

**How does foraging success affect chick growth? The case  
of the Magellanic penguin (*Spheniscus magellanicus*)**

Melissa Johnston BSci

Submitted to Swansea University in fulfilment of the requirements for the  
Degree of MRes Biosciences

*Swansea University*

2021

## **Abstract**

Seabirds are extreme examples of income breeders whereby chick growth is entirely dependent on the foraging skills of the parents and the availability of food. It has consequently been proposed that prey availability can be assessed by examining chick growth rates. For this to be verified, studies need to compare chick growth with a parental 'Catch per Unit Effort' (CPUE) metric as a measure of prey abundance. However, there is limited research on how CPUE affects chick growth and what it might mean in terms of parental quality and food abundance. I examined chick growth in Magellanic penguins (*Spheniscus magellanicus*) and compared it to CPUE using animal-attached accelerometer metrics assuming prey capture and time spent underwater as effort and showed that there is no significant relationship between CPUE and chick growth rates, in part due to high inter-individual variability. However, the growth rate of chicks was significantly affected by both the number of chicks within the nest (one and two chicks) and by the year (2015 and 2016), with the highest rate of growth in one-chick broods in 2016 (73.9 g/day) and the lowest in two-chick broods in 2015 (32.8 g/day). Variability of growth rates and CPUE can be caused by the size and species of prey that penguins catch during a foraging trip, whether the birds choose to allocate food accrued to themselves or their chicks, where and when the prey are found, and on prey aggregation size. Variability of food delivery on a day-to-day basis can cause misrepresented relationships between CPUE and chick growth rate. Therefore, chick growth rate and CPUE should be used with careful consideration as proxies for prey abundance in the area.

**Keywords:** Income breeder, CPUE, VeDBA, Prey capture, Foraging ability, Parental quality, Seabird, Food abundance, Variability

## Lay summary

Animals which care for their young need an effective transfer of food between parents and offspring, which is achieved by them being either capital or income breeders. Seabirds are income breeders as food is collected by the parents during foraging trips and is fed directly to the chicks, rather than being stored as fat or milk. Chick growth and survival is thus entirely dependent on food availability and the parent's ability to catch prey. Determination of bird success at acquiring prey can help us understand the impact of food availability on seabird populations and how they respond to environmental change. However, because many seabirds feed underwater and far from land, it is difficult to assess foraging success. As chicks rely entirely on provided food to grow, it has been suggested that prey availability can be monitored using chick growth because fast growing chicks are assumed to have been fed lots of food and *vice versa*. To see if chick growth can be used to tell us about prey availability, I needed to see whether parents successful at foraging also have chicks with high growth. I used data from a Magellanic penguin (*Spheniscus magellanicus*) colony in Argentina where foraging of parent birds was monitored with animal-attached tags recording time and acceleration. 'Catch per Unit Effort' (CPUE) was used to assess the parents' foraging success by dividing the total prey caught by the total time spent underwater (a single prey capture event was identified by a sudden increase in acceleration). The chicks were weighed every two days from the day they hatched, up to 25 days old to see how much weight they gained (or lost) per day (growth rate). The CPUE and growth rate were analysed along with the total prey caught by the parent in one foraging trip. This showed that CPUE and the total catch had no effect on chick growth rate, mainly because there was huge variability in how successful parents were. This may be due to the different size and species of prey caught (not indicated by the tags), whether the parents are lucky enough to find a good patch of prey, if they travelled in the right direction to find prey, or whether they fed for themselves or chose to feed their chicks. This changing rate of food delivery indicates a constant change of prey availability and accessibility, which can cause low or decreased growth rates even if, on average, the parents bring back lots of food in a short time. As there are many factors affecting the foraging performance of the parents, even if food is abundant, chick growth should be used with careful consideration as an indicator of prey abundance. This research is important as it has highlighted future and better ways of monitoring prey abundance using chick growth which can be useful to help with the conservation of seabird species in terms of their supply of food.

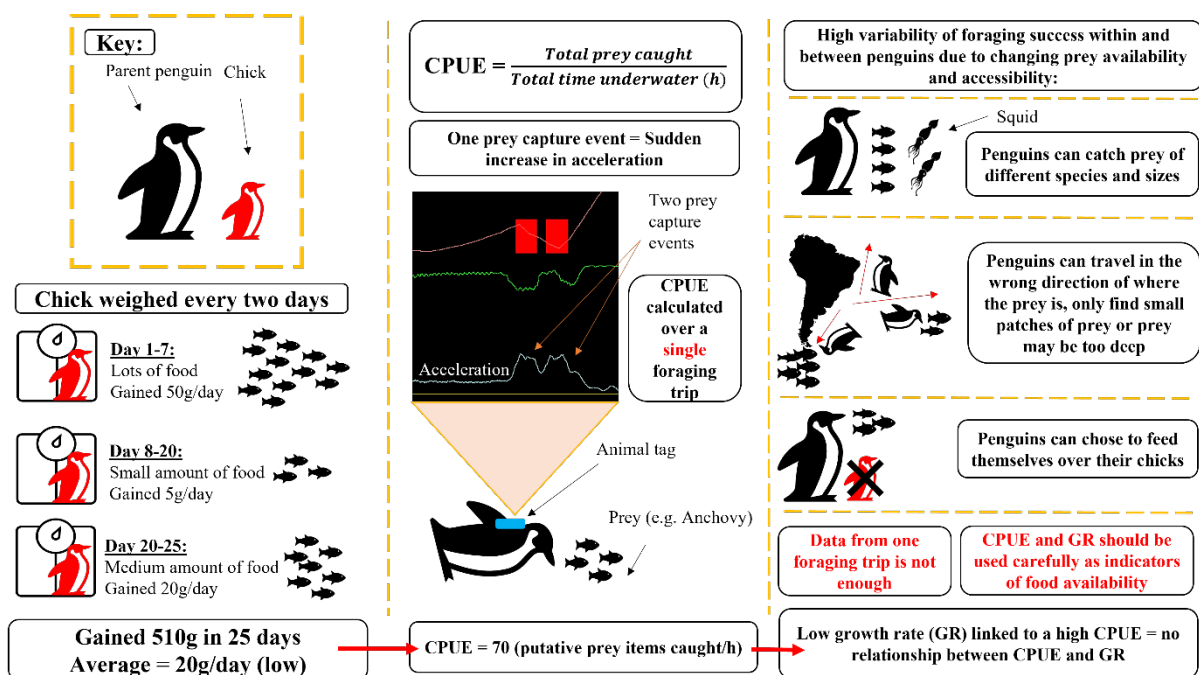


Figure 1. An example of the study's methodology including a summary of the outcome of the study

## University Declarations and Statements

### STATEMENT 1

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

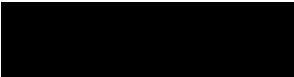
Signed .....  ..... (candidate)

Date .....16/03/2022.....

### STATEMENT 2

This thesis is the result of my own investigations, except where otherwise stated. Where correction services have been used, the extent and nature of the correction is clearly marked in a footnote(s).

Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended.

Signed ...  ..... (candidate)

Date .....16/03/2022.....

