll et al. 2007). Indeed, in the current “*golden age of bio-logging*” (Wilmers et al. 2015), this information is considered to be the “holy grail” in understanding the multi-faceted workings of a predators foraging ecology.

The overall objective of the present study was to understand the fine-scale factors influencing the foraging behaviour and energetics of penguins. The results have demonstrated that penguin behaviour is largely dependent on, not only the presence of prey, but the type, amount and calorific value of the prey field. As energy consumption is a major aspect in determining behaviour (Shaffer 2011), this finding was unsurprising. Nevertheless, it is rarely quantified due to limitations in directly

observing predator-prey interactions in the marine environment. Variability in prey type and abundance prompted individuals in the present study to deviate from optimal foraging assumptions (Chapter 2 and 5), use contrasting habitats (i.e. benthic vs pelagic; Chapter 4) and make foraging decisions at various temporal scales to increase foraging success and efficiency (Chapter 4 and 5). Accelerometers were found to be a reliable estimate of foraging effort (Chapter 3) and the validation of this technique supported the use of accelerometers in Chapters 4 and 5 to develop prey capture models and estimates of foraging effort and efficiency. This body of work provides some of the first evidence of the functional links in seabirds and the immediate prey field. Accounting for the factors associated with prey field revealed how fine-scale foraging decisions are made over various spatio-temporal scales to maximise foraging success, effort and efficiency (Figure 6.1).

The following chapter expands on the major findings of these combined studies. The application of techniques used in the preceding chapters are discussed with reference to the broader context of seabird ecology and the impacts of climate change. Finally, this chapter provides suggestions for future research to advance our understanding of marine predator ecology.

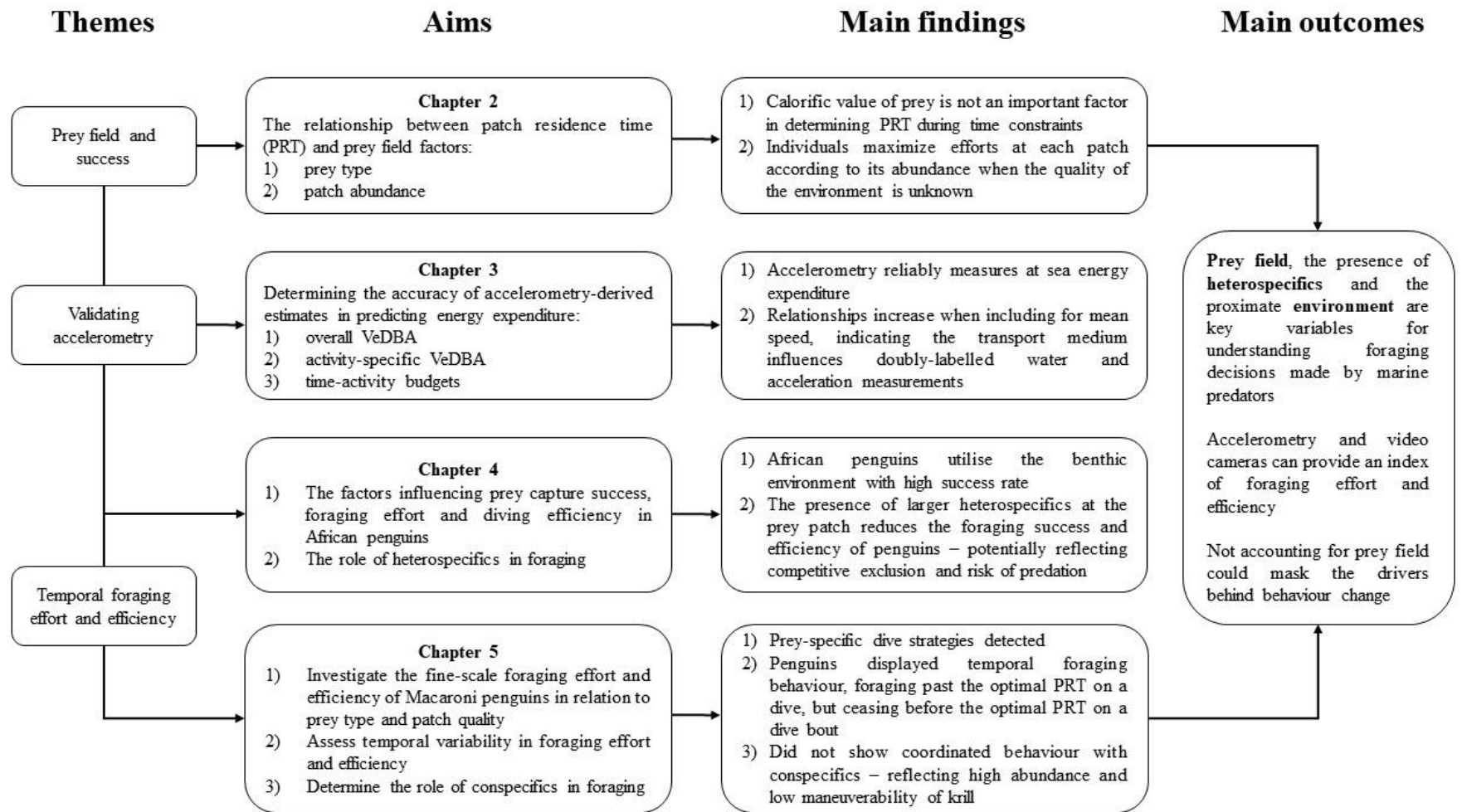


Figure 6. 1: Thesis structure, specific central chapter aims and main findings.

Accelerometry and prey detection

In combination with other data loggers, animal-borne accelerometers are widely used to investigate several aspects of an animal's life. Over the two decades since their first application to remotely monitor behaviour, they have been employed to gain insights into the daily patterns of a wide range of species (Chakravarty et al. 2019; McClune et al. 2014; Wang et al. 2015; Wilson et al. 2008). Dynamic body acceleration (VeDBA or ODBA) is most the widely used proxy for energy expenditure (Halsey et al. 2011b). However, how energy is expended relates to both animal movement and physiological processes (Champagne et al. 2012). Therefore, accelerometers must be calibrated against a genuine measure of energy expenditure to determine their predictive capability. Several studies have attempted to correlate doubly-labelled water estimates of energy expenditure with accelerometry derived estimates using animals in captivity (Bidder et al. 2017; Payne et al. 2011; Wright et al. 2014) but with more difficulty in free-ranging populations (Elliott et al. 2013; Hicks et al. 2020; Jeanniard-du-Dot et al. 2017; Pagano & Williams 2019).

The correlation between energy expenditure and DLW in the present study ($r^2 = 0.83$) was higher than those reported for other vertebrates measured in captivity (between 0.47-0.60) (Fahlman et al. 2008; Gleiss et al. 2010; Halsey et al. 2011a). The proportion of variation in energy expenditure explained by VeDBA was also slightly higher than some other avian diving species (Elliott et al. 2013; Stothart et al. 2016). This is likely due to the ability to account for on land periods in the present study's estimations of total daily energy expenditure at-sea. Including mean travel speed in models strengthened the relationship ($r^2 = 0.87$), revealing that individual's

energy expenditure is influenced by behaviour, but also the medium in which the travels.

The positive relationship between energy expenditure estimated by DLW and VeDBA validated the use of accelerometers for measuring foraging effort and efficiency in Chapters 4 and 5. In these chapters, accelerometers were used to develop machine learning algorithms (SVMs). These were based on a kernel separator which divided data into prey capture and swimming behaviour. Cameras were necessary in the development of these models as true prey capture signals acted as the classifier barrier to validate capture signals (Carroll et al. 2014), which has limited the applicability of this method in penguins until recently. To bypass the use of cameras, previous studies have identified prey capture signals using head mounted accelerometers (Kokubun et al. 2011; Volpov et al. 2015; Watanabe & Takahashi 2013). The use of cameras in this study (Chapters 4 and 5) has shown the high positive rate of back mounted accelerometers in detecting prey encounters, thus reducing the need for more invasive methods of device attachment (i.e. head attachment) which can increase hydrodynamic drag and impact an animal's behaviour (Bannasch et al. 1994).

