

**DIVING INTO THE COLD: INDIVIDUAL VARIATION IN THE WINTER FORAGING
BEHAVIOUR OF THE GENTOO PENGUIN**

by

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Abstract

Within any population, certain individuals outperform other members of their species. However, the precise basis for their advantage largely remains a mystery in ecology. In the last decade, research on the variability in foraging behaviour and diet between individuals has become a focus for ecologists as a potential mechanism for individual advantage. The numbers of breeding pairs of gentoo penguins in the Falkland Islands fluctuate annually, and while the precise cause of deferred breeding is unknown, carryover effects from the previous winter period is likely an important factor. Blood oxygen-carrying capacity and body mass are proposed to be critical carryover effects from winter influencing the reproductive trade-off of participating in breeding in the following spring, given their proposed influence on the diving ability and hence foraging capacity of penguins. In this thesis, I investigate (1) if interindividual variation in diving efficiency is associated with the condition of oxygen stores through i) blood oxygen-carrying capacity, using blood hemoglobin (Hb) and hematocrit (Hct) as indicators, and ii) body mass, and (2) if pre-breeding foraging effort differs between individuals based on their condition of oxygen stores and breeding status. Through monitoring penguins with time-depth recorders, I explored how Hb, Hct, and body mass influenced a penguin's ability to dive efficiently (maximize bottom time) over their natural range of foraging depths. Subsequently, I monitored breeding participation and egg lay date to assess the reproductive status of individuals. Reduced blood oxygen-carrying capacity was found to negatively impact dive efficiency, and the effect was most influential during deeper dives. Penguins with higher Hb and an apparent optimum Hct of 52 % performed best. Pre-breeding foraging effort was predictive of reproductive status, as early laying penguins exhibited lower foraging effort and spent less time at sea than non-

breeding penguins. How diving behaviour corresponds to breeding participation is essential to understand the effects ecosystem changes have on populations, and knowledge gained here could have broad implications for the conservation of this genus and many diving species.

Lay Summary

A key question in ecology is how some individuals outperform others within a species. Penguins can breed each year, but some do not and skip breeding seasons. Penguins are long-lived and prioritize their long-term success by avoiding negative costs and risks of breeding if they are in poor condition. Before the breeding season, winter foraging success determines their health and may influence whether they breed that year or not. My thesis explores how differences in diving ability and the physiological condition of oxygen stores are related, and how diving effort differs based on condition and breeding status in gentoo penguins. Better oxygen stores allowed penguins to dive longer and benefitted their foraging ability. Penguins that spent the least amount of time at sea laid eggs the earliest. How animals forage differently from each other and whether this difference influences breeding is valuable for conservation and predicting how environmental changes affect animals.

Preface

This project was initiated by Dr. Glenn Crossin and my supervisor Dr. Marie Auger-Méthé in collaboration with Dr. Megan Tierney, Dr. Paul Brickle, and Dr. Phil Trathan. I was the primary designer of the specific research aims described in this thesis and received suggestions and support from Dr. Marie Auger-Méthé and Dr. Glenn Crossin. I performed all data collection and analysis, including the programming, attachment, and processing of tracking devices, and I trained and led a team of 3 research assistants during the recapture field season in the Falkland Islands. I also assayed all hemoglobin samples under the guidance of Dr. Tony William and his lab at Simon Fraser University. Chapter 2 was written as a manuscript for which co-authors Dr. Marie Auger-Méthé and Dr. Glenn Crossin provided comments.

I completed the ethics training requirement of the Canadian Council on Animal Care (CCAC), and all protocols conformed to the CCAC guidelines. This research was conducted under Falkland Islands Scientific Research Licence (R12/2017), University of British Columbia Animal Care Permit A17-0243 and Dalhousie University Animal Care Permit 17-100.

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List of Abbreviations

ACF	Autocorrelation function
ADL	Aerobic dive limit
AIC	Akaike's information criterion
ARMA	Autoregressive-moving-average model
C	Colony
D	Depth
DE	Dive efficiency
GAMM	Generalized additive mixed modelling
Hb	Hemoglobin
Hct	Hematocrit
M	Body mass
Mb	Myoglobin
PCA	Principal component analysis
PC1	Principal component 1
PC2	Principal component 2
PDSI	Post-dive surface interval
R	Reproductive status
S	Sex
SD	Standard deviation
TDR	Time-depth recorder

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To children in small towns with big dreams, to my amazing family, and to the penguins.



Chapter 1: Introduction

1.1 The need to dive, and the importance of efficiency

In the last decade, research on the individual variability in foraging behaviour and diet amongst individuals has become a focus for ecologists (e.g., Bonnot et al. 2015, McHuron et al. 2018a). For species that forage at sea, such as seabirds and marine mammals, variation in foraging is often studied as differences in diving behaviour (Baylis et al. 2015). In these cases, foraging ability is tightly coupled to specific aspects of diving behaviour, where dietary specializations impact the preferred diving depth and foraging behaviour of individuals (Baylis et al. 2015, Horswill et al. 2017). Understanding how individuals select foraging habitat is vital to comprehend the foraging ecology of animals and understand the impacts both natural and anthropogenic ecosystem changes can have on populations (dit Durell 2000, Bearhop et al. 2006, Cury et al. 2011, Phillips et al. 2017).

Across the animal kingdom, we find a diverse array of diving ability. Within diving avians alone, species vary from quick, shallow dives of a few meters (e.g., great shearwaters, *Puffinus gravis*; Ronconi et al. 2010), to dives of over 500 m (e.g., emperor penguins, *Aptenodytes patagonicus*; Shiomi et al. 2012). Despite vast ranges in dive depths, all diving species share a common goal to maximize their foraging efficiency, where their diving behaviour reflects the optimal pursuit of preferred prey (Clausen et al. 2005, Takahashi et al. 2008, Horswill et al. 2017). Prey is almost always encountered during the bottom phase of dives (Simeone and Wilson 2003, Takahashi et al. 2004, 2008, Kokubun et al. 2010). To maximize dive efficiency, animals must maximize the time spent at depth while minimizing the time spent on the surface to recover (Stephens and Krebs 1986, Mori 1998, Wilson et al. 2010, Zimmer et al. 2010). As breath-hold divers, body oxygen stores become depleted while submerged,

meaning that animals must spend time to recover before diving again (Dzal et al. 2015). The precise means by which individuals differ in their storage and use of oxygen limits their ability to remain submerged and directly affects their diving efficiency and foraging ability (Crossin et al. 2015, Chimienti et al. 2017). My main goal in this thesis, therefore, is to investigate how factors relating to the improved storage of oxygen influence the degree of variation in diving behaviour between individuals using gentoo penguins as a model species.

1.2 The control of diving and the importance of oxygen stores

Breath-holding divers, especially deeper divers, are faced with physiological constraints (e.g., oxygen stores) to their diving ability (Roncon et al. 2018). A vast literature base now exists on the control of diving (reviewed in Ponganis and Kooyman 2000, Dzal et al. 2015, Roncon et al. 2018). As energy is expended throughout a dive, the available oxygen is depleted, while metabolites such as carbon dioxide (aerobic metabolism) and lactate (anaerobic metabolism) accumulate and affect how long an animal can spend without replenishing oxygen stores (Dzal et al. 2015). The aerobic dive limit (ADL) is reached when oxygen stores are no longer sufficient to support aerobic metabolism, and lactate, a metabolite, begins to accumulate due to the transition from aerobic metabolism (Kooyman et al. 1983). Diving animals have a complex suite of physiological adaptations to lengthen the time they can spend underwater, but in this thesis, I will focus on how deep divers maximize the amount of oxygen stored in the body to extend their aerobic dive limits.

The ADL is largely determined by oxygen stores within the body, which may consist of oxygen in the lungs, as well as within different body compartments. The latter are largely determined by oxygen-carrying proteins in the blood (Hemoglobin, Hb) and the muscles (Myoglobin, Mb) of animals (Mirceta et al. 2013, Roncon et al. 2018). To increase their storage

of oxygen, diving animals are adapted to have larger blood volumes, more erythrocytes (red blood cells) with increased concentrations of Hb, and higher muscle mass dense in Mb (Meir and Ponganis 2009, Roncon et al. 2018). As larger body sizes possess more blood and muscle, body mass directly contributes to oxygen stores (Ponganis and Kooyman 2000, Cook et al. 2013, Mirceta et al. 2013, Polito et al. 2015, Camprasse et al. 2017). Quantifying absolute oxygen stores necessitates many aspects of physiology to be measured, but the oxygen-carrying capacity of the blood can be estimated using simple erythrocyte variables (Johnstone et al. 2017). Hematocrit (Hct) is the percentage of packed red blood cells in the blood, indicating the relative volume of erythrocytes, and Hb concentration determines the total amount of oxygen that can be carried by the blood (Minias 2015). As Hct is based on blood cytology and Hb based on blood biochemistry, each measure provides different insights into the oxygen stores of individuals (Fair et al. 2007, Kaliński et al. 2011, Minias 2015).

Measuring indices of blood oxygen-carrying capacity, Hct and Hb, allow us to make inferences regarding the overall physiological condition of animals that, in the wild, is otherwise difficult to determine (Roncon et al. 2018). Both metrics can be measured with small amounts of blood and are essential components to physiological performance, through limiting aerobic capacity, and thus the breath-holding ability of diving animals (Minias 2015). While these erythrocyte indicators are useful in assessing diving ability, there are some limitations (reviewed in Fair et al. 2007, Minias 2015, Johnstone et al. 2017). Though inferences are valuable in estimating the underlying health of animals, a cautious interpretation is required, as their relationship to definitive physiological condition is complicated (Johnstone et al. 2017). Nevertheless, to proactively monitor the status and health of wildlife populations, researchers are

focusing more on sensitive individual-level metrics related to performance, such as blood oxygen-carrying capacity, instead of slower-responding population metrics (Cooke et al. 2013).

1.3 Penguins, order Sphenisciformes

Seabirds, especially deep diving penguins, are ideal for studying how oxygen stores relate to diving performance due to the high degree of individual variation in foraging behaviour. As colonial species, foraging ranges are restricted seasonally around colonies leading to an increased likelihood for intraspecific competition (Bearhop et al. 2006). Some penguins have shown high interindividual variation in small scale foraging habitat selection based on local availability of prey (Camprasse et al. 2017), and depending on the species, variety in diet has also been documented between sexes (Bearhop et al. 2006, Phillips et al. 2017) or age groups (Phillips et al. 2017, Sherley et al. 2017). The cause of this variation may be correlated with diving ability restricted by oxygen storage. Individual variation creates the opportunity for ecosystem changes to have different effects, through trait specific selection, on the demographics of a population (Sherley et al. 2017).

All species of penguins have similar life-history patterns. Like many other seabirds, penguins are long-lived and reproduce annually, where they lay one or two eggs and take months to rear their young (Boersma 2008). Their annual cycles all contain courtship, breeding, moulting, and non-breeding periods, although the timing of these phases differs by species (Ancel et al. 2013). Fossil evidence indicates penguins diverged 45-60 million years ago from other birds (Baker et al. 2006) with adaptations specialized for diving such as flipper-like wings for underwater propulsion and the ability to hold their breath for extended periods (Elliott et al. 2013). Since their survival and reproduction are sensitive to their foraging success and environment quality, penguins are good indicators for their local ecosystem health (Reid et al.

2005, Boersma 2008, Carpenter-Kling et al. 2019). However, this same sensitivity to environmental changes and increasing conflicts with humans have put numerous species at risk (reviewed in Black 2016). At present, penguins remain one of the most threatened families of seabirds (Croxall et al. 2012). Of the 18 species currently recognized by the International Union for Conservation of Nature over half are classified as threatened, with a status of endangered (5) or vulnerable (5), while others are near threatened (3), and only a few are of least concern (5) (IUCN 2019).

Climate change can impact prey availability and, in turn, the habitat suitability of predators to their environment, impacting survival and reproductive rates (Hinke et al. 2007, Boersma 2008). For penguins and other seabird species, locating food in winter is essential to recover energy stores depleted due to breeding and moulting and prepare for the ensuing breeding season (Sorensen et al. 2009, Crossin and Williams 2016). Consequently, winter periods are critical in determining annual survival and recruitment rates (Fraser et al. 1992, Hinke et al. 2007). Food acquisition is associated with high movement costs, due to the dynamic nature of marine environments, and food can also become scarce in late winter (Wilson et al. 1998, Clausen and Pütz 2003, Tanton et al. 2004). In unusually harsh winters, offspring and adults can experience high mortality, and adults ending winter in poor health may be less likely to reproduce in the following breeding season (Fraser et al. 1992).

1.4 Variation in diving performance and its effect on fitness measures

The precise means by which high-quality individuals outperform others in their species largely remains a mystery in ecology. Individual quality, defined here as a collection of phenotypes positively correlating with fitness (Wilson and Nussey 2010), can be assessed using the health or condition of animals, defined broadly as a combination of fat reserves, nutritional

state, and physiological performance (Minias 2015). Individual condition is one critical determinant in the decision to participate in breeding (O'Connor et al. 2014). Since penguins have long life-histories, individuals in poor health may be better to defer breeding and focus on improving their condition rather than risk their survival (Williams 1990, Williams and Rodwell 1992). According to life-history theory, all iteroparous species, characterized by multiple reproductive cycles, experience reproductive trade-offs between investing in current versus future breeding seasons to maximizing individual fitness during their lifetime (Cole 1954). The likelihood of individuals within a population to defer breeding impacts population dynamics and the response to environmental conditions in the Anthropocene (Williams 1990, Williams and Rodwell 1992, Crossin et al. 2010). Research distinguishing behavioural patterns of successful versus unsuccessful breeders is therefore critical for conservation, and penguins can be a model species to inform upon life-history trade-offs animals experience.