### STATEMENT 3

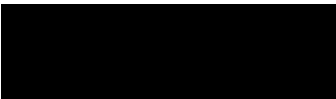
I hereby give consent for my thesis, if accepted, to be available for photocopying and for inter-library loan, and for the title and summary to be made available to outside organisations.

Signed .....  ..... (candidate)

Date .....16/03/2022.....

### STATEMENT 4

The University's ethical procedures have been followed and, where appropriate, that ethical approval has been granted

Signed.....  ..... (candidate)

Date.....16/03/2022.....

### Statement of expenditure

| <b>Category</b> | <b>Item</b>                 | <b>Description</b>  | <b>Cost</b>    |
|-----------------|-----------------------------|---|----------------|
| Electricals     | HP Probook i7 15”<br>laptop | 450 G7 Notebook Windows 10 Home<br>Intel Core i7-10510U CPU 16GB<br>Memory 512GB SSD 15” FHD Screen.<br>3 Year On Site Warranty | £790.00        |
| <b>Total:</b>   |                             |   | <b>£790.00</b> |

I hereby certify that the above information is true and correct to the best of my knowledge.

Signature: ...Melissa Johnston.....      Date: ...28/09/2021.....

## Statement of Contributions


| <b>Contributor Role</b>              | <b>Role Definition</b>  | <b>Persons involved</b>  |
|--------------------------------------|---|--|
| Conceptualization                    | Ideas; formulation or evolution of overarching research goals and aims  | Rory Wilson (RW)<br>Gabriella Blanca (GB)<br>Flavio Quintana (FQ)<br>Melissa Johnston (MJ) |
| Data Curation                        | Management activities to annotate (produce metadata), scrub data and maintain research data (including software code, where it is necessary for interpreting the data itself) for initial use and later reuse | GB, FQ   |
| Formal Analysis                      | Application of statistical, mathematical, computations or other formal technique to analyse or synthesise study data  | MJ   |
| Funding Acquisition                  | Acquisition of the financial support for the project leading to this publication  | n/a  |
| Investigation                        | Conducting a research and investigation process, specifically performing the experiments, or data/evidence collection   | GB, FQ   |
| Methodology                          | Development or design of methodology  | RW, GB, FQ, MJ   |
| Project Administration               | Management and coordination responsibility for the research activity planning and execution   | GB, FQ   |
| Resources                            | Provision of study materials, animals, instrumentation, computing resources or other analysis tools   | GB, FQ   |
| Software                             | Programming, software development, designing computer programs; implementation of the computer code and supporting algorithms; testing of existing code components  | Mark Holton (MH)<br>MJ   |
| Supervision                          | Oversight and leadership responsibility for the research activity planning and execution, including mentorship external to the core team  | RW<br>Kayleigh Rose (KR)   |
| Validation                           | Verification, whether as a part of the activity or separate, of the overall replication/reproducibility of results/experiments and other research outputs   | n/a  |
| Visualisation                        | Preparation, creation and/or presentation of the published work, specifically visualisation/data presentation   | MJ   |
| Writing – Original draft preparation | Creation and/or presentation of the published work, specifically writing the initial draft  | MJ   |
| Writing – Review and Editing         | Preparation, creation and/or presentation of the published work by those from the original research group, specifically critical review, commentary, or revision – including pre- or post-publication stages  | MJ, RW, KR   |

# Ethics Approval

## Student Details

**Name:** Melissa Johnston  
**Student Number:** [REDACTED]  
**Level:** 7  
**Course:** Biosciences  
**Project Supervisor:** Dr Kayleigh Rose  
**Last Updated Date:** 29 Jan 2021, 11:31 a.m.  
**Last Reviewed Date:** 29 Jan 2021, 4:06 p.m.  
**Reviewed by:** Kayleigh Rose

## Projects Ethics Assessment Status

| Project Title | Status  | Approval Number               |
|---------------|---|-------------------------------|
|               |  Completed | SU-Ethics-Student-290121/3700 |

## Project Ethics Assessment

It is mandatory requirement to complete this Project Ethics Assessment before starting any project in the College. Any further assessments can be submitted as and when required. A unique reference number will be generated and sent to you by email for each of the completed Ethics Assessment below.

**Approval Number:** SU-Ethics-Student-290121/3700

**Reference Number:** STU\_BIOL\_161744\_290121113137\_1

**Status:** Completed

### Project Ethics Assessment Confirmation|Cadarnhad o Asesiad Moeseg Prosiect



cosethics@swansea.ac.uk

To: JOHNSTON M. [REDACTED]

Cc: Rose [REDACTED]

Retention Policy Exchange Retention Policy (Never)

Expires Never

[Reply](#) [Reply All](#) [Forward](#) [...](#)

Fri 29/01/2021 16:06

This is an automated confirmation email for the following project. The Ethics Assessment status of this project is: APPROVED

Applicant Name: Melissa Johnston  
Project Title:  
Project Start Date:  
Project Duration:  
Approval No: SU-Ethics-Student-290121/3700

NOTE: This notice of ethical approval does not cover aspects relating to Health and Safety. Please complete any relevant risk assessments prior to commencing with your project.

Neges awtomataidd yw hon ar gyfer y prosiect canlynol. Statws Asesiad Moeseg y prosiect hwn yw: APPROVED

Enw'r Ymgaisydd: Melissa Johnston  
Teitl y Prosiect:  
Dyddiad Dechrau'r Prosiect:  
Hyd y Prosiect:  
Rhif y Gymeradwyaeth: SU-Ethics-Student-290121/3700

SYLWER: Nid yw'r hysbysiad hwn o gymeradwyaeth foeseogol yn cynnwys agweddau sy'n ymwneud ag techyd a Diogelwch. Dylech gwblhau unrhyw asesiadau risg perthnasol cyn dechrau eich prosiect.

# Health and Safety and Risk Assessments



HEALTH & SAFETY  
IECHYD A DIOGELWCH

| Risk Assessment             |  |                                    |                  |
|-----------------------------|--|------------------------------------|------------------|
| <b>College/ PSU</b>         | College of Science   | <b>Assessment Date</b>             | 29/01/2021       |
| <b>Location</b>             | Singleton Campus   | <b>Assessor</b>                    | Melissa Johnston |
| <b>Activity</b>             | Desk based study   | <b>Review Date (if applicable)</b> |                  |
| <b>Associated documents</b> | <ul style="list-style-type: none"> <li>•</li> <li>•</li> </ul> |                                    |                  |

**Part 1: Risk Assessment**

| What are the hazards?  | Who might be harmed? | How could they be harmed? | What are you already doing?   | S | L | Risk (SxL) | Do you need to do anything else to manage this risk?                | S | L | Risk (SxL) | Additional Action Required   |
|--|----------------------|---------------------------|---|---|---|------------|---|---|---|------------|--|
| Screen glare   | Computer user        | Temporary eyestrain       | Taking regular breaks from the screen                                 | 1 | 3 | 3          | Set the screen to a warm display and reduce brightness.             | 1 | 2 | 2          | Allow for sufficient lighting in the areas where the computer is used. |
| Poorly adjusted computer equipment                             | Computer user        | Back/neck ache            | Sitting in a comfortable chair with appropriate back support          | 1 | 3 | 3          | Make sure the computer is near eye level                            | 1 | 2 | 2          | Take regular breaks to walk and stretch                                |
| Spilling liquid on to a computer or other electrical appliance | Computer user        | Electricution             | Ensuring that there are no open liquid containers near the appliances | 3 | 3 | 9          | Move away from the electrician appliance when consuming any liquids | 3 | 2 | 6          | N/A  |