Habitat and foraging success

Habitat is an important factor in determining the foraging success of all animals. Specifically, a habitat's profitability (Werner & Mittelbach 1981), distance from breeding grounds (Wakefield et al. 2009) and the number of other occupying predators may influence the foraging success of an individual (Brown 1988; Nash et al. 2012). In marine environments, the pelagic habitat is often associated with high

levels of spatio-temporal variability and is largely influenced by meso-scale chemical and physical anomalies such as fronts and eddies (Wakefield et al. 2009). These features typically generate regions of increased productivity where prey, and, consequently, predators, are found in high concentrations.

Comparatively less is known about the benthic habitats than what is known about pelagic ones. In general, prey inhabiting benthic habitats are lower in abundance and overall more predictable than pelagic habitats (Fariña et al. 2003). For some marine predators, the benthic environment may be the main hunting habitat (Arnould & Costa 2006; Costa & Gales 2003) or provide an additional food resource in years of poor pelagic prey abundance (Croxall et al. 1991). Benthic diving has been suggested to be more energetically costly than pelagic foraging (Costa et al. 2004; Kirkman et al. 2019). However, in species that display a degree of both benthic and pelagic diving behaviour, little is known of the quantitative importance of benthic dives or how they compare in success and efficiency to pelagic dives (Chimienti et al. 2017).

Penguins occupy a wide geographical range with inter-species differences in diving behaviour well documented. Together with diet analyses, time-depth profiles obtained from dive recorders have indicated that the majority of penguin species are primarily pelagic feeders, preying upon swarming crustaceans and shoaling fish (Takahashi et al. 2004a). Benthic dives have been observed in some species, including the emperor penguin (Rodary et al. 2000), yellow eyed penguin (Mattern et al. 2007), Gentoo penguin (Kokubun et al. 2010), rockhopper penguin (Tremblay & Cherel 2000) and the little penguin (Hoskins et al. 2008). However, these studies do

not address the differences in foraging success and efficiency between pelagic and benthic strategies.

In the present study, African penguins exhibited different foraging modes, and, correspondingly, varying levels of success when hunting benthically versus pelagically (Chapter 4). Although benthic foraging could simply be a previously undescribed feature of African penguin foraging behaviour, the greater success from benthic dives than pelagic dives indicate the population was experiencing poor conditions. A primarily pelagic forager, the Cape fur seal (*Arctocephalus pusillus pusillus*) also showed evidence for benthic foraging in this region (Botha et al. 2020). Indeed, with the collapses of fish stocks (Crawford et al. 2011), oil spills and heat waves affecting the breeding success of marine predators breeding at colonies in Algoa Bay (Klusener et al. 2018; Sherley et al. 2020), the benthic foraging observed in marine predators in this region may be indicative of a degrading habitat.

The African penguin colonies in Algoa Bay represent the last stronghold for the endangered African penguin, with more than 50% of its population located in these sites (Crawford et al. 2011). As with other species, behavioural flexibility may act as a buffer against changes to pelagic prey availability (Grémillet & Boulinier 2009; Jakubas et al. 2020; Phillips et al. 2017). In common guillemots (*Uria aalge*), for example, switching between pelagic and benthic foraging allowed individuals to target different prey aggregations in order to take advantage of the opportunities presented (Chimienti et al. 2017). Individuals that demonstrate flexibility will generally be able to better handle environmental variation and extremes (Chiaradia & Nisbet 2006; Handley et al. 2017; Moe et al. 2004; Padilla & Savedo 2013).

However, it remains to be seen if the degree of behavioural flexibility in foraging strategies and availability of alternative prey is enough to provide a safeguard for the African penguin.

Spatio-temporal decisions and foraging effort

Any time an animal chooses one particular behaviour from a set of alternatives, it can be said to have made a “decision”. Animals make ecologically important decisions across multiple spatio-temporal scales (Embling et al. 2012; Harel et al. 2016). For example, when hunting small mobile prey, predators decide where to hunt, what prey types to consume and for how long. These decisions are trade-offs between the time and energy apportioned to the pursuit, capture and handling of their prey (Charnov 1976). Measuring a predator’s effort in relation to the potential rewards (i.e. calorie consumption), over multiple spatio-temporal scales may shed light on decision making processes.

In the present study, temporal dynamics of foraging decisions were investigated in respect to optimal foraging theory. Specifically, temporal dynamics were investigated within the framework of the marginal value theorem (MVT). Briefly, the MVT is used to understand how a forager apportion its time within a hierarchical patch environment (McNair 1982). The MVT states that individuals should move from one patch to another when the capture rate drops to the average prey capture rate across the environment. Therefore, short-term patch quality positively affects patch residence time, whereas long-term patch quality negatively affects patch residence time.

Using the temporal units defined by penguins themselves (i.e. dives, dive bouts and trips), individuals in the present study were shown to respond to the MVT assumption in different ways. However, in all cases, there were exceptions to the rules. For example, the MVT indicates that animals should alter their patch residency time (PRT) in response to changes in quality (i.e. calorific gain) of the prey field. However, in chapter 2, little penguins did not adhere to this assumption as they foraged according to patch abundance, irrespective of its quality. In chapter 4, factors other than prey field influenced the prey capture success of African penguins. While Macaroni penguins (Chapter 5) responded to the MVT theory on a dive scale, they ceased foraging at prey patches earlier than deemed optimal at a prey patch scale.

Although the present study indicates that penguins do conform the MVT in some ways, the theoretical assumptions of the MVT may not apply to such a highly spatio-temporally variable environment. Indeed, the majority of MVT studies have focussed on terrestrial environments where prey field is immobile or more easily predictable (Krebs et al. 1974; MacArthur & Pianka 1966; McNickle & Cahill 2009; Nonacs 2001). Previous studies in marine environments have focussed on the benthic environment or on a krill feeding species, where prey is more uniformly distributed (Foo et al. 2016; Watanabe et al. 2014) but still differ somewhat from the expected assumptions. The deviations observed in these marine MVT studies, and the present study, likely reflect the unpredictability of the marine environment and the limitations of the theory itself to incorporate the complexity of predator-prey interactions. This highlights the importance quantifying the factors associated with

prey field as these are crucial when assessing the temporal foraging decisions of predators.

Prey field, foraging success and efficiency

Marine predators operate in a heterogeneous seascape and must respond to environmental cues at multiple scales in order to forage efficiently. During the breeding season, the availability of prey and how close it is to the breeding colony are important factors in determining the reproductive success and, therefore, the fitness of breeding individuals (Birt et al. 1987; Fauchald 2009). In the present study, prey characteristics were found to be the most significant drivers in the determining an animal's foraging decisions.

Trip parameters obtained from tracking data on the penguins in the present studies demonstrated how prey field can influence the foraging range of penguins. For the piscivorous species (i.e. little and African penguins) individuals rarely foraged further than 40km from the colony. Maximum foraging distances were similar between little and African penguins and did not dramatically increase due to the larger body size. However, African penguins left at night to make use of hours of low light levels to travel to foraging locations.

Macaroni penguins foraged at maximum distances of around 70 km from the breeding colony. While previous studies have found Macaroni penguins travel longer distances (Bon et al. 2015; Horswill et al. 2017), the present study was conducted in the early chick-rearing phase where females typically make shorter trips (Barlow & Croxall 2002). The greater maximum distances displayed by Macaroni penguins in comparison to African penguins (which are of similar body size) may have to do with

greater competition at Macaroni penguin colonies. These penguins breed in large, densely populated colonies, so competition in foraging grounds in closer proximity to the colony might be higher (Ainley et al. 2004; Corman et al. 2016). Indeed, previous studies suggests a relationship between seabird colony size and foraging effort due to competition (Ballance et al. 2009; Masello et al. 2010; Wakefield et al. 2013).