Reproductive trade-offs can be explored through the concept of carryover effects. Carryover effects are interactions, both positive and negative, between an individual's previous history and their current performance (O'Connor et al. 2014). The initial concept of carryover effects linking life-history stages focused on the energy reserves of animals, that ultimately determined the resources available to invest in reproduction (Harrison et al. 2011, O'Connor et al. 2014). For example, diet quality in some species of birds has been found to determine the timing of breeding (Perrins 1970, Verhulst and Nilsson 2008, Lescroël et al. 2009, Sorensen et al. 2009), reproductive investment (Wagner et al. 2008, Horswill et al. 2017), and reproductive success (Waluda et al. 2017). The timing of breeding is relevant as an indication of individual quality in birds as, on average, individuals breeding earlier have better reproductive success (Perrins 1970, Verhulst and Nilsson 2008).

In addition to energy reserves, carryover effects may also be related to underlying physiological mechanisms able to influence individual condition over more extended periods (reviewed in Williams 2012, Fowler and Williams 2017). Many studies of penguins and other birds have shown individuals base timing and reproductive investment on their pre-breeding physiological condition and their ability to maintain minimum levels of hematological variables during the costs of breeding (Wagner et al. 2008, Crossin et al. 2010, Fronstin et al. 2016). Throughout the breeding season, female macaroni penguins, *Eudyptes chrysolophus*, have shown a > 10 % reduction from pre-breeding to post-laying hematocrit levels (Crossin et al. 2010). While female zebra finches, *Taeniopygia guttata*, alter clutch size to maintain acceptable levels of hematological variables (Wagner et al. 2008), penguins have almost no variation in clutch size between individuals of a species (Ancel et al. 2013). Therefore, the trade-off to maintain hematological variables essential for oxygen stores and diving could involve forgoing participation in breeding altogether in penguins. Energy reserves and physiological conditions are both carried-over from the winter pre-breeding period and are hypothesized as essential to buffer the future costs of reproducing (Sorensen et al. 2009, Alves et al. 2013, Crossin and Williams 2016). Due to the impacts of winter on reproductive status, conservation goals need to consider the implications of carryover effects on foraging ability and how likely individuals are to defer breeding (Daunt et al. 2006, O'Connor and Cooke 2015, Sorenson et al. 2017).

1.5 The northern gentoo penguin, *Pygoscelis papua papua*, and foraging specialization

Although gentoo penguins, *Pygoscelis papua*, have fared better than many other species of penguin in the changing environmental conditions of the century (Juárez et al. 2013, McMahon et al. 2019), their breeding populations experience significant annual fluctuations in some locations (Pistorius et al. 2010, Stanworth and Crofts 2019). Gentoo penguins have a wide

circumpolar distribution across Antarctic and sub-Antarctic regions, and recently their increasing colony sizes toward the southern reach of their range improved their IUCN status to least concern (IUCN 2019). However, recent literature advocates that the population in the Falkland Islands be considered a separate sub-species, *Pygoscelis papua papua*, as they are isolated from other populations by the polar front (de Dinechin et al. 2012, Levy et al. 2016, Clucas et al. 2018). The Falkland Islands are at the northern reaches of the gentoo penguin's range, with changes as great as 50 % in the number of breeding pairs occurring in a single year (Pistorius et al. 2010). While some annually monitored colonies are still increasing in their breeding population, other locations are decreasing (Stanworth and Crofts 2019). The cause of variable breeding participation remains unknown, but carryover effects from winter foraging success are likely a predominant factor (Williams 1990, Alves et al. 2013, Crossin and Williams 2016).

The foraging success of individual gentoo penguins is primarily based on nearby environmental conditions where they consume a wide variety of locally available prey (Lescroël and Bost 2005, Kokubun et al. 2010, Waluda et al. 2017). As gentoo penguins are not a migratory species, their foraging range only moderately expands during the winter in the absence of dependent chicks (Tanton et al. 2004, Thiebot et al. 2011). Most research on the foraging behaviour of gentoo penguins has primarily focused on the breeding or pre-moult interval periods (Williams et al. 1992a, Kokubun et al. 2010, Masello et al. 2010, Lee et al. 2015, Handley et al. 2016, Camprasse et al. 2017, Carpenter-Kling et al. 2017). In the Falkland Islands, they remain primarily on the continental shelf hunting opportunistically on krill, fish, and squid species (Clausen and Pütz 2003, Hinke and Trivelpiece 2011, Handley et al. 2017). Studies conducted during the winter indicate that most gentoo penguins remain diurnal foragers year-round using daylight to help catch prey and continue to return to shore at night (Clausen and Pütz

2003, Tanton et al. 2004, Hinke and Trivelpiece 2011). Yet, a few studies report some degree of individual variation in foraging activity in regards to night diving (Masello et al. 2010), trip duration (Williams et al. 1992b, Hinke and Trivelpiece 2011, Carpenter-Kling et al. 2017), and preferred prey type (Camprasse et al. 2017, Handley et al. 2017, Xavier et al. 2017). Longer trip durations may allow individuals to forage further from shore and gain access to otherwise unreachable prey resources (Clausen and Pütz 2003), and specialization in prey type can influence diving behaviour and the vertical spatial segregation of individuals (Horswill et al. 2017). This is especially the case in prey-sparse winters, when nearshore resources become depleted (Clausen and Pütz 2003), individual foraging specializations may impact the condition and energy reserves of penguins (Hinke et al. 2017, Catry et al. 2019, McMahon et al. 2019).

Since gentoo penguins have a wide range of prey comprising their diet and likely experience high levels of competition for resources, there is a more significant opportunity for interindividual variation and individual specialization in foraging strategies (dit Durell 2000, Clausen and Pütz 2003, Lescroël et al. 2004, Handley et al. 2016, Camprasse et al. 2017, Phillips et al. 2017). In foraging ecology, it is common for species to be considered either generalist foragers, that consume a variety of prey opportunistically and exploit a broad ecological niche or specialist foragers focussed on specific prey species within a narrow niche (Bolnick et al. 2003, Phillips et al. 2017). Individuals belonging to generalist species may consume a range of prey (type A generalists), or individuals may each specialize in preferred prey species (type B generalists) (Bearhop et al. 2004). Gentoo penguins have been identified as type B generalists, composed of specialized individuals (Polito et al. 2015, Camprasse et al. 2017, Herman et al. 2017). As type B species narrow individual niches that differ from each other they also tend to have exceptionally high interindividual variation in foraging. The condition of individual gentoo

penguins can be influenced due to narrow niche widths, as a change in the availability of prey will have different impacts on individuals based on their specializations and adaptability of foraging search patterns (Bolnick et al. 2003). Specialization in foraging strategies, via their impact on the condition of individuals, may then influence individual breeding participation and help explain documented fluctuations in breeding population between years (Ceia and Ramos 2015). Through using gentoo penguins as a model species, we can gather information on the types of trade-offs animals experience and the influence of that on whether they breed that season.

1.6 Research goals

The main objective of my thesis is to understand how interindividual variation in the diving behaviour of gentoo penguins relates to individual condition, and how this relates to breeding participation. Pre-breeding condition is presumed to influence reproductive status and explain the fluctuations in breeding participation seen in gentoo penguins. Here, I focus on two types of condition indicators with specific relevance to oxygen storage and diving performance that are commonly used to assess the overall health of animals: blood oxygen-carrying capacity and body mass. Oxygen stores within the blood are essential for breath-holding divers such as penguins through limiting their ability to remain at depth, thus restricting foraging time and efficiency (Crossin et al. 2015, Chimienti et al. 2017). Body mass is relevant as larger individuals are proposed to dive deeper and have higher oxygen-carrying capacity from larger blood volumes and muscle mass (Cook et al. 2013, Mirceta et al. 2013, Polito et al. 2015, Camprasse et al. 2017). My first research goal was, therefore, to explore how interindividual variation in pre-breeding diving behaviour relates to the condition of oxygen stores: i) blood oxygen-carrying capacity, in terms of Hb and Hct levels, and ii) body mass. Due to the long life-

history of penguins, they must trade-off current reproduction efforts against future reproduction and survival (Cole 1954). Individual foraging ability and condition should both be crucial in the decision to participate in breeding. Consequently, my second research goal was to explore how interindividual variation in pre-breeding diving behaviour and foraging effort is related to condition indices of oxygen storage and breeding participation in gentoo penguins.

As the Falkland Islands are home to approximately one-third of the world gentoo penguin population and are now suggested to be a different subspecies (de Dinechin et al. 2012, Levy et al. 2016, Clucas et al. 2018), breeding instabilities and their link to winter ecosystems need to be investigated as they could have impacts on the global status of this species. Understanding how oxygen stores impact diving efficiency, and what this impact means for breeding participation, can help us understand the types of life-history trade-offs in penguins through knowledge on how likely individuals are to defer breeding. The adaptability of populations to environmental change is likely affected by the interindividual variation, and individual specialization, in foraging strategies (dit Durell 2000, Phillips et al. 2017, Morgan et al. 2019). Knowledge of the limitations to diving, and how these limitations influence population dynamics, is needed not only for gentoo penguins but for many diving avian species.

Chapter 2: Pre-breeding dive efficiency associated with differences in oxygen storage in a foraging seabird

2.1 Introduction

The mechanism by which high-quality individuals outperform others in their species largely remains a mystery in ecology. Individual quality, defined here as a collection of phenotypes positively correlating with fitness (Wilson and Nussey 2010), can be assessed using the condition of animals, defined broadly as a combination of fat reserves, nutritional state, and physiological performance (Minias 2015). Individual quality is closely related to foraging success, and for diving animals is closely coupled to diving ability (Baylis et al. 2015, Horswill et al. 2017). Determining traits common to high-quality individuals is complicated due to the intricate relationships between animals and their environment that make interpreting physiological-ecology studies difficult. Variation in quality also may only be apparent when exaggerated under especially harsh environmental conditions (Vleck and Vleck 2002, Williams 2012), but nonetheless it is increasingly important to understand how individual quality impacts population responses to changing environmental conditions (Ceia and Ramos 2015).

Seabirds, especially penguins, are ideal for studying variation in individual quality as they severely deplete their energy reserves during breeding and moulting periods and must replenish these reserves by foraging intensively in winter to recover their condition (Sorensen et al. 2009, Crossin and Williams 2016). Consequently, winter periods partly determine annual survival and recruitment rates in penguins (Fraser et al. 1992, Hinke et al. 2007, Rebstock and Boersma 2018) and carryover effects from winter influence breeding participation (i.e., the capacity to reproduce in the following breeding season) (Alves et al. 2013, Crossin and Williams

2016). There is a high likelihood of intraspecific competition for prey around colonies, and this is especially true for gentoo penguins, *Pygoscelis papua*, as they are not migratory but remain constrained near-shore with restricted foraging ranges year-round (Clausen et al. 2005, Bearhop et al. 2006, Kokubun et al. 2010). Of concern is that the numbers of breeding pairs in the Falkland Islands fluctuate drastically, with changes of 50 % occurring in a single year (Pistorius et al. 2010, Stanworth and Crofts 2019). I hypothesized that this disparity in breeding investment is the result of individual differences in winter foraging behaviour, particularly during challenging years.

How diving animals differ in their access to, or acquisition of, resources may be physiologically driven and thus limited by the condition of oxygen stores (Roncon et al. 2018). As a generalist species, gentoo penguins consume a wide variety of locally available prey found at a range of depths down to approximately 200 m (Tanton et al. 2004, Thiebot et al. 2011, Camprasse et al. 2017). However, recent work identified gentoo penguins as Type B generalists, that is, the population is composed of specialized individuals (Polito et al. 2015, Camprasse et al. 2017, Herman et al. 2017). Specialization in prey and associated diving behaviour might be partially driven by differences in individual diving physiology (Ceia and Ramos 2015, Crossin et al. 2015).

Diving animals have a range of adaptations to extend their breath-holding capability and maximize their aerobic capacity. As energy is expended throughout a dive, the available oxygen stores are depleted while metabolites such as carbon dioxide (aerobic metabolism) and lactate (anaerobic metabolism) accumulate and affect how long an animal can spend without replenishing oxygen stores (Dzal et al. 2015). The aerobic dive limit (ADL) occurs when oxygen stores in the body are no longer adequate to support metabolism wholly aerobically and

anaerobic metabolism is recruited, leading to an elevation in lactate levels (Kooyman et al. 1983). Oxygen stores include the lungs and oxygen-carrying proteins in the blood (Hemoglobin, Hb) and the muscles (Myoglobin, Mb) (Mirceta et al. 2013, Roncon et al. 2018). Body mass also directly contributes to oxygen stores as larger individuals possess more blood and muscle (Ponganis and Kooyman 2000, Cook et al. 2013, Mirceta et al. 2013, Polito et al. 2015, Camprasse et al. 2017). Thus, blood oxygen-carrying capacity and body mass are essential for breath-holding divers, such as penguins, and is one aspect of physiological performance that limits diving ability (Crossin et al. 2015, Chimienti et al. 2017). Therefore, the condition of oxygen stores can be an important constraint on foraging and diving behaviour affecting individual performance and, thus, prey selection (Crossin et al. 2013, 2015, Minias 2015).

Here, I explore how interindividual variation in pre-breeding foraging behaviour relates to blood oxygen-carrying capacity, as indicated by Hct and Hb levels, body mass, and ultimately the breeding status of gentoo penguins. Monitoring penguins with time-depth recorders (TDRs) provides valuable information on foraging behaviour such as the vertical spatial segregation of individuals (Wilmers et al. 2015, Horswill et al. 2017). The cost of reproduction is hypothesized to enforce a threshold level of condition carried over from the pre-breeding period that is required to participate in breeding. Understanding how individuals vary in their foraging ability and behaviour as they prepare for breeding is essential to understand the possible impacts natural and anthropogenic ecosystem changes can have on populations (dit Durell 2000, Bearhop et al. 2006, Cury et al. 2011, Phillips et al. 2017). Thus, I investigate (1) if diving efficiency is associated with the condition of body oxygen stores through i) blood oxygen-carrying capacity, using blood hemoglobin (Hb) and hematocrit (Hct) as indicators, and ii) body mass, and (2) if

pre-breeding foraging effort differs between individuals based on their oxygen stores and breeding status.