HEALTH & SAFETY  
IECHYD A DIOGELWCH

**Part 2: Actions arising from risk assessment**

| Actions  | Lead             | Target Date | Done Yes/No |
|--|------------------|-------------|-------------|
| Ensured computer screen has been set to a warm display | Melissa Johnston | 29/01/2021  | Yes         |
| Ensured sufficient lighting in the workspace           | Melissa Johnston | 29/01/2021  | Yes         |
| Ensured desk and chair are appropriate and comfortable | Melissa Johnston | 29/01/2021  | Yes         |
| Undergo regular breaks and stretches                   | Melissa Johnston | Continuous  | Yes         |
| Purchase of a water bottle and travel mug with a lid   | Melissa Johnston | 29/01/2021  | Yes         |



HEALTH & SAFETY  
IECHYD A DIOGELWCH

**Risk Matrix**

|            |   | Consequences  |  |  |  |  |
|------------|---|---|--|--|--|--|
|            |   | 1<br>Insignificant<br>No injuries/ minimal financial loss | 2<br>Minor<br>First aid treatment/ medium financial loss | 3<br>Moderate<br>Medical treatment/high financial loss | 4<br>Major<br>Hospitalised/ large financial loss | 5<br>Catastrophic<br>Death/ Massive Financial Loss |
| Likelihood | 5<br>Almost Certain<br>Often occurs/ once a week      | 5<br>Moderate   | 10<br>High   | 15<br>High   | 20<br>Catastrophic                               | 25<br>Catastrophic                                 |
|            | 4<br>Likely<br>Could easily happen/ once a week       | 4<br>Moderate   | 8<br>Moderate  | 12<br>High   | 16<br>Catastrophic                               | 20<br>Catastrophic                                 |
|            | 3<br>Possible<br>Could happen/ happen once a year     | 3<br>Low  | 6<br>Moderate  | 9<br>Moderate  | 12<br>High                                       | 15<br>High   |
|            | 2<br>Unlikely<br>Hasn't yet happened but could happen | 2<br>Low  | 4<br>Moderate  | 6<br>Moderate  | 8<br>High  | 10<br>High   |
|            | 1<br>Rare<br>Concievable but 1/100 year event         | 1<br>Low  | 2<br>Low   | 3<br>Low   | 4<br>Moderate                                    | 5<br>Moderate                                      |



## **Table of Contents**

|          |   |    |
|----------|---|----|
| <b>1</b> | <b>Introduction</b> .....   | 13 |
| <b>2</b> | <b>Materials and methods</b> .....  | 16 |
| 2.1      | Study site.....   | 16 |
| 2.2      | Deployment of devices .....   | 16 |
| 2.3      | Chick growth.....   | 16 |
| 2.4      | Data analysis of diving behaviour .....   | 17 |
| 2.5      | Data analysis of chick growth.....  | 20 |
| 2.6      | Statistical analysis.....   | 20 |
| <b>3</b> | <b>Results</b> .....  | 21 |
| 3.1      | Effects of brood size on chick growth .....   | 21 |
| 3.2      | Parent foraging ability .....   | 23 |
| 3.3      | Effects of CPUE on chick growth.....  | 26 |
| <b>4</b> | <b>Discussion</b> .....   | 28 |
| 4.1      | Effects of brood size, year and CPUE on chick growth rate .....   | 28 |
| 4.2      | CPUE in relation to parent foraging ability and prey abundance .....  | 29 |
| 4.3      | Using chick growth rate as an indicator of prey availability .....  | 30 |
| 4.4      | Limitations/considerations of the data .....  | 31 |
| <b>5</b> | <b>Conclusion</b> .....   | 33 |
| <b>6</b> | <b>Appendices</b> .....   | 34 |
|          | Appendix 1: Table 4 .....   | 34 |
|          | Appendix 2: Correlation Coefficient R script (Figure 2).....  | 35 |
|          | Appendix 3: Chick growth histogram R script (Figure 4).....   | 36 |
|          | Appendix 4: R script for main statistical analysis, including correlation coefficient<br>(Appendix 1).....  | 37 |
|          | Appendix 5: Mean, Standard Deviation and Standard Error values for parent foraging<br>ability (Figure 5 & 6) and t-test / Mann-Whitney test R script..... | 46 |
| <b>7</b> | <b>References</b> .....   | 48 |

## **Acknowledgements**

This thesis and research behind it would not have been possible without my secondary supervisor, Professor Rory Wilson who gave me the opportunity to work on this project, taught me everything I needed to know about DDMT and tri-axial acceleration tags, gave me an insight on penguin/seabird biology, behaviour, and ecology, and helped with editing and providing feedback to my thesis. I would also like to thank Gabriella Blanca, Flavio Quintana and team at Cabo dos Bahías for collecting the raw data needed for this project. I wish to extend my thanks to Dr Kayleigh Rose (primary supervisor), who gave me an insight on the statistical analysis needed for this project and gave me feedback where needed.

## List of tables and illustrations

|   |    |
|---|----|
| <b>Figure 1.</b> An example of the study’s methodology including a summary of the outcome of the study.....   | 3  |
| <b>Figure 2.</b> Simple linear regression graph showing the trend between total time underwater (h) and summed VeDBA (g).....   | 19 |
| <b>Figure 3.</b> Violin- and boxplots depicting the mean growth rate (g/day) for nests with one- and two-chick broods and for each year presented.....  | 21 |
| <b>Figure 4.</b> Frequency distribution of the mean growth rate (g/day) for Magellanic penguin chicks in 2015 and 2016.....   | 22 |
| <b>Figure 5.</b> Cumulative putative prey capture of tagged breeding Magellanic Penguins during a single foraging trip in 2015.....   | 24 |
| <b>Figure 6.</b> Cumulative putative prey capture of tagged breeding Magellanic Penguins during a single foraging trip in 2016.....   | 25 |
| <b>Figure 7.</b> The effect of CPUE (putative prey items caught/h) on mean growth rate (g/day) on Magellanic penguin chicks in 2015 and 2016.....   | 26 |
| <b>Figure 8.</b> The effect of CPUE (putative prey items caught/h) on mean growth rate (g/day) of Magellanic penguin chicks between nests with one- and two-chick broods.....                                       | 27 |
| <b>Table 1.</b> Mean of mean growth rate (g/day) for Magellanic penguin nests with one and two chicks in 2015 and 2016 with standard deviation and error.....   | 22 |
| <b>Table 2a.</b> The outcome of the two-way ANOVA to examine the effects of the number of chicks and year on Magellanic penguin chick mean growth rate (g/day), without the interaction effect.....                 | 23 |
| <b>Table 2b.</b> The outcome of the two-way ANOVA to examine the effects of the number of chicks and year on Magellanic penguin chick mean growth rate (g/day), with the interaction effect.....                    | 23 |
| <b>Table 3.</b> ANOVA output of the linear model to examine the effects of CPUE, year, number of chicks and total catch on Magellanic penguin chick mean growth rate (g/day).....                                   | 27 |
| <b>Table 4.</b> Outcome of the Spearman’s rank correlation coefficient between total time underwater (h) and total time at sea (h) with CPUE (putative prey caught/h), with and without the outlier (Nest 81A)..... | 34 |