While a seabirds foraging trip duration may be influenced by factors such as competition and chick age (Botha & Pistorius 2018), it may also be related to prey field. For example, krill eating penguins must consume large quantities of prey items in order to obtain a substantial meal. In comparison, a piscivorous species is expected to require considerably fewer prey items in order to meet energetic demands. For land breeding marine predators, departing and returning to the colony can be costly, with penguins being vulnerable to predation (Klimley et al. 2001) and the energetic expenditure associated with locomotion on land (Pinshow et al. 1977). Therefore, individuals should not return until obtaining a substantial meal to provide their chicks. This is potentially a more onerous process for krill eating predators, which may explain why they have longer foraging trips.

The evolutionary arms race between predators and their prey has resulted in both counterparts developing adaptations to capture and avoid being captured, respectively (Abrams 1986; Wilson et al. 2018). Prey choice is an important factor in determining the fitness of individuals with marine mammal and seabird population declines hypothesised to be linked to nutritional deficiencies and reduced availability of certain food resources (Dann et al. 2000; Vollenweider et al. 2011). Therefore, it can be postulated that novel prey items may increase predator's foraging effort. Indeed,

this was observed in the present studies with Macaroni penguins consuming larval fish at a high rate of effort and African penguins requiring increased time to handle and consume pipefish. It is, however, uncertain whether penguins were supplementing their diet with these prey to access certain nutritional benefits, or if it was because of a greater underlying process influencing the availability of higher quality prey. As penguins are limited in their foraging range during the breeding season (Croxall & Davis 1999), novel prey items may be important during these periods of temporal constraint.

The collection of work presented in this thesis demonstrates the paramount importance of quantifying an animal's prey field. Prey is an important predictor of foraging activity and has the capacity to influence the structure dynamics of predator populations, in both marine (Green et al. 2020; Wilson et al. 2005) and terrestrial environments (Butler & Gillings 2004; Hopcraft et al. 2005; Sih et al. 1985). Determining prey field characteristics is necessary to understand the trade-offs between energy gained and the costs associated with accessing certain prey types. In addition, quantifying prey field can reveal which factors drive prey selection and the development of energy maximising strategies (Hazen et al. 2015). These are important for understanding the underlying factors regulating foraging behaviour, success and, therefore, fitness of organisms in a changing environment.

Future directions

Throughout their range, penguins face numerous threats to their survival (Ropert-Coudert et al. 2019). Perhaps most pressing, several colonies have been subjected to changes in the availability in prey as a result of habitat degradation, environmental

variability and the effects of over fishing (Crawford 1998; Crawford et al. 2017; Trathan et al. 2015). These threats have resulted in negative population trajectories observed over the last 60 years for multiple penguin species (Boersma 2008; Crawford et al. 2009). To fully understand a marine species, it is essential to observe it through all aspects of its life cycle. It is quite obvious that the work of the present study would not have been possible without the numerous technological advancements in the field of bio-logging. The unprecedented detail we can now obtain about the camera wearer, has enabled the answering of complex questions with regard to fine-scale foraging and energetics. However, there are still many information gaps that need to be addressed.

Quantifying prey field has been shown to be highly important in determining the behaviour of penguins in the present study. So too is it important for both marine and terrestrial alike. As the miniaturisation of high resolution devices continue to develop, the use of such devices will continue to increase. A challenge of this will be to develop the techniques to analyse big data sets in an economical manner. For example, the time consuming process of manually analysing bulk volumes of video could be completed using deep learning algorithms (Koozadi & Charkari 2017; Zhu et al. 2005). However, developing these are difficult without a strong foundation in mathematics, statistics and coding (Barraquand et al. 2014). Therefore, academics should consider a greater investment into learning these concepts and forming multi-disciplinary collaborations.

Innovative ways to increase the battery life of devices should also be a consideration for the future. A recent study used machine learning algorithms inbuilt

into accelerometers (low battery consumption devices) to control the recording periods of animal-borne video data loggers (high battery consumption devices) (Korpela et al. 2020). In this way, data collection was concentrated on infrequent target behaviours identified in accelerometry. This approach could reduce the number of bio-loggers required to collect the same amount of data and reduce the time consuming task of processing gigabytes of video data to obtain a few important events. In addition, it should allow for further reductions in battery requirements and therefore, reduce device mass which is an important aspect of experimental design (Williams et al. 2020). This would be especially important for small flying seabirds as device mass could influence flight behaviour (Geen et al. 2019).

Due to the specificity in the amplitude and duration of prey captures, it was not possible in this study to develop one prey capture detection model for all penguin subjects. Indeed, when tested on other species, the penguin-specific models identified < 1% of prey captures. However, it might still be possible to develop a “global model”. By isolating peaks corresponding to prey captures and comparing the intensity of these in relation to normal travelling signals it might be possible to find a constant relationship between species (i.e. prey captures are 4 times the amplitude of travelling measurements). This could then be turned into species specific models to determine prey captures in all penguin species instrumented with accelerometers.

Archival dive loggers have been used more widely than accelerometers with many species having multi-year information. Therefore, it might be more useful to use accelerometers to validate signatures in other recording sensors (i.e. dive data) that can reliably predict prey captures. This has previously been achieved in Australian

fur seals (*Arctocephalus pusillus doriferus*) with ascent/descent rates providing a high predictive capacity (Volpov et al. 2016). If such a relationship can be determined in penguin dive data, it would be possible to calculate prey captures in years of where accelerometers were not used. By validating what characteristics of a dive signify a prey capture, it could then be applied to multi-year data sets to determine annual patterns in prey availability and the factors that influence foraging success (Speakman et al. 2020).

While some work has begun to link prey pursuits with dive information (Green et al. 2020; Ropert-Coudert et al. 2000), these methods still leave out the link that this thesis has showed is most important: the quantifiable prey field. Therefore, possibly the most critical research question to stem from the present collection of work may be to determine a way to link verified prey field to environmental variables. Through ongoing technological advancements, prey field should be easier and more efficiently quantified. However, determining the relationship between actual prey field and certain environmental variables could advance our knowledge of foraging behaviour for species where it is not possible to quantify prey field. This is especially important as previous studies have found weak or even negative spatial associations between predators and indices used to estimate prey availability (Fauchald 2009; Logerwell et al. 1998; Russell et al. 1992). Determining which factors best explain changes in prey availability, and enhancing the resolution of such data, should allow for a greater understanding of the fine-scale spatial and temporal associations between predators and their prey (Abrahms et al. 2020). This may assist in understanding the long-term environmental variables that influence foraging effort, success and efficiency.

Final thoughts

Ultimately, this study has revealed how prey field impacts the fine-scale foraging behaviour of penguins. All investigated species responded to the prey field in various ways. With the ever-increasing advancements in bio-logging technology, the number of fine-scale seabird tracking studies are likely to continue increasing.

Correspondingly, so should studies investigating the impacts of handling and logger attachment. As researchers, we have the ethical obligation to translate the substantial financial and logistical investments associated with gathering telemetry data, and the potential disturbance of tracked species, into a knowledge base for the future. While humans grow increasingly detached from nature, charismatic animals like penguins are particularly important in reinforcing the bond between humans and their environment. This can be strengthened through novel techniques such as animal borne video cameras to observe the activities of these species and understand more about their behaviour. Such visual imagery is paramount to highlighting the impacts of climate change and increasing public engagement (Wang et al. 2018).

With the downward trajectory of many penguin populations, it is crucial to understand what factors influence foraging success and the consequences for reproductive fitness. Accurate information on where, when and how individuals forage throughout the environment can help shape global policy framework needed for establishing appropriate management of the marine environment. These are important aspects to consider when working towards achieving meaningful conservation goals for penguins and indeed, threatened species worldwide.