2.2 Methods

2.2.1 Data collection

Adult gentoo penguins were captured post-moult between April 4, 2018, to April 10, 2018, from two colony locations 27 km apart in the Falkland Islands: Rookery Sands, Race Point (-51.4345, -59.1081, n=33) and Tamar Point, Pebble Island (-51.3241, -59.4523, n=33). The Race Point colony is included in the annual census and reported 1213 ± 3 breeding pairs in the 2018 season (Stanworth and Crofts 2019), and while not censused Pebble Island was approximately double in size in 2018. Body mass (kg) was measured using a 10kg Pesola scale and penguins were equipped with Lotek LAT1800 TDRs (62 x 13 x 13 mm, 13.6 g, Lotek Wireless Inc, St. John's, Canada) which recorded depth (0.25 m resolution), temperature (0.01°C resolution), and wet/dry state at 1 s intervals. Devices were attached to midline back feathers using TESA® tape (Beiersdorf AG, GmbH, Hamburg, Germany) and cyanocycline glue on tape seams. Devices (n=23/35 recaptured penguins; 8 Race Point, 15 Pebble Island) were retrieved between September 27, 2018, to October 21, 2018. Upon retrieval, body mass was again measured and blood samples (< 1.5 ml) were taken from the left brachial vein to determine blood oxygen-carrying capacity using heparinized syringes fitted with 25-gauge needles. Physiological indicators, Hct and Hb, were then measured from fresh whole blood following the release of each penguin (see section 2.2.2). The research was conducted under Falkland Islands Scientific Research Licence (R12/2017) and conformed to guidelines from the Canadian Committee on Animal Care (University of British Columbia Animal Care Permit A17-0243 and Dalhousie University Animal Care Permit 17-100).

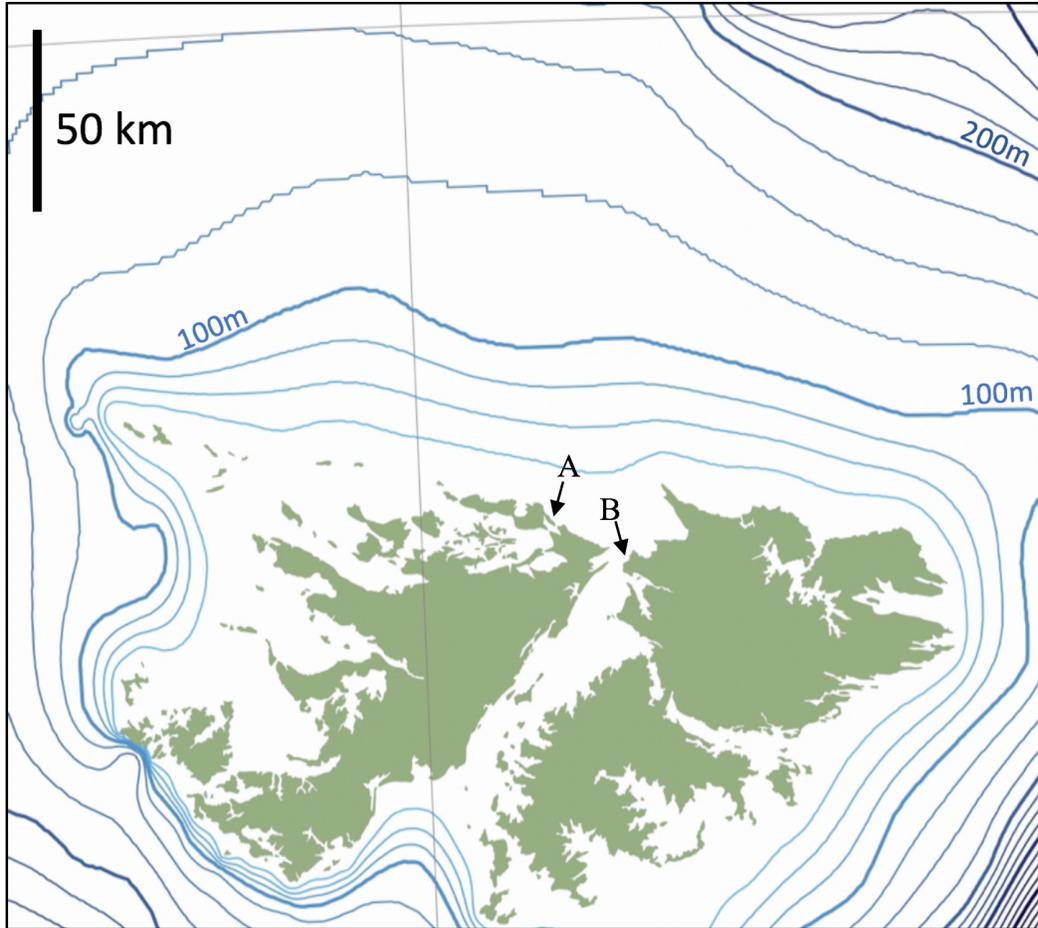


Figure 2.1 Falkland Islands showing both study sites: (A) Tamar Point, Pebble Island (-51.3241, -59.4523), (B) Rookery Sands, Race Point (-51.4345, -59.1081).

2.2.2 Physiological measurements and assays

Physiological indicators of blood oxygen-carrying capacity used in this study were hematocrit (Hct) and hemoglobin (Hb). As Hct is based on blood cytology and Hb based on blood biochemistry, each measure provides different insights into the aerobic condition of individuals (Fair et al. 2007, Kaliński et al. 2011, Minias 2015). Hct (percent packed red blood cell volume) was determined from fresh whole blood in heparinized capillary tubes centrifuged for 5 m (Centrifuge; Brinkmann Instruments, Ontario, Canada) at 10000 g and measured using digital callipers (± 0.01 mm). Hb (g/dL) was determined using the cyanomethemoglobin method (Drabkin and Austin 1932), where 5 μ l of fresh whole blood was pipetted (Gilson Pipetman P2; Gilson Medical Electronics, France) into 1.25 ml Drabkin's reagent (D541-6V, Brij 35 solution B4184-100ml; Sigma-Aldrich, Missouri, US). Samples were run in triplicate, and absorbance read at 540 nm by a microplate spectrophotometer (BioTek PowerWave 340, Vermont, USA). The inter-assay coefficient of variation was 1.70 % between plates.

2.2.3 Diving data analysis

To quantify TDR series, I extracted a set of diving metrics using the software Divebomb (1.0.7, Nunes 2019) in Python (3.4.10, Python Software Foundation 2019). Analysis was limited to dive behaviour within 40 days prior to when birds were re-captured. The maximum duration that the blood samples were likely representative of dives was based on the approximate rate of erythropoiesis in birds (30 – 42 days, Rodnan et al. 1956). Dive data were first zero-offset corrected for drift (Luque and Fried 2011). Dive metrics comprising dive start, dive duration, maximum depth, bottom time, and post-dive surface interval were identified. As I was interested in foraging efficiency, I discarded all dives shallower than 5 m, which were most likely associated with travelling (Kokubun et al. 2010, Lee et al. 2015, Carpenter-Kling et al. 2017).

Additionally data analysis only included post-dive surface interval (PDSI) < 200 s, a previously identified indicator of the end of a foraging previously identified for gentoo penguins, to eliminate inclusion of long surface periods not associated with active foraging (Kokubun et al. 2010, Lee et al. 2015). Correct determination of dive metrics was verified through visually inspecting 100 random dives across all individuals. Divebomb gave precise measurements of descent, bottom, ascent, and surface phases of dives 94 % of the time, with minor errors distinguishing the bottom phase in cases where undulations in depth occurred over the transition from descent or to ascent phases.

2.2.4 Behavioural observations

To assess the reproductive status of penguins, teams of two observers monitored breeding behaviour of marked birds. Individual presence at the colony was recorded daily at Race Point from September 27, 2018, to October 24, 2018, and Pebble Island from September 29, 2018, to October 24, 2018, through colony scans and monitoring arriving individuals until dusk (13h00 – 19h00). Focal follows were conducted for > 5 minutes on individuals observed in the colony and lasted until presence or absence of eggs in an occupied nest could be confirmed. Pair bonding behaviours monitored included nest building, copulation, pair calling, and pair bowing (Williams 1995). Due to a later than predicted initiation of the breeding season in 2018, lay date was unable to be acquired for most penguins, which would have provided a continuous metric to assess reproductive status. Thus, three categories of reproductive status were instead determined to be non-breeding (NB), breeding (B), and early laying (L) individuals. Penguins classified as non-breeders were found most often at different locations than nesting penguins, typically towards the edge of colonies, and rarely displayed pair-bonding behaviours. Penguins categorized as breeders were observed conducting pair-bonding behaviours at stable nest site locations. Early

laying penguins were observed to be incubating at least one egg within nests prior to my departure date from the colony, October 24, 2018.

2.2.5 Statistical analysis

All data analyses were performed using R (3.5.0, R Core Team 2018). Values presented in results are mean \pm SD unless otherwise noted, and statistical tests were considered significant at a 0.05 level. First, I assessed if different indices of higher blood oxygen-carrying capacity increased diving efficiency as an indirect measure of foraging ability. I defined dive efficiency as $\frac{\text{bottom time}}{\text{dive duration} + \text{PDSI}}$ (Simeone and Wilson 2003, Lescroël and Bost 2005, Lee et al. 2015).

Generalized additive mixed modelling (GAMM) were used to determine the relationship between diving efficiency at different maximum depths and various indicators of oxygen storage, represented by Hb, Hct and body mass. The models also tested for differences between colony locations and sex. Body mass was not scaled by a morphometric index, as mass alone has been determined as more ecologically relevant for most species and is more reliably measured (Schamber et al. 2009, Labocha and Hayes 2012). Prior to analysis, relationships between variables were investigated with scatter plots, boxplots, and Pearson correlation coefficients (PCC), to check for collinearity (Zuur et al. 2009, Dormann et al. 2013). No pairs of continuous variables had $|\text{PPC}| > 0.7$.

In the dive efficiency GAMM, a random intercept was included so that dives were nested by penguin ID. Temporal autocorrelation was assessed through the autocorrelation function (ACF) and reduced through sub-setting every 5th dive (20 % of data) and applying a correlation structure to residuals using an autoregressive-moving-average model (ARMA). ARMA combinations of autoregressive terms (p) 0, 1, 2 and moving average terms (q) 0, 1, 2 were tried,

with model selection based on the lowest Akaike's information criterion (AIC) resulting in $p = 0$ and $q = 1$ (Zuur et al. 2009). As data exploration had revealed non-linear patterns between dive efficiency and dive depth, a LOESS cubic regression splines smoother was used to model relationships with maximum dive depth. To investigate the interaction between depth regression splines and the indices of oxygen stores, Hb, Hct, and mass were included within splines to assess how the dive efficiency of penguins in different condition was affected by depth. Model selection included dropping covariates and interactions terms between depth and Hb, Hct and mass (Table 1). Models were ranked using AIC to determine the best fitting model (Zuur et al. 2009). Consideration was given to all models of $AIC < 4$ (Burnham and Anderson 2002). High dive efficiency can be achieved by either extending the bottom time and/or by reducing surface recovery between dives. To determine which behavioural trait most influenced dive efficiency for deep dives, individual mean post-dive surface interval and bottom times were compared between penguins with low (10-20 g/dL, $n=8$) and high (20-31 g/dL, $n=9$) Hb. Dive efficiency and Hb were positively related, hence apparent patterns should be identifiable through dividing the data from the median (Johnstone et al. 2017). Dives included occurred deeper than 140 m depth to capture the deep foraging cluster, and Welch's Two Sample t-test used to determine if differences between groups were significant at the 0.05 level. To determine if Hb influenced the choice of foraging dive depth, Welch's Two Sample t-tests were also used to compare individual proportions of dives below 140 m and 70 m in high and low Hb penguins.

Table 2.1 Dive efficiency GAMMs applied to TDR series from 19 gentoo penguins. The notation $f()$ signifies the term is modelled as a LOESS smoothing function.

Expression	df	AIC	Δ AIC
$f(d:hb) + f(d:hct) + f(d:m)$	13	-20344.33	-
$f(d:hb) + f(d:hct) + f(d:m) + s$	14	-20342.52	1.81
$f(d:hb) + f(d:hct) + f(d:m) + c$	14	-20342.35	1.98
$f(d:hb) + f(d:hct) + f(d:m) + s + c$	15	-20340.64	3.69
$f(d:hb) + f(d:hct)$	11	-20305.40	38.93
$f(d:hb) + f(d:hct) + m$	12	-20303.46	40.87
$f(d:hct) + f(d:m)$	11	-20297.32	47.01
$hb + f(d:hct) + f(d:m)$	12	-20295.48	48.85
$f(d:hct)$	9	-20247.48	96.85
$f(d:hb) + f(d:m)$	11	-20227.11	117.22
$f(d:hb) + hct + f(d:m)$	12	-20226.52	117.81
$f(d:m)$	9	-20141.89	202.44
$f(d:hb)$	9	-20109.01	235.32
$f(d)$	6	-20032.87	311.46

DE, dive efficiency; d, depth; hb, hemoglobin; hct, hematocrit; m, mass; s, sex; c, colony.