## **Definition of Abbreviations**

- CPUE – ‘Catch per Unit Effort’
  - The indirect measurement of the abundance of prey caught by the penguin
  - $CPUE = \text{Total prey caught} / \text{Total time spent underwater (h)}$
  
- PPCE – Putative prey capture event
  - An assumed capture of a single item of prey by the penguin
  
- DBA – Dynamic Body Acceleration
  - Uses tri-axial accelerometers to detect overall body acceleration to deem energy expenditure of the animal from muscle contraction
  
- VeDBA – Vectorial Dynamic Body Acceleration
  - A proxy for energy expenditure derived from an approach that uses DBA to quantify the vibrance of animal movement, normally due to movement of the limbs

# **1 Introduction**

The life history of animals shows that an effective energy and matter transfer between parents and progeny is vitally important to the fitness and survival of the population (Giordano et al., 2014; Jönsson, 1997; Roff, 2002). For this, animals are often deemed to be capital or income breeders (Houston et al., 2006; Stephens et al., 2009). Capital breeders are species which store energy as body reserves which are used for reproduction later on (Crocker et al., 2001; Lourdais et al., 2015; Madsen and Shine, 1999). This is seen in female elephant seals (*Mirounga leonine*) where they store reserves prior to birth, after which they supply their offspring with milk for weeks of their initial growth despite not feeding (Crocker et al., 2001; Oosthuizen et al., 2019). Income breeders, such as the European roe deer (*Capreolus capreolus*) (Andersen et al., 2000), effectively transfer nutrients using current energetic income directly from the environment (Sainmont et al., 2015). In mammals, this may still take the form of lactating, although in income breeders, body reserves of the lactating females are considered minimal (e.g. Antarctic fur seal (*Arctocephalus gazella*)) (Boyd, 2003).

Birds are known to be an extreme example of income breeders, such as the rockhopper penguin (*Eudyptes chrysocome*) and common diving petrels (*Pelecanoides urinatrix*), where the young are provisioned by the parents and the food accumulated during foraging trips is transferred directly from the environment to the brood (Chastel et al., 1995; Hull et al., 2004) without passing as milk, an exception being pigeons where both parents regurgitate milk from their crops, an organ which produces pigeon milk, in addition to storing food (Gillespie et al., 2011; Luo et al., 2017). For birds, this means that chick growth is entirely dependent on the foraging skills of the parents and the availability of the food (Drent and Daan, 1980; Jönsson, 1997). In this, it is notable that the closer and more abundant the food is to the nest, the less energy and time the parents have to invest to acquire it, generally resulting in increased provisioning rates, increasing the chicks chance of survival (Green et al., 2007; Sherley et al., 2013).

Seabirds must cope with a heterogenous environment in which prey abundance and availability vary greatly across temporal and spatial scales due to abiotic (e.g. frontal systems, upwelling) and biotic factors (e.g. fisheries) (Hennicke and Culik, 2005; Ramírez et al., 2014; Weimerskirch, 2007). Workers examining seabird populations have identified that prey availability can impact seabird survival, especially during breeding seasons, when central placed foraging limitations are present (Crawford et al., 2006; Orians and Pearson, 1979), and acquiring the right amount of food at the time the chicks hatch is critical (Saraux et al., 2012).

Indeed, it has been suggested that identifying prey capture events can help us understand the impact of food availability on seabird populations and their response to environmental change (Carroll et al., 2018). However, it is particularly challenging to assess foraging success in seabirds as they often feed underwater and far from land (Petersen et al., 2006; Thaxter et al., 2012). Noting the assumed link between prey abundance and seabird reproductive performance (Crawford et al., 2006; Sherley et al., 2013), it has been proposed that prey availability can be assessed through looking at chick growth rates (Williams and Croxall, 1990). If chicks are provisioned poorly then growth rates will be lower than chicks with high levels of provisioning (Ballard et al., 2010; Salihoglu et al., 2001; Wanless et al., 2005; Williams and Croxall, 1990).

While it is clear that fast-growing chicks will have been well provisioned, which can only occur when food is easily accessible to seabirds (Salihoglu et al., 2001), the reverse is not necessarily the case. For example, food may be abundant but inaccessible (e.g., located under ice in the Arctic/Antarctic) (Ancel et al., 2017; Irvine et al., 2000), or foraging may be precluded or disadvantaged by other factors, such as the presence of competitors (Ainley et al., 2006; Trivelpiece et al., 2011), or simply poorly acquired by first-time breeders which have a lack of experience in foraging and reproduction (Angelier et al., 2007; Lecomte et al., 2010; Olsson, 1997).

Several studies have examined foraging success and chick growth alongside each other. This has been done by comparing different colonies foraging successes using temperature-depth and stomach-temperature recorders and then comparing their relative chick growths as a separate entity (Hennicke and Culik, 2005). Other studies have used time-depth recorders to assess foraging effort (as time spent diving) and looked at the relationship of this to chick growth (Takahashi et al., 2003). Critically though, studies need to examine both prey capture success and foraging effort to put foraging success into perspective because the energy used by provisioning adults to forage must be deducted from the overall energy capture (Cavallo et al., 2020; Grémillet, 1997), with the difference being given to the broods (Grémillet, 1997). Specifically, in order to compare ‘foraging success’ with chick growth, studies should elect some ‘Catch per Unit Effort’ (CPUE) metric (Wilson, 1992), as do commercial fisheries (Bannerot and Austin, 1983) as the measure of prey abundance. There is, however, limited research on how it affects chick growth and what it might mean in terms of parental quality and food abundance of the area.

This thesis examines this issue and seeks to try and disentangle the effect of hunting effort/activity on chick growth in a monomorphic seabird, the Magellanic penguin (*Spheniscus magellanicus*). The aim of the work is specifically to see if it is possible to correlate Magellanic

penguin catch per unit effort (CPUE) indices with chick growth and to discuss the implications of success or failure in this for our understanding of how seabird food abundance relates to breeding success.