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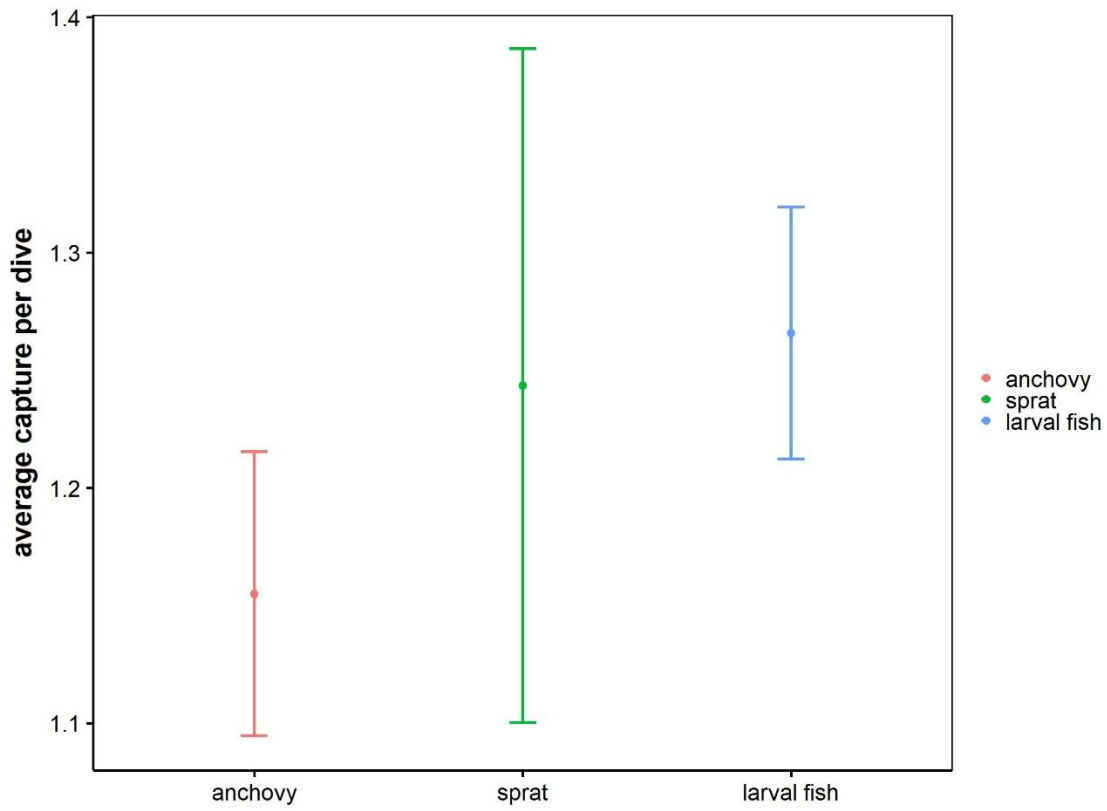
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Supplementary Information



SI Figure 2.1: Average prey capture per dive for each fish prey type consumed by little penguins.

SI Table 3.1: Model results for relationship between at-sea daily energy expenditure (DEEDLW-s $\text{kJ}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$) and mean speed ($\text{km}\cdot\text{h}^{-1}$) and mean depth (m) per foraging trip.

| Response variable | Predictor Variables | Estimate | S.E | Statistic | <i>P</i> | CI | r^2 |
|-------------------|---------------------|----------|-------|-----------|----------|--------------|-------|
| DEEDLW-s | Intercept | 177.2 | 315.4 | 0.6 | <0.5 | -397, -737.4 | 0.64 |
| | Mean speed | 543.3 | 131.3 | 3.5 | <0.01 | 282.1, 887.8 | |
| | Mean depth | 13.9 | 18.3 | 0.8 | 0.5 | -27.3, 57.1 | |

SI Table 3.2: Full model selection table for model 1a. Models averaging was performed for candidate models with a delta < 4.

| Model 1a | | | | | | | | | |
|-----------|---------------------|------------|--------------|-------------------|---|--------|--------|-------|--------|
| Intercept | Horizontal distance | Mean Speed | VeDBA-mean-s | Vertical distance | K | logLik | AICc | delta | weight |
| -877.67 | NA | NA | 10647.7 | NA | 3 | -59.66 | 129.32 | 0 | 0.6 |
| -785.23 | NA | 209.77 | 8284.09 | NA | 4 | -57.81 | 131.62 | 2.3 | 0.19 |
| -740.84 | NA | NA | 8815.05 | NA | 4 | -58.28 | 132.56 | 3.24 | 0.12 |
| -856.12 | NA | NA | 10494.34 | 0 | 4 | -59.64 | 135.28 | 5.96 | 0.03 |
| -639.29 | 5.4 | 216.95 | 6290.8 | NA | 5 | -55.42 | 135.84 | 6.52 | 0.02 |
| 63.07 | 10.18 | 409.94 | NA | NA | 4 | -60.41 | 136.81 | 7.49 | 0.01 |
| 138.56 | NA | 542.31 | NA | 0.02 | 4 | -60.94 | 137.88 | 8.56 | 0.01 |
| 263.7 | NA | 551.28 | NA | NA | 3 | -64.15 | 138.3 | 8.98 | 0.01 |
| -825.94 | 10.27 | NA | 8574.16 | -0.01 | 5 | -56.79 | 138.58 | 9.26 | 0.01 |
| -628.27 | NA | 273.64 | 6647.6 | 0.01 | 5 | -56.87 | 138.73 | 9.41 | 0.01 |
| 592.79 | 15.15 | NA | NA | NA | 3 | -65.15 | 140.29 | 10.97 | 0 |
| 1278.77 | NA | NA | NA | NA | 2 | -68.98 | 143.67 | 14.35 | 0 |
| 434.64 | 21.43 | NA | NA | -0.02 | 4 | -64.55 | 145.11 | 15.79 | 0 |
| 76.83 | 7.25 | 447.39 | NA | 0.01 | 5 | -60.25 | 145.49 | 16.17 | 0 |
| 1129.38 | NA | NA | NA | 0.02 | 3 | -67.85 | 145.71 | 16.39 | 0 |
| -682.58 | 7.02 | 183.63 | 6600.11 | 0 | 6 | -55.27 | 150.54 | 21.22 | 0 |

SI Table 3.3: Full model selection table for model 2a. Models averaging was performed for candidate models with a delta < 4.

| Model 2a | | | | | | | | | |
|-----------|---------------------|------------|-----------------------|-------------------|---|--------|--------|-------|--------|
| Intercept | Horizontal distance | Mean Speed | DEE _{PRED-s} | Vertical distance | K | logLik | AICc | delta | weight |
| 195.07 | 8.32 | NA | 0.5 | NA | 4 | -57.11 | 130.21 | 0 | 0.39 |
| 20.26 | 7.48 | 214.45 | 0.37 | NA | 5 | -52.86 | 130.72 | 0.5 | 0.3 |
| 377.12 | NA | NA | 0.63 | NA | 3 | -61.37 | 132.73 | 2.52 | 0.11 |
| 57.21 | 14.08 | NA | 0.49 | -0.02 | 5 | -54.09 | 133.18 | 2.96 | 0.09 |
| 143.4 | NA | 259.3 | 0.46 | NA | 4 | -59.09 | 134.18 | 3.96 | 0.05 |
| 63.07 | 10.18 | 409.94 | NA | NA | 4 | -60.41 | 136.81 | 6.6 | 0.01 |
| 382.32 | NA | NA | 0.59 | 0.01 | 4 | -60.9 | 137.81 | 7.59 | 0.01 |
| 138.56 | NA | 542.31 | NA | 0.02 | 4 | -60.94 | 137.88 | 7.66 | 0.01 |
| 263.7 | NA | 551.28 | NA | NA | 3 | -64.15 | 138.3 | 8.09 | 0.01 |
| 96.04 | NA | 321.77 | 0.35 | 0.01 | 5 | -56.71 | 138.43 | 8.21 | 0.01 |
| 592.79 | 15.15 | NA | NA | NA | 3 | -65.15 | 140.29 | 10.08 | 0 |
| 1278.77 | NA | NA | NA | NA | 2 | -68.98 | 143.67 | 13.45 | 0 |
| 1.4 | 10.47 | 156.29 | 0.4 | -0.01 | 6 | -52.07 | 144.13 | 13.92 | 0 |
| 434.64 | 21.43 | NA | NA | -0.02 | 4 | -64.55 | 145.11 | 14.89 | 0 |
| 76.83 | 7.25 | 447.39 | NA | 0.01 | 5 | -60.25 | 145.49 | 15.28 | 0 |
| 1129.38 | NA | NA | NA | 0.02 | 3 | -67.85 | 145.71 | 15.49 | 0 |

SI Table 3.4: Full model selection table for model 3a. Models averaging was performed for candidate models with a delta < 4.