Second, to determine if pre-breeding dive behaviour changes between individuals based on their oxygen stores and breeding status, I investigated three measures of pre-breeding foraging effort; mean trip duration, time at sea, and diving effort. Trip duration was approximated using the saltwater sensor of the TDRs to obtain the proportion of time at sea. Binary wet-dry data was collected every second, and because penguins occasionally jump while swimming this creates brief periods where tags recorded dry conditions although the animal was still at sea. To prevent these anomalies from ending dive trips prematurely, wet-dry data were averaged over a 10-minute rolling window and any window with an average > 0 was classified as wet. A criterion of one hour with a dry sensor then terminated each trip, and subsequent trips began once the penguin returned to the sea. Time spent at sea was the sum of all trip durations within the 40-day period prior to re-capture. Last, to measure diving effort, I used a dive rate, defined as the total vertical distance travelled while penguins were at sea, calculated by

$$\frac{\sum \text{maximum depth (m)} \times 2}{\text{time at sea (d)}} \text{ (Lescroël and Bost 2005, Booth et al. 2018).}$$

Principal component analysis (PCA) was then used to quantify the individual variance in pre-breeding foraging effort. Subsequently, linear models were used to determine the best explanatory variables of the first (PC1) and second (PC2) principal components (Table 2, 3). Explanatory variables included indices of oxygen-carrying capacity, Hb, Hct, and body mass, as well as sex and reproductive status of individual penguins. I also investigated for a possible interaction between sex and reproductive status. Model selection included step-wise dropping covariates, and ranking models using AIC to determine the best fitting model (Zuur et al. 2009). Consideration was given to all models of $AIC < 4$ (Burnham and Anderson 2002). To avoid possible confounding effects of location on the metrics of foraging effort colonies were not

pooled together, and due to a limited sample size, only Pebble Island penguins were included in this analysis.

Table 2.2 Model selection on the linear model of the first principal component, with 49 % of explained variation in foraging effort, from the 14 gentoo penguins recaptured and blood sampled at Pebble Island.

Expression	df	AIC	Δ AIC
hb + hct + m + s	12	36.09	-
hb + hct + m	12	37.06	0.97
hb + hct + m + s + r	12	37.43	1.34
hb + hct + m + s + r + s:r	12	40.95	4.86
hb + hct + s	12	41.56	5.47
hct + m + s	12	42.45	6.36
hb + m + s	12	45.63	9.54

hb, hemoglobin; hct, hematocrit; m, mass; s, sex; r, reproductive status.

Table 2.3 Model selection on the linear model of the second principal component, with 42 % of explained variation in foraging effort, from the 14 gentoo penguins recaptured and blood sampled at Pebble Island.

Expression	df	AIC	Δ AIC
s + r	12	36.85	-
r	12	37.56	0.71
hb + s + r	12	37.96	1.11
hb + m + s + r	12	39.69	3.84
s	12	41.65	4.80
hb + hct + m + s + r	12	41.68	4.83
hb + hct + m + s + r + s:r	12	44.46	7.61

hb, hemoglobin; hct, hematocrit; m, mass; s, sex; r, reproductive status.

2.3 Results

2.3.1 Oxygen stores impact diving efficiency at depth

Out of the re-sighted penguins ($n = 35$), 23 TDRs were retrieved (8 Race Point, 15 Pebble Island) and blood samples were collected for 19 of these individuals (5 Race Point, 14 Pebble Island). For indices of oxygen storage, pre-breeding mass was 6.8 ± 0.6 kg (5.8 – 7.9 kg), Hb was 20.5 ± 5.0 g/dL (10.6 – 30.6 g/dL) and Hct was 49.3 ± 4.4 % (42 – 58 %) and as expected Hb and Hct were the most correlated indices (Fig. 2.2). In total, over the 40 days prior to capture, I recorded 124,682 dives (> 5 m depth) and 113,495 potential foraging dives with a post-dive surface interval < 200 s. Penguins spent an average of 130.0 ± 60.8 s submerged, with the maximum dive time recorded of 520 s occurring at a depth of 174.5 m, and an average of 56.6 ± 32.1 s in the bottom phase of dives, with the maximum bottom time of 228 s occurring at 45.3 m. Mean individual dive efficiency was 0.30 ± 0.03 (0.26 – 0.38). Penguins dove to a mean maximum depth of 166.4 ± 28.7 m that varied substantially between individuals (74.8 – 217.8 m). Across all dives, clusters of dive depths occur in shallow depths below 10 m, in mid-range depths around 40 m and 60 m, and in deep depths of ~ 150 m (Fig. 2.3).

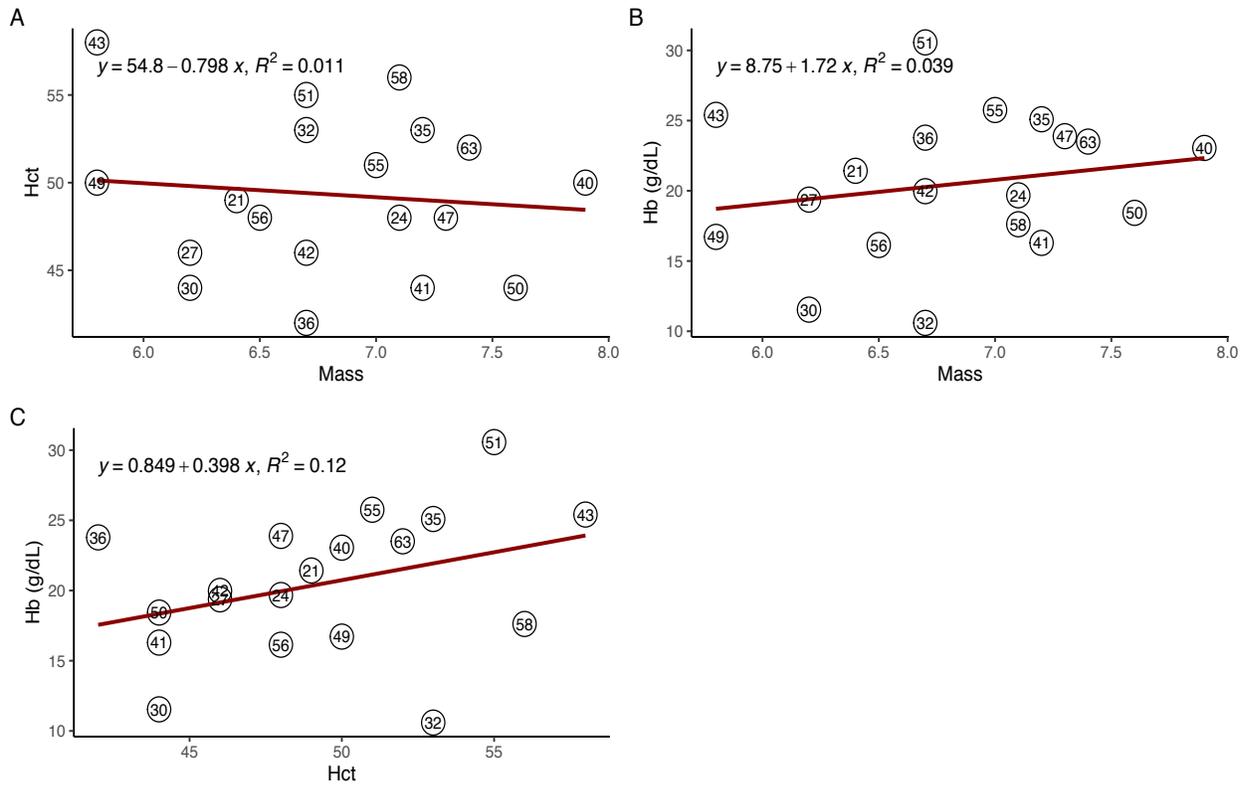


Figure 2.2 Correlation between indices of oxygen storage (A) Hematocrit (Hct) and body mass (mass), (B) Hemoglobin (Hb, g/dL) and mass, and (C) Hb and Hct for all 19 gentoo penguins.

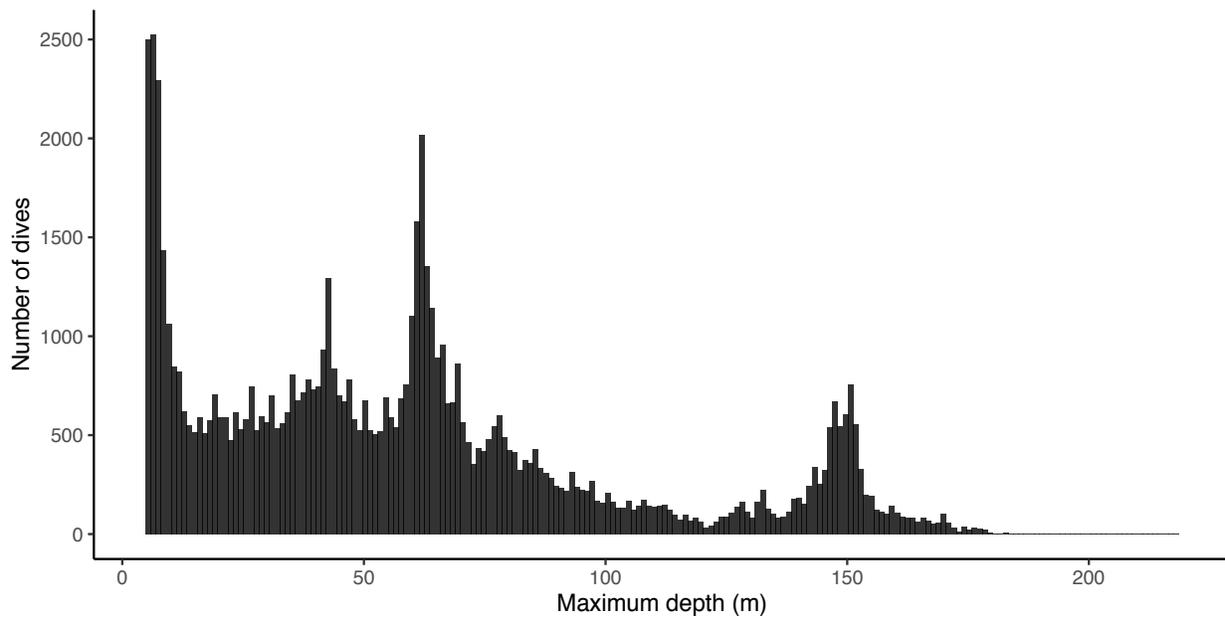


Figure 2.3 Distribution of maximum dive depths performed by 19 penguins over 40 days (5 Race Point, 14 Pebble Island, Falkland Islands).

The best fitting GAMM for dive efficiency was a model where all three condition indices of oxygen storage (Hb, Hct, and mass) were selected to have significant interaction with the depth of dives within LOESS smoothing functions (Table 2.1). All other models with $\Delta\text{AIC} < 4$ included the same three interactions as well but were more complex models. Across all interaction surfaces, dive efficiency was low in very shallow dives before increasing to a maximum dive efficiency at approximately 50 m in depth across variations in the indices of oxygen storage (Fig. 2.4).

Most striking was the interaction between depth and the indices of blood oxygen-carrying capacity at deeper depths. Penguins with higher Hb were observed to have significantly improved diving efficiency, especially when diving deeper than 100 m ($F_{12.93} = 5.008$, $P < 0.001$). Similarly, those with lower Hb had notably decreased efficiency at deeper depths. Interestingly for Hct, all values had similar dive efficiency at 100 m depth, but in deeper depths both high and low Hct perform poorer than mid-level Hct ($F_{14.96} = 9.117$, $P < 0.001$). At depths around 150 m, peak performance occurred for penguins of approximately 52 % Hct. For mass, heavier individuals performed only moderately more efficient than lighter individuals between 80-150 m in depth ($F_{18.26} = 6.964$, $P < 0.001$).

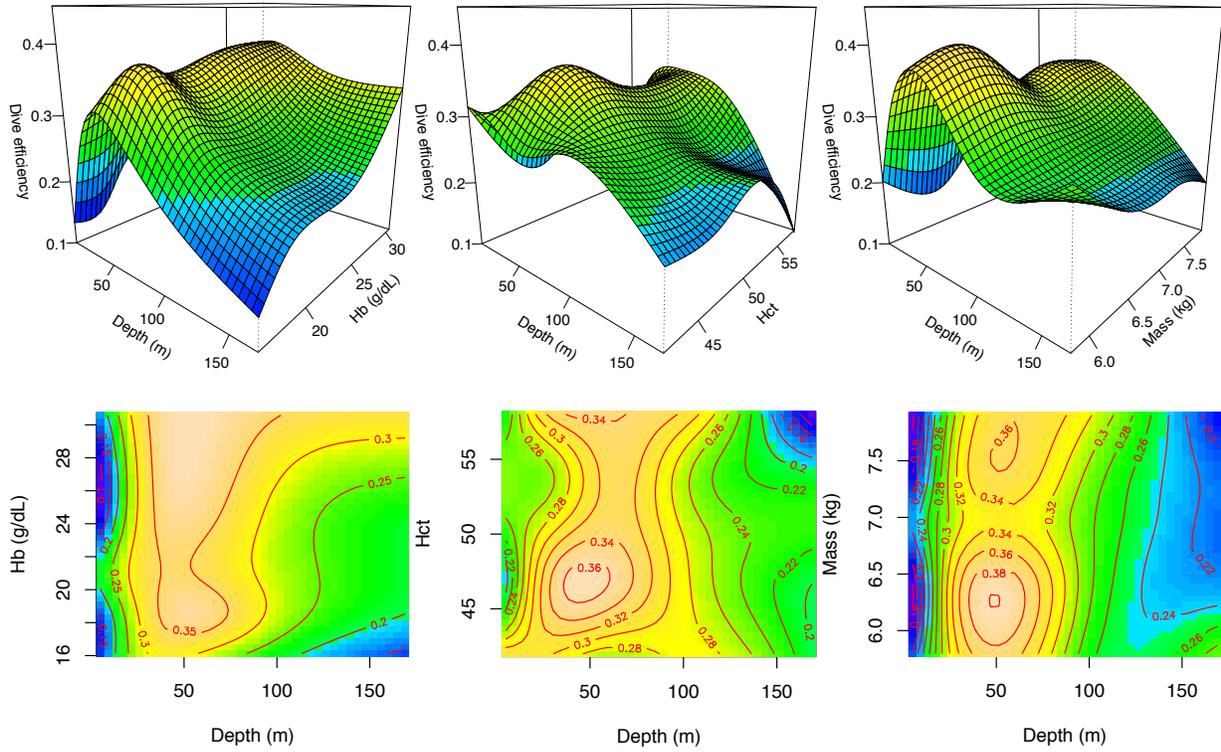


Figure 2.4 GAMM 3D interaction surfaces (top) and contour plots (bottom) for LOESS smoothing functions between dive depth (m) and hemoglobin (Hb, g/dL, A), hematocrit (Hct, %, B), or mass (kg, C). Red lines in contour plots represent dive efficiency values, where yellow is high dive efficiency and blue is low dive efficiency.