The Magellanic penguin is the most widespread and abundant seabird breeding on Argentina's Patagonian coast, with 900,000 monogamous breeding pairs (Falabella et al., 2019). The breeding season lasts from September to February, with breeding females being at least four years old and males being at least five years old (Davis et al., 2010; Boersma et al., 2013). Once the chicks have hatched after the 40-day incubation period, both parents take it in turns to feed them approximately once a day for the first 30 days, with feeding becoming more infrequent afterwards, until they fledge at around 60 days old (Otley et al., 2004; Boersma et al., 2013). Magellanic penguins primary food source is pelagic schooling fish such as Argentine anchovy (*Engraulid anchoita*) which accounts for 60-100% of their stomach contents and Argentine hake (*Merluccius hubbsi*) accounting up to 40% (Frere et al., 1996; Gandini et al., 1999; Gosztonyi, 1984; Wilson et al., 2005), whereas squid (*Loligo* spp., *Illex argentinus*) are a subsidiary food source, accounting for 1-19% of their stomach contents (Boersma et al., 2009; Fernandez et al., 2019; Gandini et al., 1999; Gosztonyi, 1984; Wilson et al., 2005). One of the key threats to Magellanic penguins is the reduction of their prey resources from fisheries (Boersma et al., 2013; Gandini et al., 1999). This can either be directly, through the already exploited hake fishery (Alemany et al., 2013; Vaz-dos-Santos et al., 2010) or the developing anchovy fishery (Skewgar et al., 2014, 2007) or through bycatch of anchovy and juvenile hake by northern Argentine Patagonia fisheries (BirdLife, 2020). Magellanic penguins were classed as 'Near Threatened' (from 2004 to 2018) due to their declining populations, but since 2020 they have been classified as 'Least Concern', although their populations are still in decline (BirdLife, 2020). This seeming inconsistency needs data. Thus, anything that helps monitor penguin reproductive success through the analysis of chick growth and foraging success can provide useful statistics to inform policy and potentially help conservation measures.

Currently, there is not a clear and detailed idea of how parental foraging effort affects the growth rate of chicks of seabirds in general and Magellanic penguins in particular. In order to fulfil the aim for this study, I used previously collected chick growth and foraging effort data from a Magellanic penguin colony in Argentina. Tag data from parent penguins was analysed to identify prey captures and to derive CPUE metrics, and effort was considered to be the total time spent underwater. Chick growth was measured during the period their parents were equipped with tags.

## **2 Materials and methods**

### **2.1 Study site**

Fieldwork was conducted during the early chick-rearing period at the Cabo dos Bahías (44°54'S, 65°32'W) Magellanic penguin colony by Gabriella Blanca, Flavio Quintana and team. This was carried out between November 23<sup>rd</sup> and December 19<sup>th</sup>, 2015, and November 27<sup>th</sup> and January 27<sup>th</sup>, 2016.

### **2.2 Deployment of devices**

Fifty-three Magellanic penguins (29 in 2015 and 24 in 2016), brooding at least one chick (less than 14 days old), were fitted with multichannel data loggers with relevant channels including tri-axial (orthogonal) acceleration and pressure (depth) as well as GPS (Axy-Trek Marine, 40 x 20 x 8 mm [L x W x H], 14-59 g (TechnoSmart – <https://www.technosmart.eu/axy-trek-marine/>)). The data loggers were programmed to record acceleration at 25 Hz and depth at 1 Hz.

Each bird was carefully removed from their nest and equipped with devices on their lower back, to minimise hydrodynamic drag, with overlapping strips of Tesa® tape (Wilson et al., 1997). The procedure took less than five minutes, which minimised the stress caused, after which the birds were immediately returned to their nest. Each penguin was left to forage for a single trip before the devices were retrieved when the birds returned to the nest. As a result, no individual penguin contributed more data than any other.

Due to an error in programming with some of the tags, a total of 41 penguins (21 in 2015 [13 female and 8 male] and 20 in 2016 [9 female, 4 male, 7 unknown]) contributed to the data set (the age of the tagged penguins was not known).

### **2.3 Chick growth**

Each chick corresponding with the tagged parent penguin was weighed approximately every two days, from the day it hatched, up to 25 days old. For this, each chick was placed in a bag and weighed (in g) with a Pesola spring balance before being returned to their nest. The number of chicks in the nest on weighing days was also recorded, allowing the hatching or loss (by predation or other natural causes) of a chick to be documented.



N.B. The terms, “one and two chicks” and “one- and two-chick broods” (both having the same definition – the number of chicks in the brood) will be interchanged throughout this manuscript.

## **2.4 Data analysis of diving behaviour**

The diving behaviour of penguins was analysed using bespoke software (DDMT; Wildbyte Technologies, <http://www.wildbytetechnologies.com/>). The ‘behaviour builder’ option (a Boolean approach for identifying events) (Wilson et al., 2018a) within DDMT is specially designed, using algorithms, to detect specific behaviours. Based on Del Caño et al (2021), who used video footage to show that prey capture by Magellanic Penguins is accompanied by high-speed swimming and corresponding acceleration metrics from bird-attached accelerometers, putative prey capture events (PPCE) were identified based on depth and Vectorial Dynamic Body Acceleration (VeDBA). VeDBA is a proxy for energy expenditure derived from an approach that uses dynamic body acceleration (DBA) to quantify the ‘vibrancy’ of animal movement, normally due to movement of the limbs (Wilson et al., 2020).

DBA is based on the concept that contracting muscles produce a change in overall body (trunk) acceleration and that this can occur in any, or all, of the three dimensions of space (Gleiss et al., 2011; Wilson et al., 2020). The more muscles contract, in terms of the frequency of contraction, extent- and speed of contraction (all of which relate directly to energy expenditure), the greater the trunk acceleration over a given time. Thus, if accelerometers are placed on an animal’s trunk and set to record at high frequencies, they should provide information that codes for the rate at which energy is expended (Wilson et al., 2020, 2006). However, data loggers fitted with tri-axial accelerometers record both muscle contraction-derived acceleration and gravitational acceleration (due to the Earth’s gravity) in the three orthogonal axes: surge, heave and sway (Wilson et al., 2020). To access the muscle contraction component, the gravitational acceleration component needs to be subtracted (Gleiss et al., 2011). For this, each raw acceleration data stream is smoothed (nominally over two seconds - (Shepard et al., 2008)), which provides the gravitational component in the acceleration signal (Gleiss et al., 2011). This is then subtracted from the raw data stream for each acceleration axis to provide the acceleration signal due to muscle contraction (Gleiss et al., 2011).

These ‘dynamic’ muscle-linked acceleration data streams, one for each of the orthogonal axes, are then added together, vectorially, to provide VeDBA (Vectorial sum of the Dynamic Body Acceleration) *via*:

$$VeDBA = \sqrt{DA^2x + DA^2y + DA^2z}$$

where “*D*” is the dynamic acceleration resulting from the subtraction of the smoothed acceleration data from the raw and x, y and z axes, representing the three orthogonal acceleration axes, respectively (Wilson et al., 2020). This metric quantifies total body acceleration in all directions about the animal’s trunk and acts as a powerful proxy for total energy expenditure (Gleiss et al., 2011; Wilson et al., 2020).