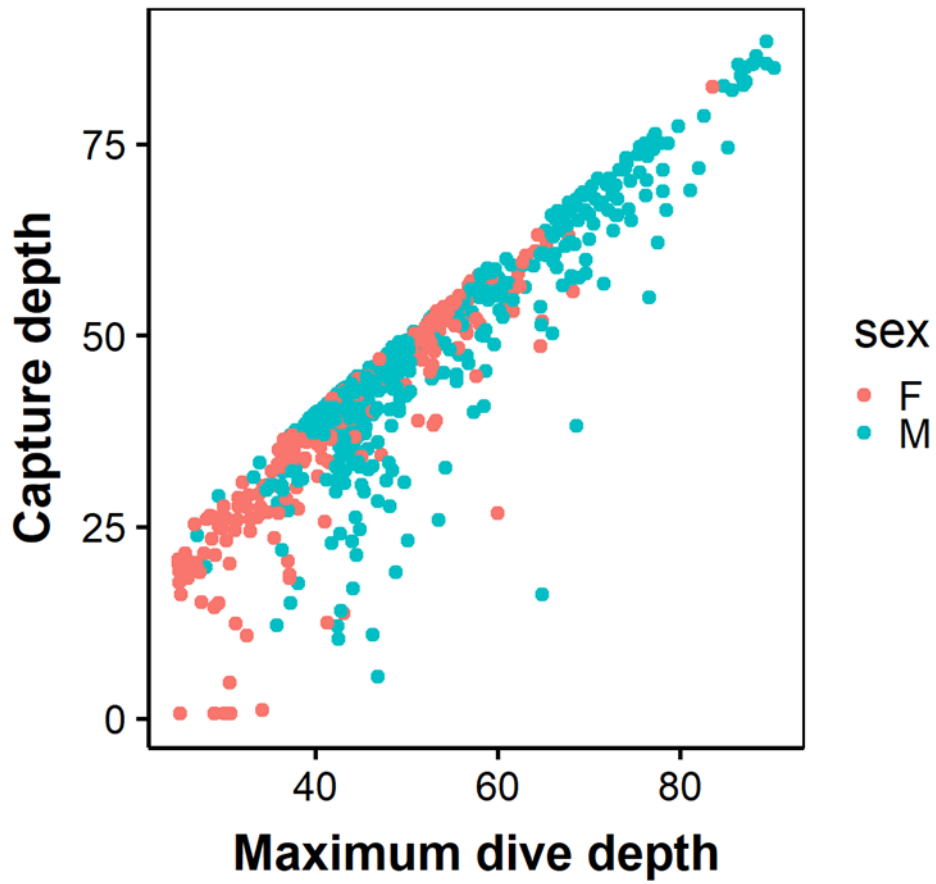
| Model 3a | | | | | | | | | |
|-----------|-----------------------|---------------------|------------|-------------------|---|--------|--------|-------|--------|
| Intercept | DEE _{CALC-S} | Horizontal distance | Mean Speed | Vertical distance | K | logLik | AICc | delta | weight |
| -928.93 | 1.05 | NA | 460.86 | NA | 4 | -59.83 | 135.65 | 0 | 0.31 |
| -1863.8 | 1.87 | 24.38 | NA | -0.06 | 5 | -55.74 | 136.48 | 0.83 | 0.21 |
| 63.07 | NA | 10.18 | 409.94 | NA | 4 | -60.41 | 136.81 | 1.16 | 0.18 |
| 138.56 | NA | NA | 542.31 | 0.02 | 4 | -60.94 | 137.88 | 2.23 | 0.1 |
| 263.7 | NA | NA | 551.28 | NA | 3 | -64.15 | 138.3 | 2.65 | 0.08 |
| -709.71 | 0.75 | 6.61 | 395.52 | NA | 5 | -57.18 | 139.36 | 3.71 | 0.05 |
| 592.79 | NA | 15.15 | NA | NA | 3 | -65.15 | 140.29 | 4.64 | 0.03 |
| -566.45 | 1.43 | NA | NA | NA | 3 | -66.1 | 142.2 | 6.55 | 0.01 |
| 1278.77 | NA | NA | NA | NA | 2 | -68.98 | 143.67 | 8.02 | 0.01 |
| -287.56 | 0.83 | 10.99 | NA | NA | 4 | -63.85 | 143.69 | 8.04 | 0.01 |
| -660.93 | 0.77 | NA | 481.38 | 0.01 | 5 | -59.43 | 143.86 | 8.21 | 0.01 |
| 434.64 | NA | 21.43 | NA | -0.02 | 4 | -64.55 | 145.11 | 9.46 | 0 |
| 76.83 | NA | 7.25 | 447.39 | 0.01 | 5 | -60.25 | 145.49 | 9.84 | 0 |
| 1129.38 | NA | NA | NA | 0.02 | 3 | -67.85 | 145.71 | 10.06 | 0 |
| -1515.18 | 1.46 | 17.4 | 199.9 | -0.04 | 6 | -52.88 | 145.77 | 10.12 | 0 |
| -691.41 | 1.55 | NA | NA | 0 | 4 | -66.08 | 148.16 | 12.51 | 0 |

SI Text 4.1: Additional methods in developing Support vector machine (SVM) for detecting prey captures in African penguins.

An SVM seeks to find the best “margin”, or kernel, that separates all positive (i.e. prey captures) and negative (i.e. swimming) events (Meyer & Wien 2015). After testing the suitability of a range of kernels (radial, linear, polynomial) the radial kernel was chosen as this model showed the highest overall accuracy. The model was further tuned by selecting the best values for gamma (how far the influence of a single training example reaches) and cost (controlling the trade-off between overfitting and under fitting of the support vector) and the following evaluation metrics were determined for each model: Accuracy - the number of correct predictions divided by the total number of predictions; Recall - the number of positive predictions divided by the number of total positive class values in the test data; and False positive rate -the number of incorrect positive predictions divided by the total number of positive predictions. The model with the highest accuracy and recall and the lowest false positive rate utilised a radial kernel where tuning parameters gamma and cost were 0.01 and 1, respectively. This model was then applied to the whole foraging trip of each individual in order to identify potential prey capture events in the periods without corresponding video data. To avoid the misclassification, a positive signal (irrespective of it being detected in a benthic or pelagic environment) had to be detected in 3 or more consecutive rolling windows (>0.9 s).

SI Table 4.1: Model selection table for models determining factors influencing probability of success for African penguins performing benthic and pelagic dives. Colony (St. Croix or Bird Island), Type (benthic or pelagic) and Sex (male or female) represented as “C”, “T” and “S”, respectively. “:” indicating interaction term between parameters.

| Retained variables | df | logLik | AICc | Δ AIC | weight |
|-------------------------------|----|---------|--------|--------------|--------|
| C, S, T, C:S, C:T, S:T, C:S:T | 9 | -3813.2 | 7644.5 | 0.00 | 0.22 |
| C,T,C:T | 5 | -3817.4 | 7644.8 | 0.29 | 0.19 |
| C, S, T, C:T, S:T | 7 | -3815.6 | 7645.1 | 0.63 | 0.16 |
| C, S, T, C:S, C:T, S:T | 8 | -3815.0 | 7646.1 | 1.55 | 0.10 |
| C, S, T, C:T | 6 | -3817.2 | 7646.4 | 1.90 | 0.08 |
| T | 3 | -3820.2 | 7646.5 | 1.98 | 0.08 |
| S, T, S:T | 5 | -3818.7 | 7647.5 | 2.95 | 0.05 |
| C, S, T, C:S, C:T | 7 | -3816.8 | 7647.6 | 3.09 | 0.05 |
| S, T | 4 | -3820.0 | 7648.1 | 3.56 | 0.04 |
| C, T | 4 | -3820.2 | 7648.3 | 3.79 | 0.03 |