The difference in dive efficiency in dives that exceed 140 m was explained by penguins altering the bottom time of dives and was also related to the aforementioned differences in physiological variables. For example, deep diving penguins with low Hb 10-20 g/dL (n=8) spent only 73 ± 7 s at the bottom, while penguins with high Hb 20-31 g/dL (n=9) spent 89 ± 11 s ($t_{13.82} = -3.622$, $P < 0.01$). Post-dive surface interval recovery across all Hb levels remained similar (121 ± 21 and 125 ± 16 s respectively; $t_{13.09} = -0.415$, $P = 0.68$, Fig. 2.5), and attributed less than bottom time to the differences in calculated diving efficiency between high and low Hb penguins. Hemoglobin concentration also influenced the behaviour of penguins. From the cluster of deep foraging dives below 140 m, 71% of dives (n = 7356) were performed by penguins with Hb above 20 g/dL. Proportionately, individuals with high Hb performed 18 ± 13 % of dives to depths below 140 m whereas only 6 ± 3 % of low Hb penguins dove below 140 m ($t_{8.951} = -2.700$, $P < 0.05$, Fig. 2.6). Even when considering foraging dives below 70 m, penguins with low Hb performed significantly fewer dives below this depth (21 ± 14 %) than high Hb penguins (41 ± 15 %, $t_{16.38} = -2.870$, $P < 0.05$, Fig. 2.6).

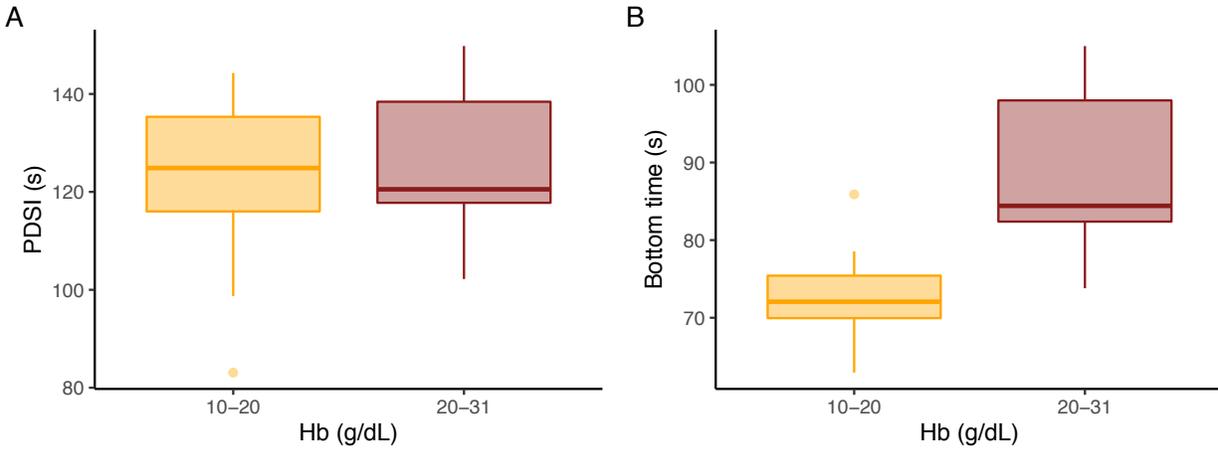


Figure 2.5 Differences between individual means of post-dive surface interval (PDSI, A) and mean bottom time (B) between low (10-20 g/dL, n=8) and high (20-31 g/dL, n=9) hemoglobin (Hb) gentoo penguins. Dives included occurred between 140-160 m depth based on the cluster of deep foraging depths.

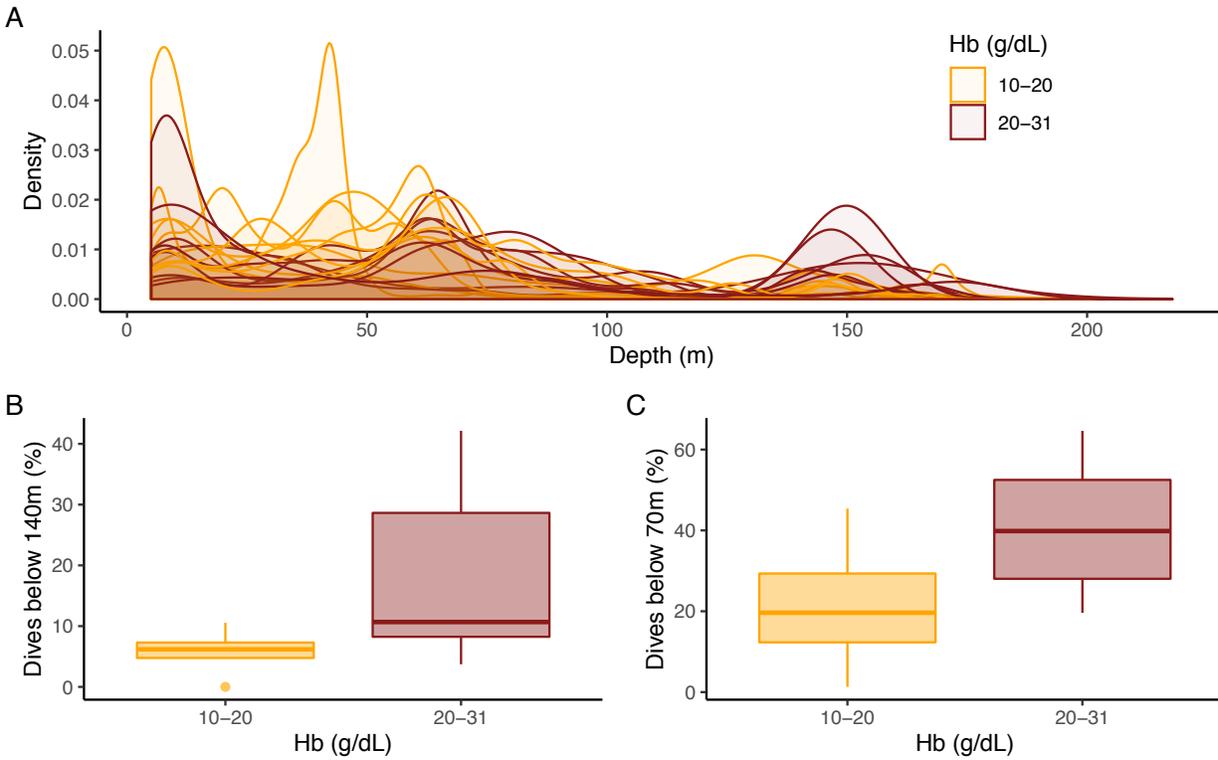


Figure 2.6 Density distributions of maximum depth (A) comparing low (10-20 g/dL, n=8) and high (20-31 g/dL, n=9) hemoglobin (Hb) gentoo penguins. Differences between individual means of the proportion of dives with a maximum depth below 140 m (B) and 70 m (C) deep are also shown.

2.3.2 Foraging effort influenced by oxygen stores and reproductive status

As just 5 Race Point penguins were recaptured with successful blood samples, it was decided to assess only the Pebble Island colony ($n=14$) for connections between foraging effort, oxygen stores, and reproductive status. Behavioural observations resulted in classification of 4 individuals as non-breeders (NB), 6 breeders (B), and 4 early laying (L) individuals, with 8 males (1 NB, 4 B, and 3 L), 5 females (3 NB, 1 B, and 1 L), and one penguin of undetermined sex (1 B). Over the 40 days pre-breeding, penguins spent an average of 23.2 ± 4.3 days at sea ($14.4 - 30.2$ days) and mean diving effort was 23.0 ± 7.3 km/day while at sea ($10.6 - 36.1$ km/day). Penguins went on 13 ± 4 trips, for which mean trip duration lasted 2.6 ± 3.5 days at sea. While 69.8 % of all trips lasted under one day, 9.0 % lasted over five days in length, with the longest trip spanning 24.3 days.

The first principal component (PC1), explaining 49 % of variation between individuals, partially describes variation in all 3 metrics of foraging effort and accounts for almost all variation in trip duration (Fig. 2.7). All models for PC1 with $\Delta\text{AIC} < 4$ had all three indices of oxygen storage: Hct, Hb, and mass. Individuals that spent less time at sea with shorter trip durations but increased diving effort had higher Hct ($t_{12} = 3.382$, $P < 0.001$) and higher mass ($t_{12} = 2.493$, $P < 0.05$), while higher Hb was associated with less diving effort and longer time at sea and trip durations ($t_{12} = -2.686$, $P < 0.05$). While the best model according to AIC included sex as a covariate, the second-best model, with ΔAIC of only 0.97, had all other covariates but did not include sex (Table 2.2). The second principal component (PC2) described the variation in penguins with high diving effort spending more time at sea and explaining 42 % of variation between individuals. Reproductive status occurred in all models with $\Delta\text{AIC} < 4$, with the earliest

laying penguins significantly different ($t_{12} = -2.666$, $P < 0.05$) from both breeding and non-breeding penguins, which were not different from each other ($t_{12} = -0.666$, $P = 0.52$). Although according to AIC sex was again included as a covariate in the best model, it was not significant ($t_{12} = -1.454$, $P = 0.18$) and the second-best model, with ΔAIC of only 0.71 did not include it (Table 2.2).

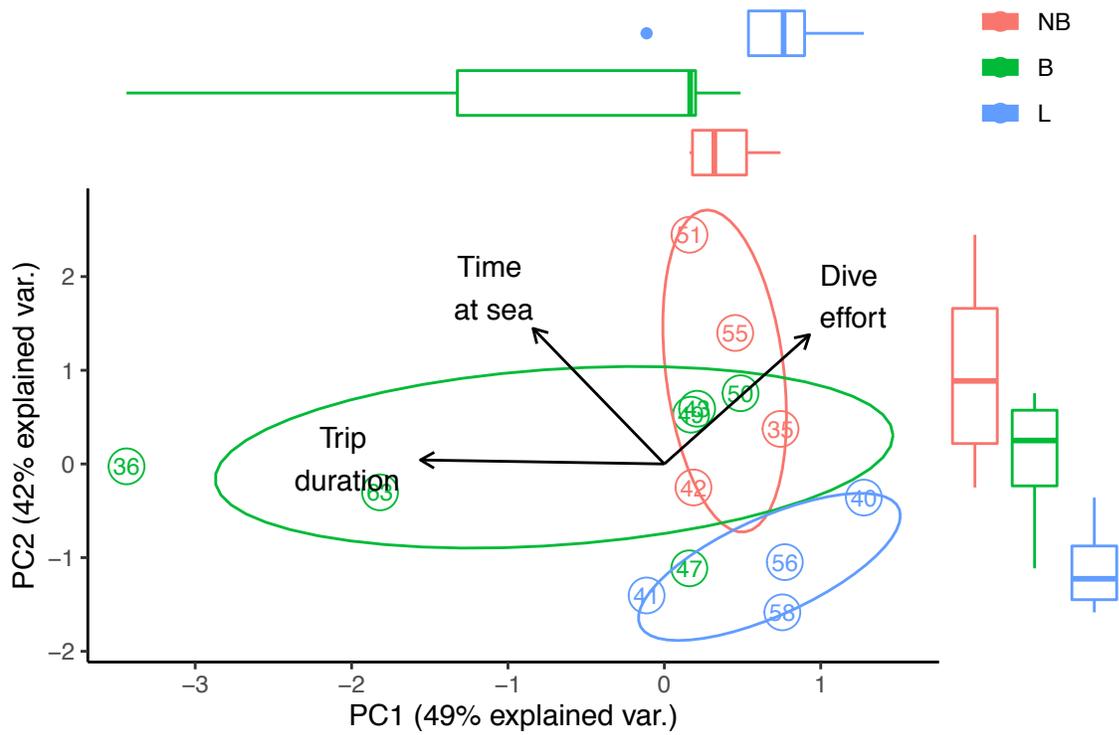


Figure 2.7 Principal component analysis of foraging effort performed by 14 gentoo penguins in the pre-breeding period from the Pebble Island colony. Differences in effort spent by penguins in different stages of reproductive status are highlighted between earliest laying penguins (L), breeding penguins (B), and non-breeding penguins (NB).

Table 2.4 Significance of linear model coefficients for PC1 (2.3) and PC2 (3.5) models.