VeDBA was used, within the ‘behaviour builder’ option within DDMT, to isolate prey capture events for each tagged penguin. Here, I assume that prey capture occurred when the depth was greater than 2 m and when VeDBA was greater than 0.4 g. I make this assumption based on research that has shown that penguins typically only catch prey at depths deeper than 2 m (Del Caño et al., 2021) and that prey pursuit in Magellanic Penguins requires more power than normal swimming (Wilson et al., 2002), and normal swimming and diving does not exceed VeDBA values of 0.4 g (Wilson et al., 2010). The algorithm took the form;

If (SM (VeDBA smoothed | 25) > 0.4 AND SM (Pressure smoothed | 25) > 2), then Mark  
Events

where the numbers after the SM (smoothed) term refer to the smoothing window (which, at 25 Hz, equated to 1 s). Periods when the algorithm was found to be true were marked within DDMT and exported to an Excel spreadsheet along with the duration of each event and considered to be a PPCE.

A second algorithm was created to identify the Catch per Unit Effort (CPUE) for each penguin. This approach considered that each identified prey pursuit (see above) resulted in the capture of a single prey (Simeone and Wilson, 2003) and that the total number of prey could be determined by summing these events. The overall cost of the foraging effort could be approximated by either summing the total VeDBA of the foraging trip or by determining the total time spend underwater. An algorithm in ‘behaviour builder’ was used to determine the time underwater when the depth exceeded 1 m, with these ‘marked events’ being exported to

an Excel spreadsheet along with the duration and the sum of the VeDBA for each dive. The algorithm took the form:

If (SM (Pressure smoothed | 25) > 1), then Mark Events

Since a simple linear regression graph and Spearman's Rank Correlation Coefficient showed that both VeDBA and time underwater were very closely correlated (Figure 2) ( $R^2 = 0.97$ ,  $P < 0.001$ ), time underwater was subsequently used as the effort metric in the CPUE equation.

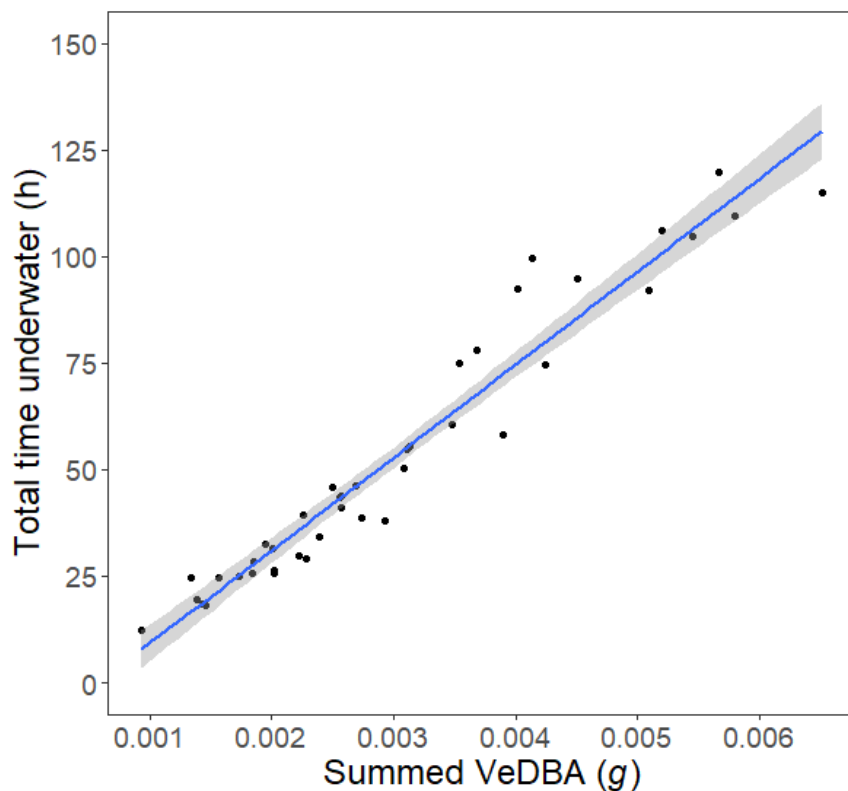


Figure 2. Simple linear regression graph showing the trend between total time underwater (h) and summed VeDBA (g) during single foraging trips as an effort metric for the CPUE equation. Each point shows the results from a single individual penguin for one foraging trip.

With the data from these two algorithms, CPUE was calculated for each tagged penguin to define the overall rate at which prey were caught per hour of their foraging trip according to:

$$CPUE = \frac{\text{Total prey caught}}{\text{Total time spent underwater (h)}}$$

## **2.5 Data analysis of chick growth**

Using the chick weight data, linear correlation graphs were constructed to provide regression equations which allowed determination of the average weight gain (g) of each chick per day, both for nests with one and two chicks for the complete chick monitoring period. Rate of weight gain from the chicks was combined with the CPUE data in a spreadsheet for each penguin for further analysis in R.

N.B Chick weight data from individuals less than two days old and more than 22 days old was disregarded as it was considered to have occurred during the non-linear phase of growth (Ricklefs, 1967; Tjørve and Tjørve, 2010).

## **2.6 Statistical analysis**

Statistical analysis was conducted within R studio (version 4.1.0, “Camp Pontanezen”, <https://www.R-project.org/>). A two-way ANOVA was carried out to consider all possible interactions between the number of chicks and the year to see if either factor had a significant effect on the mean growth rate of the chicks. This was followed by a stepwise back-deletion of non-significant interaction terms. An AIC (Akaike information criterion) determined that there was minimal difference between the models, so if the model with the interaction effect was insignificant then the model without the interaction effect was used.

A linear model was constructed to consider all possible interactions between CPUE, year, number of chicks and total catch, to see which had a significant effect on the mean growth rate of chicks. Again, this was followed by a stepwise back-deletion of non-significant interaction terms. An AIC determined that there was minimal difference between the models, so the model without the interaction effects was used for statistical analysis. A two-sample t-test was carried out to see if there was a significant difference of the total catch between the years. Spearman’s Rank Correlation Coefficient test was used to see if there was a relationship between CPUE and total time underwater and CPUE and total time at sea (Appendix 1, Table 4). Statistical differences were considered significant when  $P < 0.05$ . Graphs were constructed within Excel and R studio using GG plot. A Bartlett test was undertaken for the two-way ANOVA and a Shapiro test for the two-way ANOVA, linear models and two-sample t-test to check that assumptions for homogeneity of variance and normality were met. The Shapiro test for the two-sample t-test did not meet the assumptions so the non-parametric Mann-Whitney U-test was carried out instead.

### 3 Results

A total of 41 birds and 67 chicks (41 broods) provided complete data amounting to 41 foraging trips totalling 977 h at sea with 416 h of that time spent underwater. Nest 164 for 2015 and Nests 29, 105A and 57A for 2016 were excluded from the CPUE linear model as their tags recorded less than six hours of a foraging trip due to an error with programming.

#### 3.1 Effects of brood size on chick growth

In both 2015 and 2016, nests with one chick had a higher mean and median mean growth rate than nests with two chicks (Figure 3; Table 1).