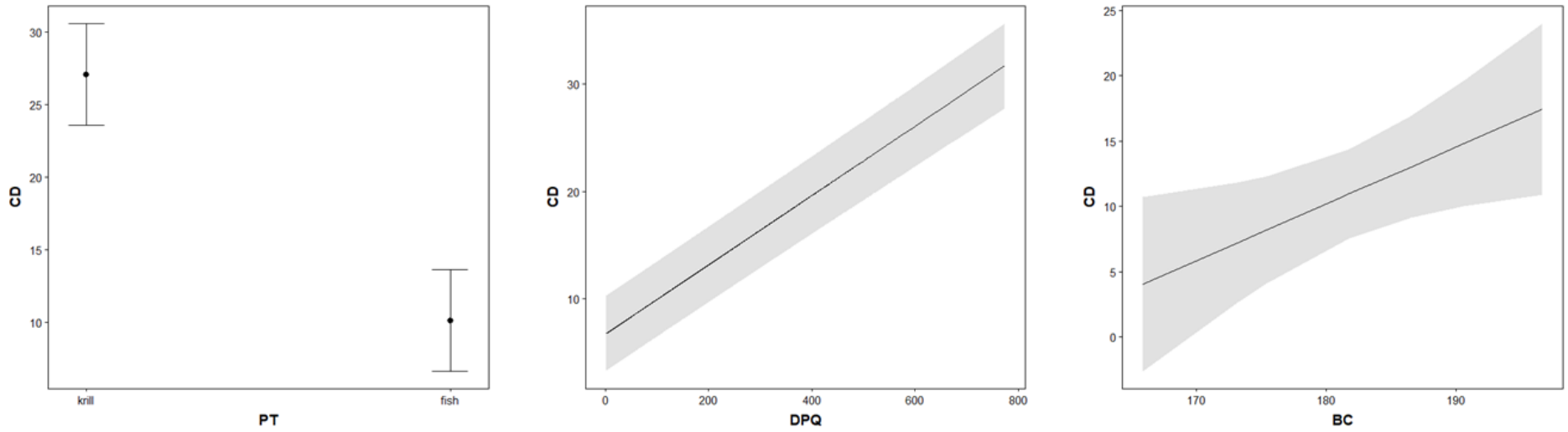


SI Figure 4.1: Maximum dive depth against depth of capture of African penguins performing benthic dives ($r^2 = 0.91$).

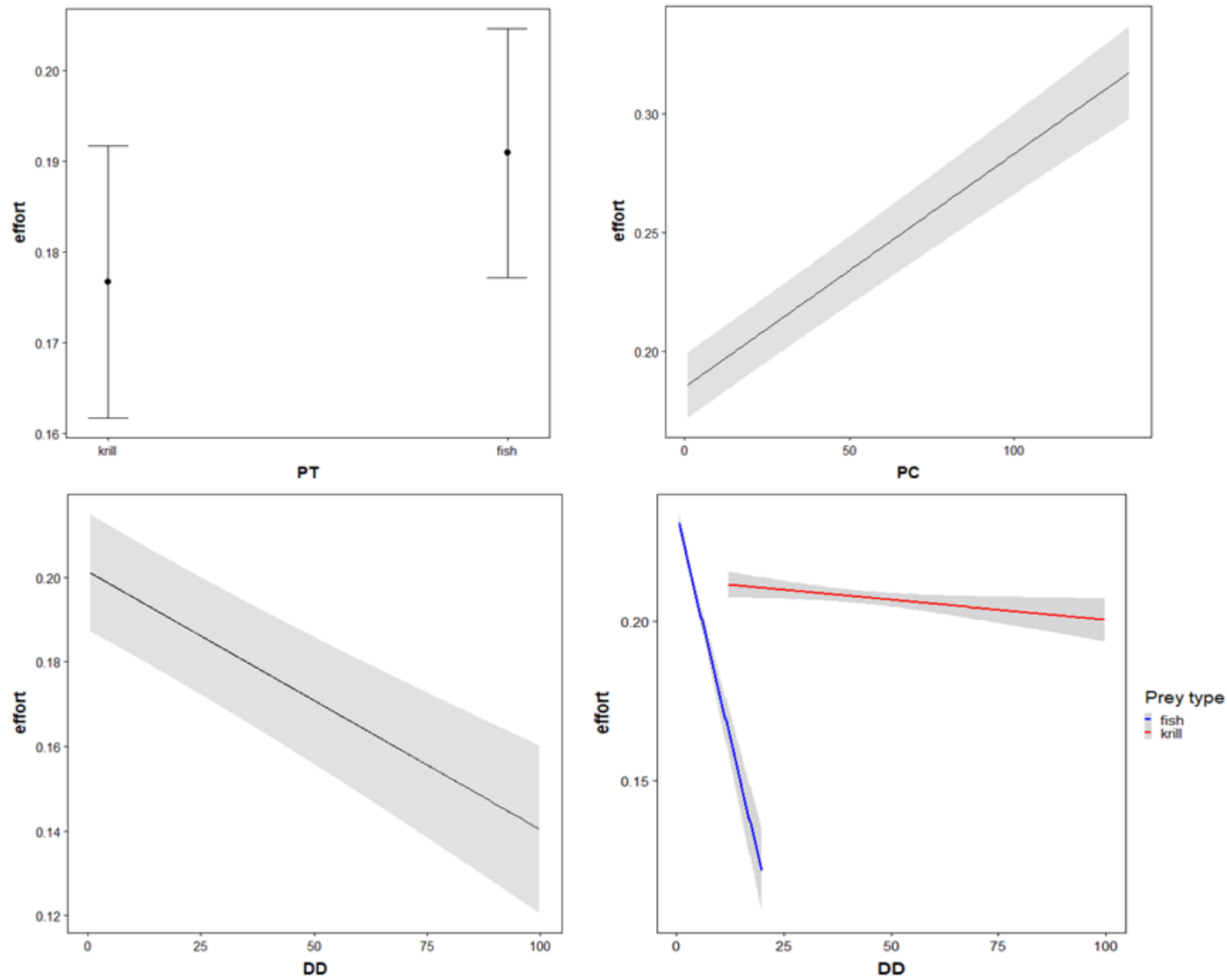
SI Table 5.1: Full models for models predicting capture depth, rate of effort (mean VeDBA, g), efficiency (number of prey captured/total VeDBA) and patch residency time in foraging Macaroni penguins. The abbreviations BC (Body condition), BPQ (Bout patch-quality), DPQ (Dive patch-quality), IBT (Inter-bout time), DD (Dive depth), PT (Prey Type), and the symbol “:” indicating an interaction term between explanatory variables are provided where necessary. Individual bird ID was included in all models to account for pseudo replication.

| Model | Response variable | Parametric coefficients | Smoothed term | Model Type |
|-------|----------------------|------------------------------|-----------------|------------|
| 1 | Capture depth | PT + DPQ + BC | Time of day (h) | GAMM |
| 2 | Effort | PT + PC + DD + BC | Time of day (h) | GAMM |
| 3 | Efficiency | PT + DPQ + DD + BC | Time of day (h) | GAMM |
| 4 | Patch residency time | PT + BPQ + IBT + BPQ:PT + DD | - | LME |