Model	Coefficient	Estimate	SE	t_{12}	p -value
2.3	Hct	0.1839	0.05438	3.382	0.00961 **
	Hb	-0.1721	0.06406	-2.686	0.0277 *
	Mass	0.9703	0.3892	2.493	0.0374 *
	Sex: M	-0.8004	0.5587	-1.433	0.190
	Intercept	-11.43	4.308	-2.654	0.0291 *
3.5	Reproductive status: B	-0.4151	0.6229	-0.666	0.522
	Reproductive status: L	-1.699	0.6373	-2.666	0.0258 *
	Sex: M	-0.7831	0.5386	-1.454	0.180
	Intercept	1.188	0.4301	2.762	0.0220 *

2.4 Discussion

The central goal of this chapter was to explore how differences in pre-breeding diving behaviour related to indices of oxygen storage and breeding participation. Diving performance is essential to foraging ability, survival, and reproduction, and traits related to improved foraging ability also likely to improve individual quality (Roncon et al. 2018). In gentoo penguins, diving efficiency was correlated with indicators of blood oxygen-carrying capacity. Especially for dives below 100 m in depth, penguins with high Hb experienced greater diving efficiency than low Hb penguins. Penguins with midrange Hct also had improved diving efficiency at depth than those with low or high values, likely as a result of high Hct increasing blood viscosity and restricting blood flow. The consequence of reduced blood oxygen-carrying capacity was evident in the proportion of deep foraging dives across individuals, as penguins with lower Hb executed shallower dives. Indices of oxygen storage were also correlated with foraging effort in trip duration, time at sea, and diving effort exerted during the pre-breeding period. Penguins with advanced reproductive status spent less time at sea and had lower diving effort than non-breeding penguins and I will further explore these associations below.

2.4.1 Impact of oxygen stores on diving efficiency and foraging

The diving efficiency of gentoo penguins was influenced by the condition of individual oxygen stores. Consistent with previous evidence of blood oxygen-carrying capacity being essential to breath-holding divers, I found high levels of Hb were associated with increased diving efficiency. This relationship was more prominent during deeper dives. This is logical, as Hb limits the total amount of oxygen able to be carried by the blood (Minias 2015). Mass was found to moderately influenced diving efficiency as well, although the relationship was not as clear.

Also pertinent is the discovery of the bell-shaped relationship between Hct and diving efficiency that becomes apparent after 130 m in depth. This shape suggested gentoo penguins have an apparent optimum Hct value for diving to deep prey, where penguins with Hct at approximately 52 % outperformed both higher and lower values. Hct increases linearly with the number of oxygen-carrying red blood cells, but it also exponentially increases blood viscosity causing either increased cardiac workload or decreased blood flow (Birchard 1997, Schuler et al. 2010, Reinhart 2016). In most research employing Hct as an index of condition, higher values are often assumed to be indicative of better physiological performance (reviewed in Fair et al. 2007, Minias 2015). From my results, this appears not to be the case as high Hct penguins performed inferior at deep depths with lower diving efficiency. The complex relationships between red blood cell count, blood flow, and cardiac workload need to be considered to assess the influence of Hct on condition accurately. It is important to be mindful when extrapolating these findings that Hct levels for optimum body functioning differ between individuals, as numerous factors such as age and disease influence individual ideal Hct levels (Reinhart 2016, Johnstone et al. 2017). Nevertheless, I have revealed an apparent optimum Hct for maximizing the diving efficiency of gentoo penguins at depth, and this is useful in interpreting the ecological significance of Hct values.

Improved dive efficiency is important to gentoo penguins for two main reasons. First, higher dive efficiency increases the time available to search for and capture prey during foraging trips, and second, it improves access to resources available at deep depths and potentially reduces intraspecific competition. For a given dive duration, dive efficiency will increase with increasing bottom time and decreased surface recovery time. Surface recovery is largely determined by the amount of oxygen consumed during the dive that must be replenished, which is related to energy

expenditure (Shepard et al. 2009). As post-dive surface recovery was not different between high and low Hb groups, it can be assumed penguins with lower blood oxygen-carrying capacity take approximately the same time to recover their oxygen stores. Hence, a delay in subsequent dives did not significantly influence diving efficiency during foraging bouts. Rather, changes in efficiency were largely the result of an increased proportion of the dive time spent as bottom time. Increased bottom time directly translates into time spent where prey is most likely to be encountered. For dives below 140 m, penguins with high Hb (20-31 g/dL) increased their mean bottom phase of by 22 % from penguins with low Hb (10-20 g/dL). Prey are almost always encountered during the bottom phase of dives (Simeone and Wilson 2003, Takahashi et al. 2004, 2008, Kokubun et al. 2010), thus increasing bottom time likely increases the chance of foraging success at deeper depths.

According to optimal foraging theory, penguins should dive in order to maximize their bottom time and minimize energy spent travelling down to where prey is located (Stephens and Krebs 1986, Wilson et al. 2010, Zimmer et al. 2010). Strategically, shallow dives should be preferred, as they require less travel time and energy to swim down to depth (Shepard et al. 2009, Zimmer et al. 2010). This pattern was apparent in my data, as peak dive efficiency occurred in shallow foraging habitat at approximately 50 m deep. Optimal dive efficiency of 25-30m has been previously reported for gentoo penguins (Lee et al. 2015). The small discrepancy is likely due to differences in colony locations or the timing of monitoring, as breeding penguins with hatched chicks are constrained closer to shore, possibly anemic from reproducing, and may have experienced seasonally different prey. So, why did some penguins choose to forage beyond the depths of highest dive efficiency and expend more energy to dive deep (e.g., Wilson et al. 2010)? The answer may be related to the availability of energy rich prey at depth, for deeper dives are

only profitable when prey capture rates, size, or caloric value outweigh the energetic costs of diving (Sala et al. 2014b).

Clausen et al. (2005) compared the diet of gentoo penguins in colonies around the Falkland Islands with surveys of prey abundance during the 2000 pre-breeding season. They highlight preferential foraging of squid and fish over krill, a shift that has also been highlighted in the historical diet of gentoo penguins (McMahon et al. 2019). Based on information from colonies close to my research location, prey likely to be essential for Pebble Island and Race Point penguins include benthic-demersal lobster krill, *Munida spp.*, found in depths 26-116m, and squid, *Loligo gahi*, found at depths 60-96m, both of which were in high abundance close to the colonies in 2000 (Clausen et al. 2005). A deeper squid species, *Moroteuthis Ingens*, 100-166m, and various rockfish, Patagotothen spp., 40m-205m, were also found abundant further offshore and found in their diet (Clausen et al. 2005). In a more recent assessment of prey, rockfish was found to be a principal prey item for gentoo penguins in the Falkland Islands (Handley et al. 2016). Generally for marine species, prey size increases with depth (Masello et al. 2010, Miller et al. 2010). Thus, deeper dives may provide greater access to larger prey that may be more valuable to gentoo penguins than the smaller prey in shallower habitat.

Not only are penguins with lower blood oxygen-carrying capacity limited in foraging bottom time, but it appears deeper foraging strategies are costly enough to discourage penguins of low Hb to forage regularly at those depths. The vast majority of dives below 140 m deep were performed by high Hb penguins, and high Hb penguins dove below 140 m three times more (18 %) often as low Hb penguins (6 %). Low Hb penguins performed an average of 20 % of dives deeper than 70 m, whereas high Hb penguins performed twice as many dives, 41 %, deeper than 70 m. Similar findings have been documented in macaroni penguins, *Eudyptes chrysolophus*,

where penguins select foraging habitat within their aerobic capacity to reach (Crossin et al. 2015). Although I can only speculate what individuals observed in this study were foraging on, it is clear that penguins with higher blood oxygen-carrying capacity may have access to a wider variety of prey items and likely experiencing less competition from diving deeper (e.g., Cimino et al. 2016). Physiological indicators for birds have previously been associated with greater variation in diet (e.g., Storey et al. 2017), and Hb has also been specifically correlated with higher quality diets (reviewed in Minias 2015). Sub-optimal blood oxygen-carrying capacity and aerobic performance is then likely to restrict the foraging niches of individuals by limiting access to resources at depth.

One potential confounding variable is related to the assumption that animals typically dive to their ADL each foraging dive independent of their prey. This simplistic view of complex animals is inherently flawed and does not account for the numerous factors influencing dive time and efficiency, for example, predators adapting foraging strategies based on prey conditions (e.g., Magellanic penguins, *Spheniscus magellanicus*; Sala et al. 2014a). Diving animals may additionally modify foraging behaviour based on prey abundance, where dives in poor prey conditions are abandoned early (e.g., Thums et al. 2013, Viviant et al. 2016) and thus do not reflect the ADL of individuals. While these concerns are valid, a large volume of dives were included in this analysis where prey and other environmental conditions encountered were accounted for within average dive times. Furthermore, deep diving is more energetically costly to undertake (Shepard et al. 2009, Zimmer et al. 2010). For this reason, prey conditions become less important and the influence of total body oxygen stores on the behaviour of diving animals becomes more apparent when deciding to forage at deeper depths (Thompson and Fedak 2001, Viviant et al. 2016).

2.4.2 Hemoglobin and hematocrit as indices of blood oxygen-carrying capacity

While Hct and Hb are both associated with oxygen-carrying capacity, they were not found to be closely correlated in my results. This contrasts with expectations where a correlation between Hct and Hb was anticipated because mature red blood cells (RBCs) have similar amounts of Hb. Values of both Hb and Hct align with previously reported values for gentoo penguin: mean Hb of 20.5 ± 5.0 g/dL closely associates to 20.7 ± 1.6 g/dL and the mean Hct 49.3 ± 4.4 % aligns well with 50 ± 4 % (Ibañez et al. 2015, n=26). Both measures were within expected ranges, and while the weak correlation found is noteworthy it is not completely unexpected. Weaker correlations have been documented, particularly in other seabird species (e.g., Kaliński et al. 2011), as Hct and Hb are affected differently by ecological stressors (Bańbura et al. 2007, Wagner et al. 2008, Johnstone et al. 2017).

Possible explanations for the disassociations between Hb and Hct in the data lie in the underlying condition of the penguins. Anemic birds with low Hb concentrations can attempt to improve it through actively regenerating red blood cells, or they may be unable to improve their condition in more severe situations (Jaensch and Clark 2004, Fair et al. 2007, Campbell et al. 2010). In the second case, Hb and Hct could remain closely correlated, but this is may be affected by erythropoiesis, the production of new RBCs. Erythropoiesis increases the number of immature red blood cells that are larger in size and initially have lower Hb content, disproportionately increasing Hct but not Hb (Wagner et al. 2008, Campbell et al. 2010, Johnstone et al. 2017). In my study, a non-breeding penguin (number 32) had the lowest Hb and yet the 4th highest Hct (Fig. 2.2). Further evidence for a state of poor condition, this same penguin was the only individual in my study to have lost mass between April and October measurements (Fig. A1). While the cause of poor health can only be speculated, as no signs of

injury were evident at the time of re-capture, individuals of compromised health will influence the ratio of Hb to Hct (reviewed in Johnstone et al. 2017). Health conditions can cause more permanent anemic states, such as heavy parasite loads or severe injury (Vleck et al. 2000, Jaensch and Clark 2004, Fair et al. 2007, Clark 2015). Measuring multiple indices of oxygen-carrying capacity allows us to assess individual health better (Johnstone et al. 2017).

2.4.3 Foraging effort, oxygen storage, and reproductive status.

While the previous results indicate the benefit of high Hb and optimum Hct values on a penguin's ability to dive efficiently, the next question we must ask is whether it also makes them more efficient foragers. For the Pebble Island colony, indices of oxygen storage were found correlated to foraging effort during the pre-breeding period, with Hb, Hct, and body mass all relating to the broader patterns of foraging detected within PC1. Hemoglobin was positively associated with trip duration and more time spent at sea, but also exerting less diving effort, defined as the total vertical distance travelled while penguins were at sea. These results likely align with a deeper diving strategy for higher value prey items that requires longer horizontal travel time to reach deep water further from shore. In contrast, Hct and mass increased with vertical diving effort but spending less time at sea with shorter trip durations. Therefore, variation in foraging effort may align with the unique foraging strategies that penguins in different conditions of oxygen storage exhibit.

A prominent feature of PC1 was trip duration, which accounts for most of the variation in this axis. Trip duration is interesting as shorter trips are thought to be associated with higher foraging efficiency and breeding success (Daunt et al. 2006, Horswill et al. 2017, Masello et al. 2017). While PC1 did not relate to reproductive status, both breeding penguins 36 and 63 had noticeably longer mean trip durations than other penguins, which was unexpected as they were

both observed later to be participating in breeding. When further investigating the data, it was found that many individuals performed long trip durations, particularly at the beginning of the 40 days observed before recapture, as 43 % of individuals went on trips longer than 10 days. The higher mean trip durations for 36 and 63 was more a factor of undergoing fewer shorter trips at the end of the 40-day period before recapture, 3 and 7 total trips respectively, when the average penguin went on 13 ± 4 trips. Long trip durations such as these have been rarely reported for gentoo penguins and may be evidence of a pre-breeding exodus (e.g., Mallory et al. 2008).

PC2 indicated that differences in foraging effort regarding time at sea and diving effort were predictive of eventual reproductive status. Gentoo penguins who laid early spent significantly less time at sea than non-breeding penguins. The successful acquisition of resources is essential as the quality of diet relates to earlier laying, which is assumed to also influence reproductive success (Sorensen et al. 2009). It is interesting that the earliest breeding penguins spent the least amount of time at sea, especially as they should have higher energetic requirements than non-breeding individuals for nest defense and egg production in females (Williams 2012). This difference in foraging effort is potentially indicative of having high foraging efficiency, where less time is required to meet energetic demands, as well as potential competing social obligations involved in breeding. More successfully breeding Adélie penguins were also found to be more efficient foragers (Lescroël et al. 2010). Previous work has also found high diving activity related to lower breeding success (Masello et al. 2017), skipped breeding (Shoji et al. 2015), and lower population growth (Sala et al. 2014b) in other seabird species.