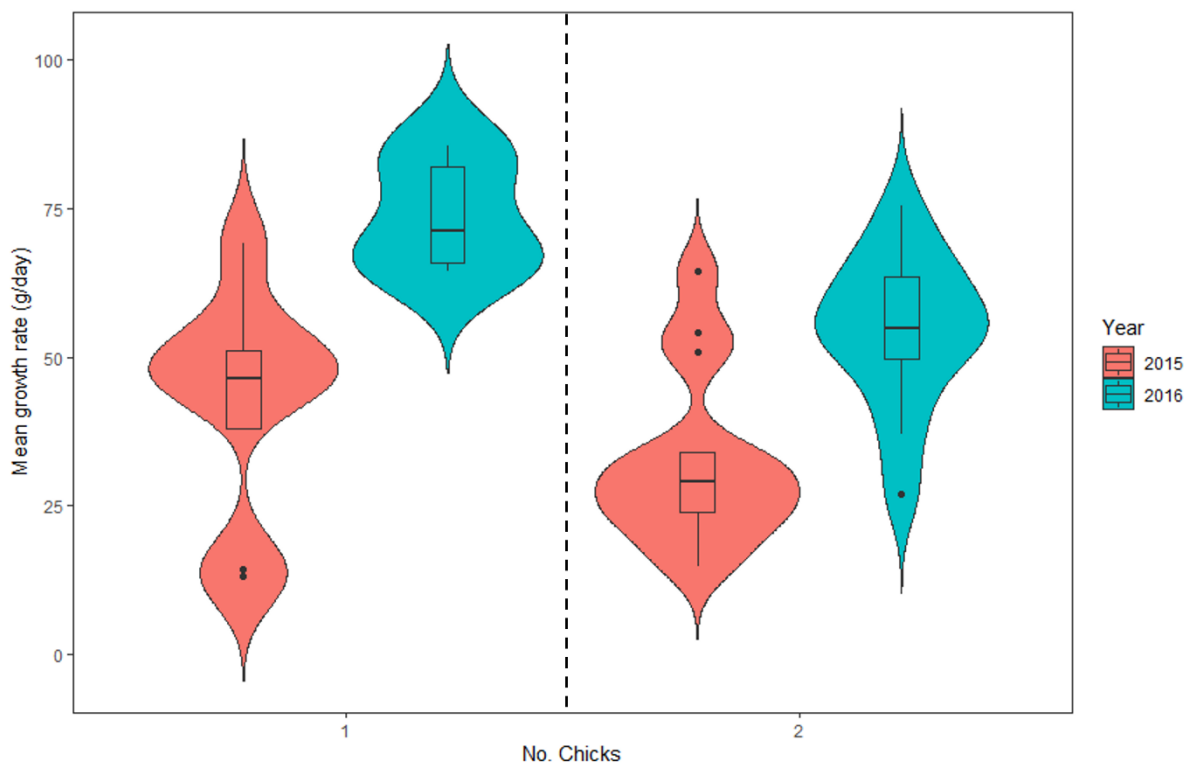


Figure 3. Violin- and boxplots (indicating median and quartiles with whiskers reaching up to 1.5 times the interquartile range) depicting the mean growth rate (g/day) for nests with one- and two-chick broods and for each year presented. The violin plot outlines the kernel probability density where the width of the violin plot represents the proportion of the data located there (One chick 2015: N = 8, Two chicks 2015: N = 13; One chick 2016: N = 7, Two chicks 2016: N = 13).

Table 1. Mean of mean growth rate (g/day) for Magellanic penguin nests with one and two chicks in 2015 and 2016 with standard deviation and error.

| Year | Number of chicks | Mean (g/day) | Standard deviation | Standard error | Number of samples |
|------|------------------|--------------|--------------------|----------------|-------------------|
| 2015 | 1                | 42.5         | 19.3               | 6.84           | 8                 |
| 2015 | 2                | 32.8         | 14.8               | 4.11           | 13                |
| 2016 | 1                | 73.9         | 9.35               | 3.54           | 7                 |
| 2016 | 2                | 54.4         | 13.0               | 3.60           | 13                |

Overall, 2016 had a significantly higher mean ( $\pm$  SE) chick growth rate of  $61.2 \pm 3.35$  g/day compared to 2015 with a mean growth rate of  $36.5 \pm 3.69$  g/day (Table 2a) although there was considerable interindividual variability (Figure 4).

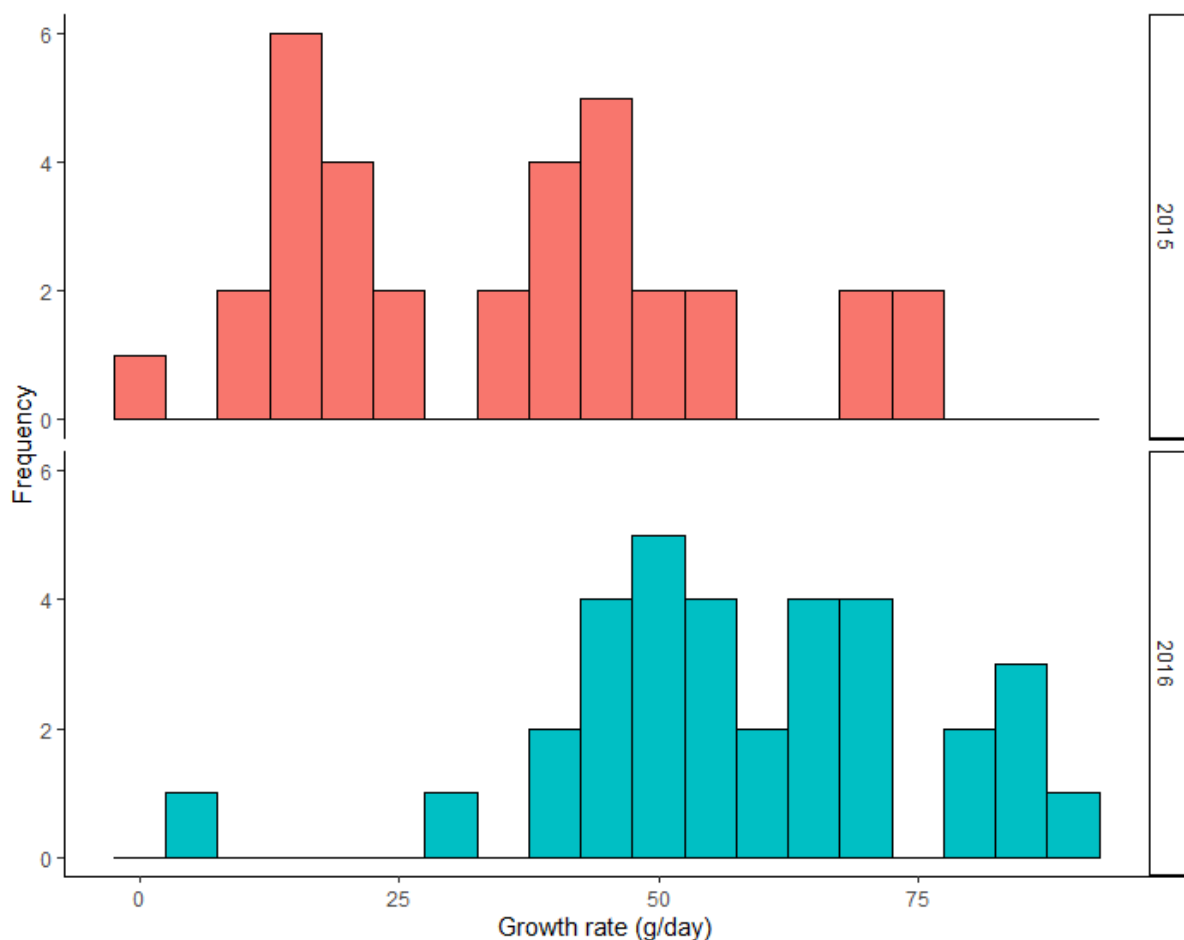


Figure 4. Frequency distribution of the mean growth rate (g/day) for Magellanic penguin chicks in 2015 and 2016. Bin width = 5 g/day. (2015: N = 21; 2016: N = 20).