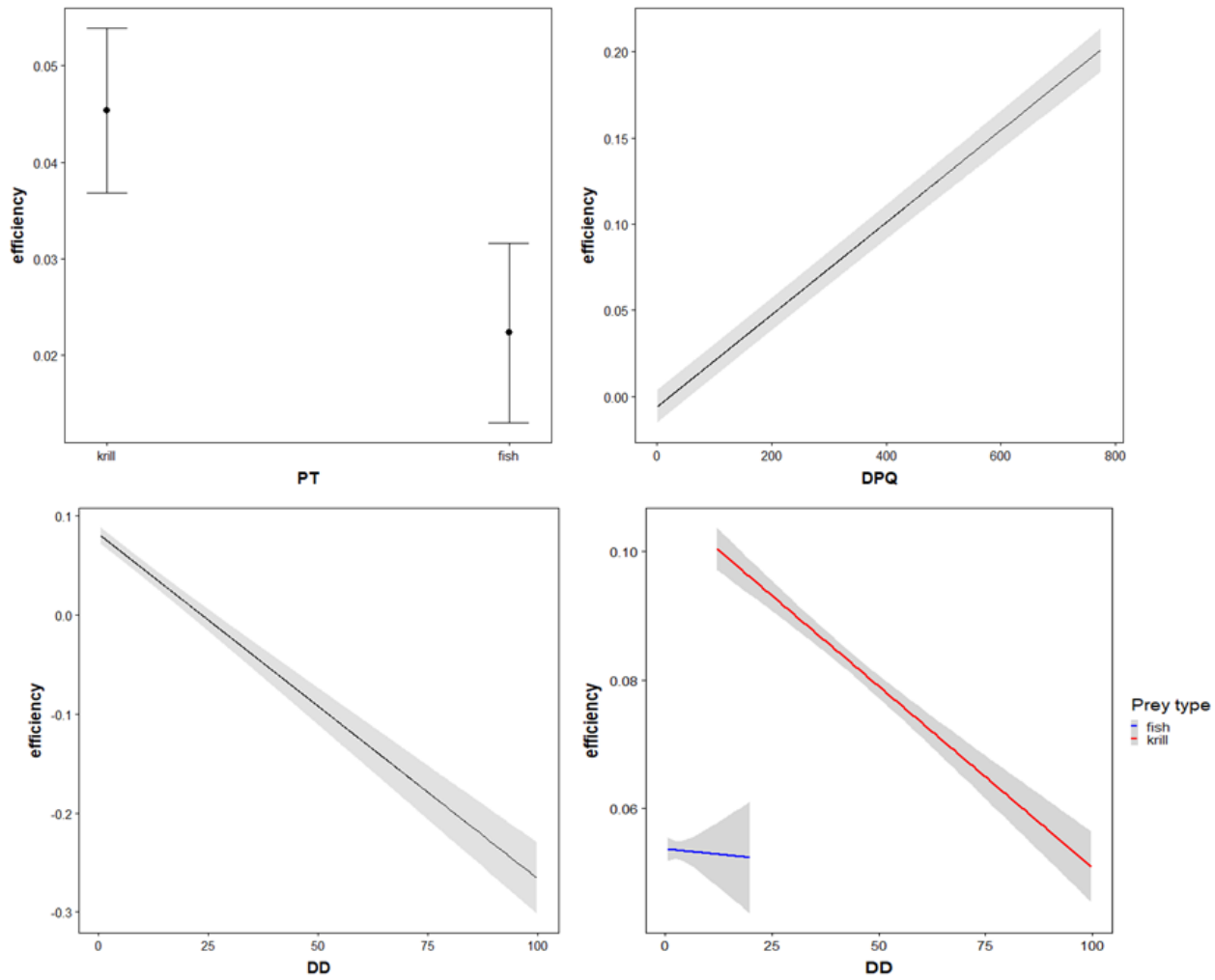
SI Figure 5.1: Model estimates of capture depth (CD) against prey type (PT), dive-patch quality (DPQ) and body condition (BC).



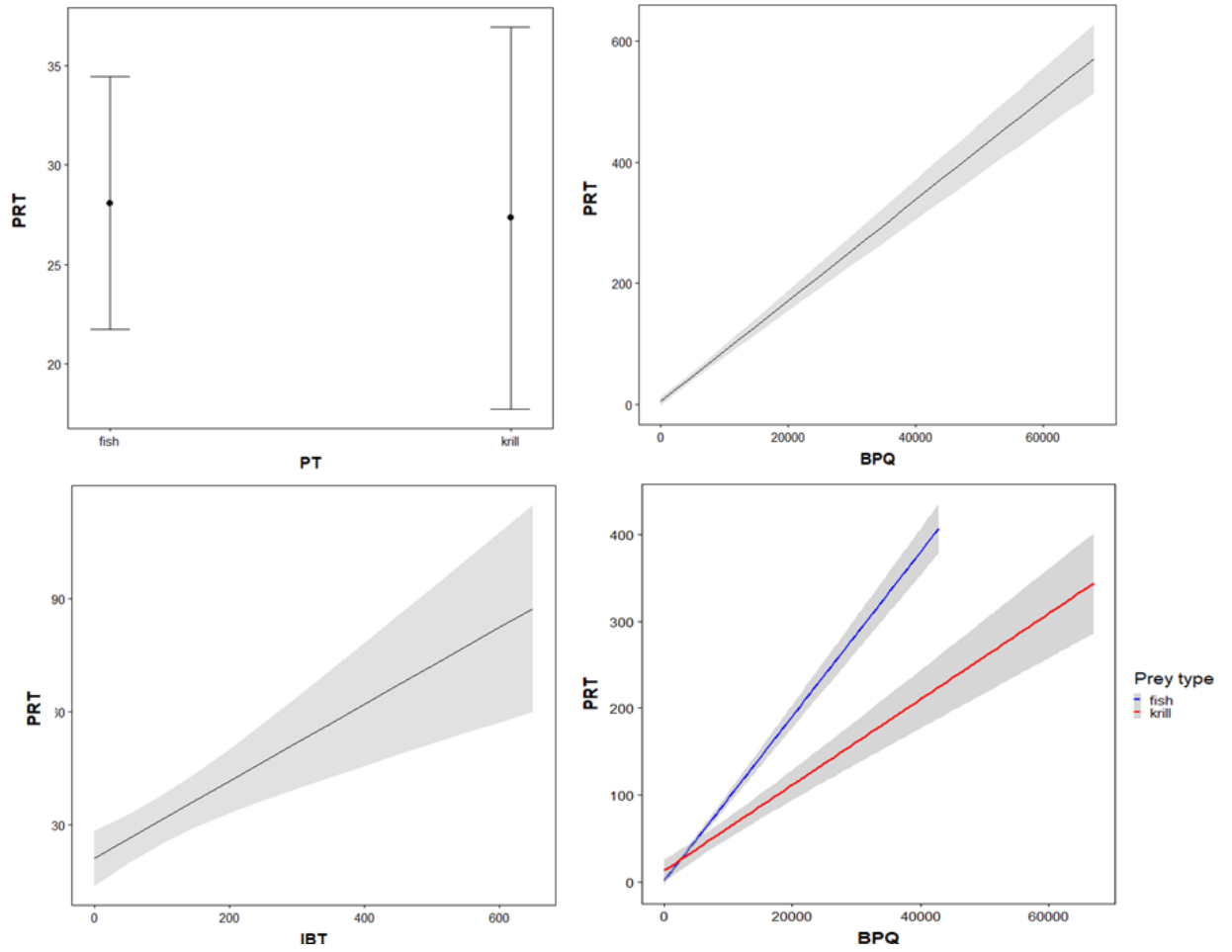
SI Figure 5.2: Model estimates of foraging effort per dive (CD) against prey type (PT), number of prey captures (PC), dive depth (DD) and the interaction between dive depth and prey type.



SI Figure 5.3: Model estimates of efficiency (CD) against prey type (PT), dive-patch quality (DPQ) and dive depth (DD) and the interaction between dive depth and prey type.



SI Figure 5. 4: Model estimates of patch residency time (PRT) against prey type (PT), bout-patch quality (BPQ) and inter-bout time (IBT) and the interaction between prey type and bout-patch quality.