Social constraints that require breeding penguins to spend more time on land could also affect their foraging behaviour, but it was not likely to be a significant reason for the at-sea times

seen in this study. Participating in breeding compels individuals to defend nest locations and partake in pair-bonding behaviours, requiring many species of penguins to fast during this time (Williams 1995). While gentoo penguins do not fast during breeding, they still must maintain a nest site for approximately two weeks before egg-laying which increases their time spent on land (Black 2016). Egg production lasts 16-20 days in penguins (Grau 1982, Astheimer and Grau 1990). All monitored gentoo penguins, except one non-breeder, were captured at least 11 days (14.5 ± 2.2 days, September 30 to October 07) before eggs were first seen in the colony on October 18. By the last observation on October 23 approximately one-quarter of the Pebble Island colony nests had eggs. Towards the end of the 40-day TDR observation period, penguins that became breeders and laid first may have spent more time on land, but it also seems likely that higher-quality individuals achieved their food requirements in less time during the pre-breeding period (Daunt et al. 2014).

While none of the indices of oxygen storage were selected for in the final PC2 model, mass and Hb were included in comparable models with $AIC < 4$. Non-breeding penguins weighed on average 93 % the mass of the earliest laying penguins. Similar results were documented in Adélie penguins, where non-breeding individuals were 90 % the mass of breeders (Vleck and Vleck 2002). Hb has been shown in many bird species, and particularly in females, to correlate with earlier breeding and other fitness traits (reviewed in Minias 2015). With a larger sample size, stronger associations between condition and breeding may have been observed by separating sexes, as their physiology is affected differently by breeding (Williams 2012, Desprez et al. 2018). While breeding numbers in 2018 were above average for gentoo penguins (Stanworth and Crofts 2019), in a harsher year, inadequate environmental conditions may also amplify the consequences of inferior foraging strategies and show more apparent impacts on

condition (Fronstin et al. 2016). In summary, reproductive status was correlated to foraging patterns, where early laying penguins spent less time at sea and exerted less diving effort than penguins that defer breeding, but this was not significantly related to any index of the condition of oxygen stores observed here. Monitoring the link between pre-breeding foraging strategies and breeding participation across seasons of variable environmental conditions would provide better insight into why some individuals defer breeding.

2.5 Conclusion

Seabirds are long-lived and favour conservative breeding strategies prioritizing their survival when conditions are sub-optimal for breeding (Storey et al. 2017). Here, I confirmed that variation in the oxygen stores of gentoo penguins affects their dive efficiency and foraging behaviour. Higher Hb was related to an increased tendency to forage at deeper dive depths, along with an apparent optimal Hct of approximately 52 %. The discovery of a non-linear relationship between Hct and diving efficiency, in particular, helps to inform some of the key limitations involved in using Hct as an indicator of blood oxygen-carrying capacity and individual condition (Johnstone et al. 2017). Variation in foraging effort during the pre-breeding period was related to individual oxygen stores even when looking at coarse summary metrics of behaviour. Pre-breeding behaviour was related to the eventual reproductive status of gentoo penguins, where deferred breeders spent more time at sea and expended more vertical diving effort. Foraging is an essential activity to survival and understanding how blood oxygen-carrying capacity and body mass impacts dive performance and foraging habitat selection is vital to comprehending foraging ecology. How diving behaviour, foraging effort, and condition correspond to breeding participation is essential to understand the effects natural and anthropogenic ecosystem changes can have on populations.

Chapter 3: Conclusion

3.1 Summary of Findings

The goal of my study was to understand how variation in individual diving behaviour in gentoo penguins relates to their oxygen stores and breeding decisions. Gentoo penguins exhibit high interindividual variation in diving and foraging behaviour (Polito et al. 2015, Camprasse et al. 2017, Herman et al. 2017), which can influence their condition and reproductive investment (Ceia and Ramos 2015). Diving ability is essential to the foraging success of penguins and other air-breathing divers (Roncon et al. 2018). The ability to dive efficiently is partly reliant on the capacity to store oxygen, where the disparity in oxygen-carrying-capacity influences the physiological performance and diving ability of individuals (Dzal et al. 2015). To better understand interindividual variation in diving behaviour, I assessed how indicators of oxygen storage were correlated with the diving ability and selection of foraging depth in penguins as well as their breeding participation.

This thesis explored two questions in chapter 2. First, I focused on how variation in dive efficiency correlated with blood oxygen-carrying capacity and body mass. I attached post-moult penguins with TDR devices to observe foraging behaviour throughout the winter until the subsequent breeding season. I then measured their diving efficiency, depth preference and foraging effort as well as collected information on body mass through measuring post-moult and pre-breeding mass and assessed their pre-breeding levels of blood oxygen-carrying capacity using Hb and Hct. I explored how Hb, Hct, and mass influenced a penguin's ability to dive efficiently over their natural range of foraging depths. Hb was found to have the most considerable influence on diving efficiency and a penguin's ability to maximize bottom time. While higher mass also improved diving efficiency to a small degree, medium Hct levels was

associated with the greatest diving efficiency which was reduced at high or low Hct values. The presence of an apparent optimum Hct for diving efficiency highlights the need for the relationships between red blood cell count, blood flow, and cardiac workload to be considered when interpreting Hct as a proxy of blood oxygen-carrying capacity.

Subsequently, I sought to explore how interindividual variation in pre-breeding diving behaviour and foraging effort expended during the pre-breeding period related to oxygen storage and breeding participation. Blood oxygen-carrying capacity and body mass were correlated to foraging effort exerted during the pre-breeding period. Penguins with high Hb had longer trip durations, spent more time at sea, but exhibited less diving effort, while for mass and Hct, the opposite was found. This variation in foraging effort may align with different foraging strategies. As reproductive status was not involved in this axis of variation, either strategy seemed to be adequate for breeding in 2018. Foraging effort, in terms of time at sea and diving effort, was however correlated with the eventual reproductive status where early laying penguins exerted less foraging effort during pre-breeding. Further monitoring across seasons of variable environmental conditions would further our understanding of factors influencing the decision to breed.

3.2 Strengths and weaknesses

The ability to monitor at-sea behaviour is only possible through technological advances that allow the attachment of recording devices like TDRs (Wilmers et al. 2015). As such, one limitation with any study utilizing devices fastened to animals is whether the effect of tags, in terms of discomfort or drag, influenced the behaviour, energy expenditure, or condition of animals (Wilson et al. 1986, Vandenabeele et al. 2015). In my study, the potential influence of devices was limited through a streamline design and attachment in a caudal position shown to

minimize drag (Bannasch et al. 1994). Furthermore, the overall weight of devices was $< 1\%$ of the average body mass recorded, and larger devices have been seen not to impact foraging behaviour (Kokubun et al. 2010). However, tags were deployed for an extended period, where negative impacts could be amplified. To investigate the potential impact of our tags, I also assessed the oxygen stores and breeding behaviour of control individuals ($n = 20$) that were caught after every tagged individual was recaptured ($n = 20$) on Pebble Island. The mean mass of penguins with tags (7.0 kg) was 5% lighter than those without (7.3 kg). However, control and tagged individuals did not significantly differ in their mass ($t_{33.34} = -1.928$, $P = 0.0625$), Hb (21.6, 21.0; $t_{36.74} = 0.456$, $P = 0.651$), or Hct (49.3, 49.2; $t_{37.83} = 0.0708$, $P = 0.944$). Tagged and control penguins also had no significant difference in reproductive status with similar ratios of non-breeding, breeding, and early laying individuals (Likelihood ratio G-test, $G_2 = 1.042$, $P = 0.594$). Therefore, carrying TDR devices did not appear to significantly affect the blood oxygen-carrying capacity, body mass, or breeding behaviour of gentoo penguins.

All indicators of individual conditions are limited in the amount of information they contain. One advantage in my study design was to include multiple indices of oxygen storage through measuring two metrics of blood oxygen-carrying capacity, Hb and Hct, as well as body mass. Many studies use mass as a proxy of energy stores of individuals, but mass alone may not be a sensitive enough indicator to represent the true underlying health of animals (Williams 2012). The inclusion of measuring blood oxygen-carrying capacity improves our ability to estimate the physiological condition of individuals. It is common for research to only report either Hct or Hb when inspecting physiological performance (Fair et al. 2007, Minias 2015). More often, Hct is chosen due to its more efficient method of assessment in the field and reliability of measurements (Fair et al. 2007). However, as Hct measures the percent volume of

erythrocytes, it is less directly associated with oxygen-carrying capacity, as the age and capacity to bind oxygen of cells are not accounted for. Measurements of Hb provide a more accurate representation of oxygen binding ability within the blood but also require a high degree of pipette precision where human-caused error can be introduced to samples (Minias 2015). Triplicating samples of both Hct and Hb in the field would increase confidence in measures but require larger blood samples. Despite the limitations of Hb and Hct, both metrics are useful as indicators of blood oxygen-carrying capacity and physiological performance, and future work should continue to compare them (Wagner et al. 2008, Campbell et al. 2010, Minias 2015, Johnstone et al. 2017). Extending the hematological effort to include more detailed blood profiles, and measuring myoglobin concentrations to assess the oxygen storage within the muscle tissue of individuals, would help complete the assessment of total body oxygen (Johnstone et al. 2017). Other physiological mechanisms possibly involved in carryover effects could also be explored for a more in-depth assessment of how pre-breeding condition and performance influence reproductive status (Williams 2012, Fowler and Williams 2017). Measuring multiple indices of condition together increases their usefulness as indicators and allows us to evaluate the individual quality of animals better (Williams 2012, Johnstone et al. 2017).

Working in the field with wild animals additionally has many inherent challenges, of which I will mention three encountered in my research. First, the sample sizes at Race Point and Pebble Island colonies were smaller than hoped, as many TDRs were lost throughout the winter, and only one-third of devices were recovered. Now that the recapture probability of extended deployments on gentoo penguins is more clearly known, concentrating all 66 tags in one location would be logical if repeating a study of similar design. Avoiding the division of tags makes retrieval more feasible, as only one colony is required to be monitored, and a larger sample size

would allow for a more in-depth exploration of how sexes differ in their pre-breeding foraging effort and how their diving correlates with reproductive status. Second, Pebble Island and Race Point colonies differed substantially in their reproductive status, as no penguins at Race Point laid before October 24. Although Pebble Island and Race Point gentoo penguin colonies are only 27 km apart, other colonies even 5 km apart show asynchronous breeding by up to 2 weeks (Williams 1990). This asynchrony makes comparing the reproductive status of individuals between colonies challenging to isolate from potential confounds relating to differences in location. Finally, reproductive status is better assessed as a continuous metric instead of categorically. Even penguins seeming to participate in breeding may not all produce eggs, which occurred in 5/61 breeding pairs of Adélie penguins (Vleck and Vleck 2002). In this study, the initiation of breeding was later than anticipated, but since gentoo penguins are known to be particularly flexible in the timing of their reproduction, this was still within the expected timeframe for the species (Black 2016). Extending the observation period to assure lay date is collected as a continuous metric for more individuals would provide a more precise measure of reproductive status (Perrins 1970, Verhulst and Nilsson 2008). Ideally, lay date, hatching date and fledging date would also be included to better assess the breeding attempt (Lescroël et al. 2010). Reproductive status as categorically assessed here, and in general, is a coarse proxy to fitness, though for most diving animals measuring any proxy to lifetime fitness is difficult due to low recapture chances. Despite these limitations, the high site fidelity of penguins allows a unique opportunity to observe individuals throughout their annual cycle, and further work linking indices of condition to diving ability could provide the insight essential for other diving species.

3.3 Towards the future

To complement our findings here, future work assessing the depth of foraging dives throughout the winter period would help understand seasonal variation in foraging effort. Prey abundance is seasonal and may become sparse in inshore waters during late winter around the Falkland Islands (Clausen and Pütz 2003). Gentoo penguins could be increasingly limited in their prey selection or abundance nearshore and forced to travel further and dive deeper to find prey appropriate for efficient foraging. In a preliminary analysis of the complete data collected from 23 TDRs, vertical dive effort steadily increased throughout the winter, along with the maximum dive depth, although there is considerable individual variation (Appendix A.2). The variation in winter behaviour, and how this variation may change under seasonal conditions from April to October, will provide information on individual flexibility in foraging patterns (Hinke and Trivelpiece 2011, Black et al. 2017). While dietary specialization is difficult to detect (e.g., Bearhop et al. 2006), recording the variation in behaviour over long periods will provide a better understanding of the specialization of individuals to prey habitat depth (Hinke and Trivelpiece 2011, Black et al. 2017, Carpenter-Kling et al. 2017, Morgan et al. 2019).

Following individuals across multiple winter seasons would provide more concrete conclusions regarding individual diving specialization. When considering multi-year studies on the winter foraging behaviour of penguins, individual repeatability in behaviour, levels of blood oxygen-carrying capacity, and body mass across seasons can be assessed. Also, through contrasting environmental circumstances, we can better understand the effect of changing ecological conditions on breeding participation and success rates (Rebstock and Boersma 2018). Individuals with long life-histories optimize their reproductive investment over their lifetime, where costs of reproduction are likely masked and thus more prevalent in unfavourable

conditions (Williams 2012, Fronstin et al. 2016, Storey et al. 2017). Observing multiple years allows us to see a range of ecological circumstances and their effect on breeding participation, where seasonal matching of environmental conditions to strategy is less likely to inflate actual differences in fitness between individual strategies (Baylis et al. 2015, Masello et al. 2017, Traisnel and Pichegru 2019).

During this study, gentoo penguins experienced relatively prosperous environmental conditions resulting in a good breeding year. Nesting pair numbers and breeding success in 2018 were above the long-term annual average recorded since 2003, as reported by the island-wide census of 14 colonies, which includes Race Point but not Pebble Island (Stanworth and Crofts 2019). Especially as 2017 experienced record low fledging rates, when some colonies experienced almost complete breeding failure, 2018 was overall a successful breeding season for gentoo penguins (Stanworth and Crofts 2019). In a year of low breeding participation, the costs of an inferior strategy in inadequate environmental conditions could be more prevalent (Fronstin et al. 2016, Storey et al. 2017). Recently shown in African penguins, *Spheniscus demersus*, those with higher consistency in foraging behaviour, had higher breeding success in poor years (Traisnel and Pichegru 2019). Monitoring the link between pre-breeding foraging strategies, individual specialization, and breeding participation across seasons of variable environmental conditions, and determining more accurate annual breeding frequencies for this species, will be crucial to predicting breeding participation and population dynamics in the future (Juárez et al. 2013, Rebstock and Boersma 2018).

Last, although general information on prey availability can be inferred from monitoring foraging behaviour (e.g., Chimienti et al. 2017), comparing detailed information on local prey availability to the diet of penguins informs on what prey items penguins are selecting from

(Clausen et al. 2005). It is impossible to confidently say which depths presented the best foraging conditions for gentoo penguins during the 2018 pre-breeding season. As discussed in chapter 2, the winter diet of gentoo penguins in the Falkland Islands is believed to comprise many prey species (Handley et al. 2017), with preferential foraging of fish (Clausen et al. 2005, Handley et al. 2016). If favoured prey species are available, foraging trips and diving behaviour should reflect the optimal pursuit of preferred prey (Clausen et al. 2005, Takahashi et al. 2008, Horswill et al. 2017). However, the ocean is a dynamic environment, and foraging locations provide variable rewards based on which types of prey are most often encountered (Schreiber and Burger 2002). In the Falkland Islands, dietary information assessed simultaneously across a range of colonies has been recently updated during the breeding period (Handley et al. 2017). This information should also be updated through diet analysis of stomach contents at timely intervals throughout the winter period (e.g., Clausen and Pütz 2003, Hinke and Trivelpiece 2011), preferentially including individuals carrying TDR recorders to match prey contents with dive depths better. Advances in technology will only improve the accessibility of researching this topic, such as through paired TDR and video recorder devices able to mark the exact depths prey are seen, pursued, and caught successfully at (Takahashi et al. 2008, Handley and Pistorius 2016, Handley et al. 2018). I recommend conducting simultaneous surveys of available prey species and diet analysis as done by Clausen et al. (2005) throughout the winter to know which species become critical and when in the diet of gentoo penguins.

3.4 Applications and importance

From a life-history perspective, penguins can be a model species to tell us what types of reproductive trade-offs animals must consider. Penguins are long-lived and must trade-off reproductive investment between the current breeding season and future fecundity and survival

(Boersma 2008, Storey et al. 2017). As top marine predators, they indicate the health of their surrounding ecosystems because their survival and reproduction are sensitive to their foraging success and environment quality (Reid et al. 2005, Boersma 2008, Baylis et al. 2012). The likelihood of individuals to defer breeding impacts population dynamics and the response of populations to environmental conditions in the Anthropocene (Williams 1990, Williams and Rodwell 1992, Crossin et al. 2010). Their decision to breed integrates social, environmental, as well as physiological inputs (Vleck and Vleck 2002). While the reasons to defer breeding are not well understood, the winter foraging success of individuals are suspected of playing a role (Williams 1990, Alves et al. 2013, Crossin and Williams 2016). Penguins, and gentoo penguins, in particular, experience significant variation in breeding participation between years (Pistorius et al. 2010, Stanworth and Crofts 2019). Research, such as presented in this thesis, distinguishing behavioural patterns of successful versus unsuccessful breeders is essential to inform on reproductive trade-offs that can help predict population dynamics.

Of all avian species, seabirds, and especially penguins, are the most threatened by the changing environment occurring in the Anthropocene (Croxall et al. 2012). Polar species are impacted to a greater degree than others from anthropogenic threats like climate change (Forcada and Trathan 2009, Cury et al. 2011, Ibañez et al. 2015, Black et al. 2017). As more than half of penguin species are threatened (IUCN 2019), a deeper understanding of the impact oxygen stores have on their foraging ecology will be critical to the conservation and management of these birds. For gentoo penguins, research has shown that, in general, they can cope with more considerable environmental variability than other penguin species (Juárez et al. 2013, McMahon et al. 2019). They were, however, declining within the Prince Edward Islands (Crawford et al. 2014) and the Kerguelen archipelago (Lescroël and Bost 2006), where both declines are

attributed to conflicts with fisheries. In the Falkland Islands, the continental shelf is a popular fishing ground, and gentoo penguins are occasionally caught as bycatch and potentially compete for prey with fishing industries (Clausen and Pütz 2003, Trathan et al. 2015). Their extended winter range could overlap with exploration for hydrocarbons, and recently there is a consideration of further developing fisheries inshore (Augé et al. 2015). I recognize the considerable effort to manage fisheries located within the Falkland Islands exclusive economic zone, and the efforts of the Falkland Islands Seabird Monitoring Program (FISMP) but inshore fisheries will impact the foraging of gentoo penguins as they are restricted to nearshore habitat (Handley et al. 2017). If the prey is already locally sparse at winters end before breeding (Clausen and Pütz 2003), reducing prey availability further may be especially detrimental for penguins with low blood oxygen-carrying capacity constrained to shallower waters. I hypothesize finding prey and acquiring enough resources to participate in breeding will be more difficult for individuals restricted to shallower habitat selection if fisheries efforts are increased. Thus, insight into the winter foraging ecology of gentoo penguins and its impact on reproductive status can aid in conservation efforts.

Of the key research priorities identified as globally crucial for seabird species (Croxall et al. 2012, Lewison et al. 2012), my research enhances our knowledge of two of these: what drives foraging behaviour and which monitoring methods best reflect overall condition. Further understanding of the mechanisms underpinning the dive response are essential to understanding individual variation in foraging behaviour (McHuron et al. 2018b, Roncon et al. 2018). My research highlights the possible implications that variations in diving efficiency have on prey selection and the levels of competition experienced by penguins, as penguins experience less intraspecific competition at deeper depths. To proactively monitor the status and health of

wildlife populations, researchers are focusing more on sensitive individual-level metrics such as the condition of oxygen stores and evaluating performance instead of slower-responding population structures (Cooke et al. 2013). How blood oxygen-carrying capacity and body mass correlate with individual diving ability enables them to be more useful as indicators of condition and inform on the behaviour of animals.

My research helps quantify the effects oxygen stores have on the diving efficiency and foraging behaviour of animals. In finding high blood oxygen-carrying capacity was associated with longer bottom times and deeper foraging dives, I provide further evidence that Hb is a good indication of blood oxygen-carrying capacity and diving ability. The use of Hct as a physiological indicator, although still commonly reported, has been criticized due to inconsistent relationships with performance and fitness related traits in many species (reviewed in Fair et al. 2007, Minias 2015, Johnstone et al. 2017). Evidence that I present here provides additional awareness on how optimum Hct can influence diving ability. Acknowledging the limitations involved from non-linear relationships with performance are essential when interpreting Hct as an index of condition in future research. Knowledge of the limitations to diving, and how these limitations influence population dynamics, is needed not only for many seabird species but for diving species in general (Baylis et al. 2015, McHuron et al. 2018b). Indices of oxygen storage and diving performance provide information on how individuals acquire resources and allow us to better comprehend their foraging behaviour. Collaborative research comparing individual disparity in diving strategies, and how they relate to overall health and breeding participation, is crucial to understanding the foraging ecology and population resilience of diving animals to environmental change.

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Appendix

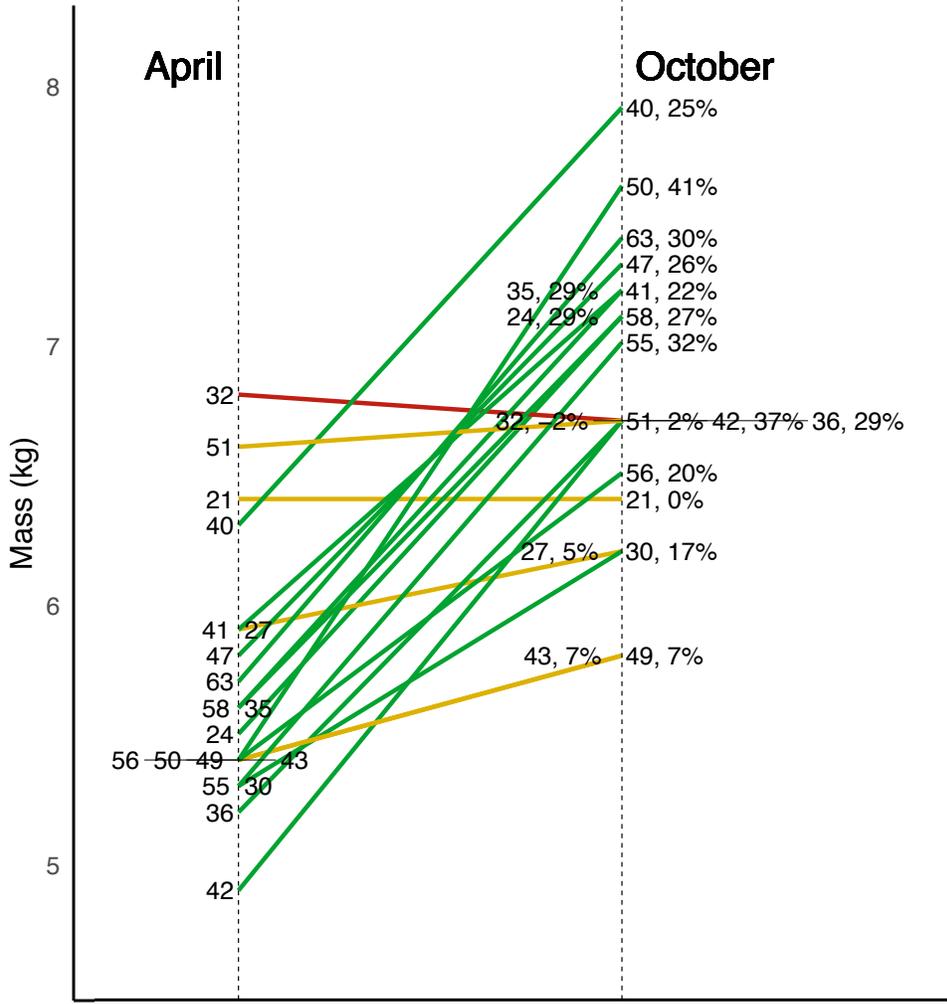


Figure A.1 The change in mass (kg) overwinter for 19 Gentoo penguins, from April post-moult to pre-breeding in October.

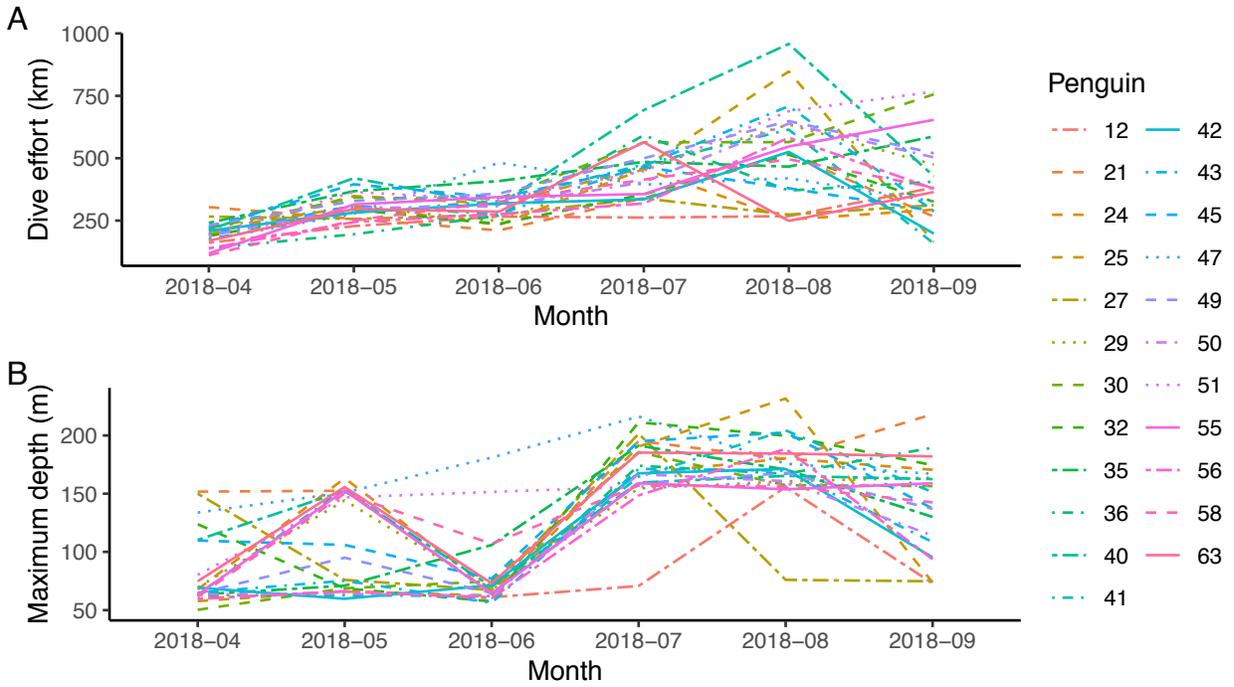


Figure A.2 Total dive effort in vertical distance dived (A, km) and maximum dive depth (B, m) for 23 gentoo penguins across all 6 months of winter in 2018. Penguins without blood samples (n = 4) were added to the 19 used in this thesis.