SUPPLEMENTARY INFORMATION - AUTHORSHIP STATEMENTS

CHAPTER 3

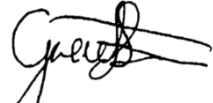
1. Details of publication and executive author

| | | |
|---|--|--|
| Title of Publication | | Publication details |
| Validating accelerometry-derived proxies of energy expenditure using the doubly-labelled water method in the smallest penguin species | | Sutton GJ, Botha JA, Speakman JR, Arnould JPY. Validating accelerometry-derived proxies of energy expenditure using the doubly-labelled water method in the smallest penguin species. Biol Open. 2021 Mar 15:bio.055475. doi: 10.1242/bio.055475. Epub ahead of print. PMID: 33722801. |
| Name of executive author | School/Institute/Division if based at Deakin; Organisation and address if non-Deakin | Email or phone |
| Grace J. Sutton | School of life and environmental sciences | gsutton@deakin.edu.au |

2. Inclusion of publication in a thesis

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| Grace Sutton conceived and designed the experiments, performed the experiments, analysed the data, prepared figures and/or tables, authored and revised drafts of the paper, and approved the final draft. | | |
| <i>I declare that the above is an accurate description of my contribution to this paper, and the contributions of other authors are as described below.</i> | Signature and date |  24/03/2021 |

4. Description of all author contributions

| Name and affiliation of author | Contribution(s) (for example, conception of the project, design of methodology or experimental protocol, data collection, analysis, drafting the manuscript, revising it critically for important intellectual content, etc.) |
|---|---|
| Jonathan Botha, Marine Apex Predator Research Unit (MAPRU), Institute for Coastal and Marine Research, Department of Zoology, Nelson Mandela University, Port Elizabeth, South Africa | Performed the experiments, analysed the data, reviewed drafts of the paper, and approved the final draft. |
| John R. Speakman Institute of Environmental and Biological Sciences, University of Aberdeen, Aberdeen, UK. Center for Metabolism, Reproduction and Aging, Shenzhen Institutes of Advance Technology, Chinese Academy of Sciences, Shenzhen, China | Analysed the data, reviewed drafts of the paper, and approved the final draft. |
| John Arnould School of Life and Environmental Sciences, Faculty of Science & Technology, Deakin University, Burwood, Victoria, Australia | Conceived and designed the experiments, analysed the data, reviewed drafts of the paper, and approved the final draft |


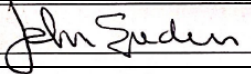
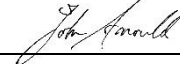
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| Jonathan Botha |  | 24/03/2021 |
| John Speakman |  | 24/03/2021 |
| John Arnould |  | 24/03/2021 |

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CHAPTER 4


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| Title of Publication | | Publication details |
| Multi-predator assemblages, dive type, bathymetry and sex influence foraging success and efficiency in African penguins | | Sutton G, Pichegru L, Botha JA, Kouzani AZ, Adams S, Bost CA, Arnould JPY. Multi-predator assemblages, dive type, bathymetry and sex influence foraging success and efficiency in African penguins. PeerJ. 2020 Jun 30;8:e9380. doi: 10.7717/peerj.9380. PMID: 32655991; PMCID: PMC7333648. |
| Name of executive author | School/Institute/Division if based at Deakin; Organisation and address if non-Deakin | Email or phone |
| Grace J. Sutton | School of life and environmental sciences | gsutton@deakin.edu.au |

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| As above | School of Life and Environmental Sciences | Fine-scale foraging movements and energetics in penguins |
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| Grace Sutton conceived and designed the experiments, performed the experiments, analysed the data, prepared figures and/or tables, authored and revised drafts of the paper, and approved the final draft. | | |
| <i>I declare that the above is an accurate description of my contribution to this paper, and the contributions of other authors are as described below.</i> | Signature and date |  24/03/2021 |

4. Description of all author contributions

| Name and affiliation of author | Contribution(s) (for example, conception of the project, design of methodology or experimental protocol, data collection, analysis, drafting the manuscript, revising it critically for important intellectual content, etc.) |
|--|---|
| Lorien Pichegru DST/NRF Centre of Excellence at the FitzPatrick Institute of African Ornithology, Institute for Coastal and Marine Research, Department of Zoology, Nelson Mandela University, Port Elizabeth, South Africa | Performed the experiments, analysed the data, authored or reviewed drafts of the paper, and approved the final draft. |
| Jonathan Botha, Marine Apex Predator Research Unit (MAPRU), Institute for Coastal and Marine Research, Department of Zoology, Nelson Mandela University, Port Elizabeth, South Africa | Performed the experiments, analysed the data, authored or reviewed drafts of the paper, and approved the final draft. |
| Abbas Z Kouzani and Scott Adams School of Engineering, Deakin University, Geelong, Victoria, Australia | Conceived and designed the methodology, reviewed drafts of the paper, and approved the final draft. |
| Charles A. Bost Centre d'Études Biologiques de Chizé, UMR7372 CNRS/Univ La Rochelle, Villiers-en-Bois, France | Conceived and designed the experiments, reviewed drafts of the paper, and approved the final draft. |
| John Arnould School of Life and Environmental Sciences, Faculty of Science & Technology, Deakin University, Burwood, Victoria, Australia | Conceived and designed the experiments, reviewed drafts of the paper, and approved the final draft |

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| Jonathan Botha |  | 24/03/2021 |
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| Abbas Z. Kouzani |  | 22/03/2021 |
| Scott Adams |  | 22/03/2021 |
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CHAPTER 5

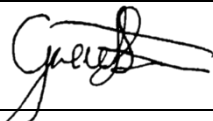
1. Details of publication and executive author

| | | |
|--|--|---|
| Title of Publication | | Publication details |
| Fine-scale foraging effort and efficiency of Macaroni penguins is influenced by prey type, patch density and temporal dynamics | | Sutton, G. J., Bost, C. A., Kouzani, A. Z., Adams, S. D., Mitchell, K., & Arnould, J. P. Y. (2021). Fine-scale foraging effort and efficiency of Macaroni penguins is influenced by prey type, patch density and temporal dynamics. <i>Marine Biology</i> , 168(1), 1-16. |
| Name of executive author | School/Institute/Division if based at Deakin; Organisation and address if non-Deakin | Email or phone |
| Grace J. Sutton | School of life and environmental sciences | gsutton@deakin.edu.au |

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| As above | School of Life and Environmental Sciences | Fine-scale foraging movements and energetics in penguins |
| If there are multiple authors, give a full description of HDR thesis author's contribution to the publication (for example, how much did you contribute to the conception of the project, the design of methodology or experimental protocol, data collection, analysis, drafting the manuscript, revising it critically for important intellectual content, etc.) | | |
| Grace Sutton conceived and designed the experiments, performed the experiments, analysed the data, prepared figures and/or tables, authored and revised drafts of the paper, and approved the final draft. | | |
| <i>I declare that the above is an accurate description of my contribution to this paper, and the contributions of other authors are as described below.</i> | Signature and date |  24/03/2021 |

4. Description of all author contributions

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| Name and affiliation of author | Contribution(s) (for example, conception of the project, design of methodology or experimental protocol, data collection, analysis, drafting the manuscript, revising it critically for important intellectual content, etc.) |
|--------------------------------|---|

| | |
|---|---|
| Abbas Z Kouzani, Kane Mitchell and Scott Adams School of Engineering, Deakin University, Geelong, Victoria, Australia | Conceived and design of methodology, reviewed drafts of the paper, and approved the final draft. |
| Charles A. Bost Centre d'Études Biologiques de Chizé, UMR7372 CNRS/Univ La Rochelle, Villiers-en-Bois, France | Conceived and designed the experiments, authored or reviewed drafts of the paper, and approved the final draft. |
| John Arnould School of Life and Environmental Sciences, Faculty of Science & Technology, Deakin University, Burwood, Victoria, Australia | Conceived and designed the experiments, analysed the data, authored or reviewed drafts of the paper, and approved the final draft |

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- xii. that there are no other authors according to these criteria,*
- xiii. that the description in Section 4 of my contribution(s) to this publication is accurate,*
- xiv. that the data on which these findings are based are stored as set out in Section 7 below.*

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|------------------|--|------------|
| Charles A. Bost |  | 22/03/2021 |
| Abbas Z. Kouzani |  | 22/03/2021 |
| Scott Adams |  | 22/03/2021 |
| Kane Mitchell | <i>Kane Mitchell</i> | 22/03/2021 |
| John Arnould |  | 24/03/2021 |

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I agree to be named as a non-author contributor to this work.

| Name and affiliation of contributor | Contribution | Signature* and date |
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| Data format | Storage Location | Date lodged | Name of custodian if other than the executive author |
|---|---|-------------|--|
| Raw data | LES Arnould Lab data master | 1/01/2017 | John Arnould |
| Raw data and additional supporting information of paper | figshare respository 10.6084/m9.figshare.12382268. | 28/05/2020 | John Arnould |

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