The number of chicks (either one- or two-chick broods) and the difference of years (2015 and 2016) had a statistically significant effect on the mean growth rate of the chicks (Two-way ANOVA:  $P < 0.05$ ) (Table 2a), but there was no significant interaction effect between the number of chicks and year ( $P > 0.05$ ) (Table 2b).

Table 2a. The outcome of the two-way ANOVA to examine the effects of the number of chicks and year on Magellanic penguin chick mean growth rate (g/day), without the interaction effect.

| <b>Factor</b> | <b>d.f.</b> | <b>F-value</b> | <b>P-value</b> |
|---------------|-------------|----------------|----------------|
| No. chicks    | 1           | 8.311          | <0.01          |
| Year          | 1           | 30.780         | <0.001         |
| Residuals     | 38          |                |                |

Table 2b. The outcome of the two-way ANOVA to examine the effects of the number of chicks and year on Magellanic penguin chick mean growth rate (g/day), with the interaction effect.

| <b>Factor</b>   | <b>d.f.</b> | <b>F-value</b> | <b>P-value</b> |
|-----------------|-------------|----------------|----------------|
| No. chicks      | 1           | 8.311          | <0.01          |
| Year            | 1           | 30.780         | <0.001         |
| No. chicks*Year | 1           | 1.067          | 0.308          |
| Residuals       | 37          |                |                |

Thus, nests with one chick in 2016 showed significantly greater mean growth per day than any other nest in either year.

### **3.2 Parent foraging ability**

In 2015 and 2016, most birds' foraging trips (2015: 70%; 2016: 58%) lasted between 18 and 26 hours with an average ( $\pm$  SD) foraging trip of  $23.86 \pm 8.47$  h (this becomes  $25.24 \pm 11.85$  h if Nest 81A for 2016 is included). In 2015 and 2016, most penguins (2015: 70%; 2016: 82%) took six hours to catch less than 200 items of prey (Figure 5 & 6). In 2015, the mean total putative catch was  $564 \pm 361$ , which was higher than 2016 which was  $516 \pm 334$ . There was no significant difference between the medians of the years (Two-Sample Mann-Whitney U-test:  $W = 185.5$ ,  $P = 0.648$ ; 2015 median: 514; 2016 median: 456). The highest total putative catch in 2015 was 1346 (Nest 56) and this also occurred over the longest foraging period of 36

hours (Figure 5). Against this, the lowest total putative catch for 2015 was 63 after the shortest foraging time of six hours (Nest 150) (Figure 5). In 2016, Nest 79 had the highest total putative catch of 1546 and Nest 81A had the longest foraging time of 75 hours (Figure 6). Nest 82A had the lowest total putative catch of 197 and Nest 4A had the shortest foraging time of six hours (Figure 6).

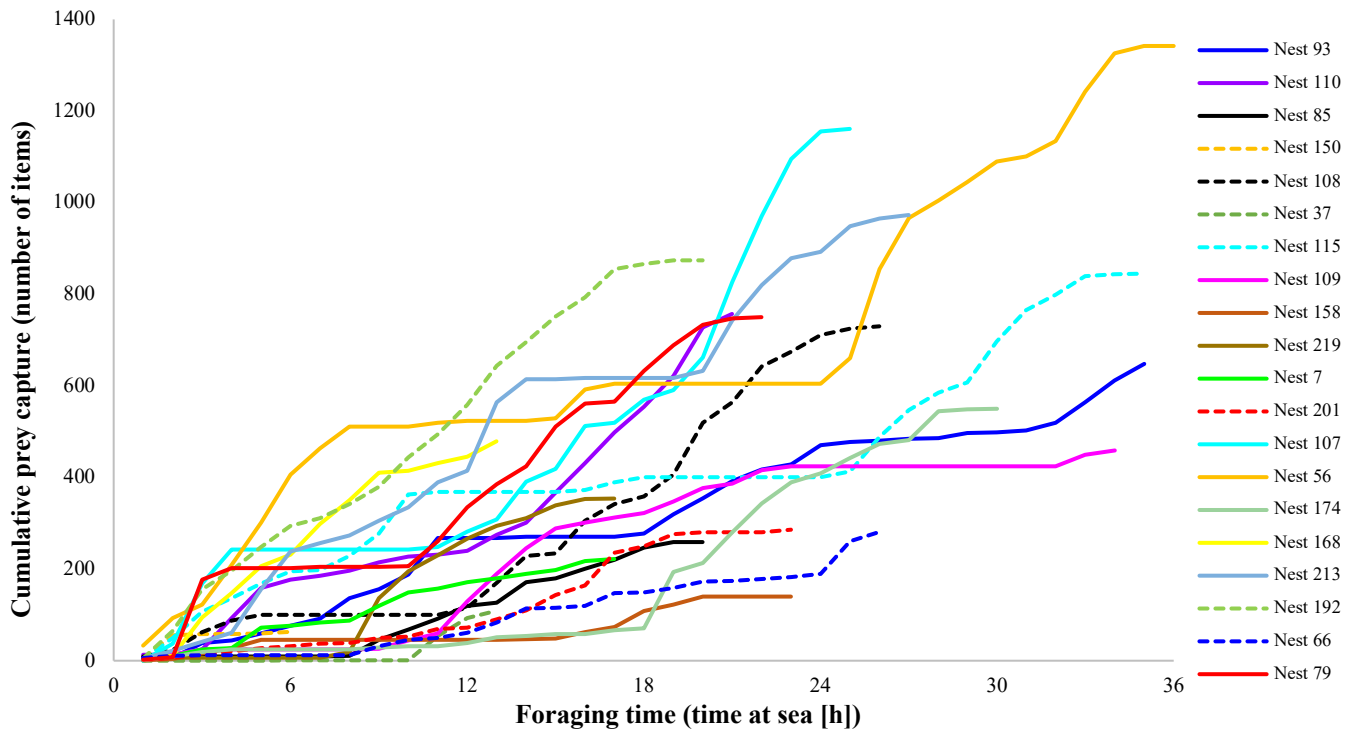


Figure 5. Cumulative putative prey capture of tagged breeding Magellanic Penguins during a single foraging trip in 2015 with corresponding nest ID, excluding trips under six hours. (N = 20).



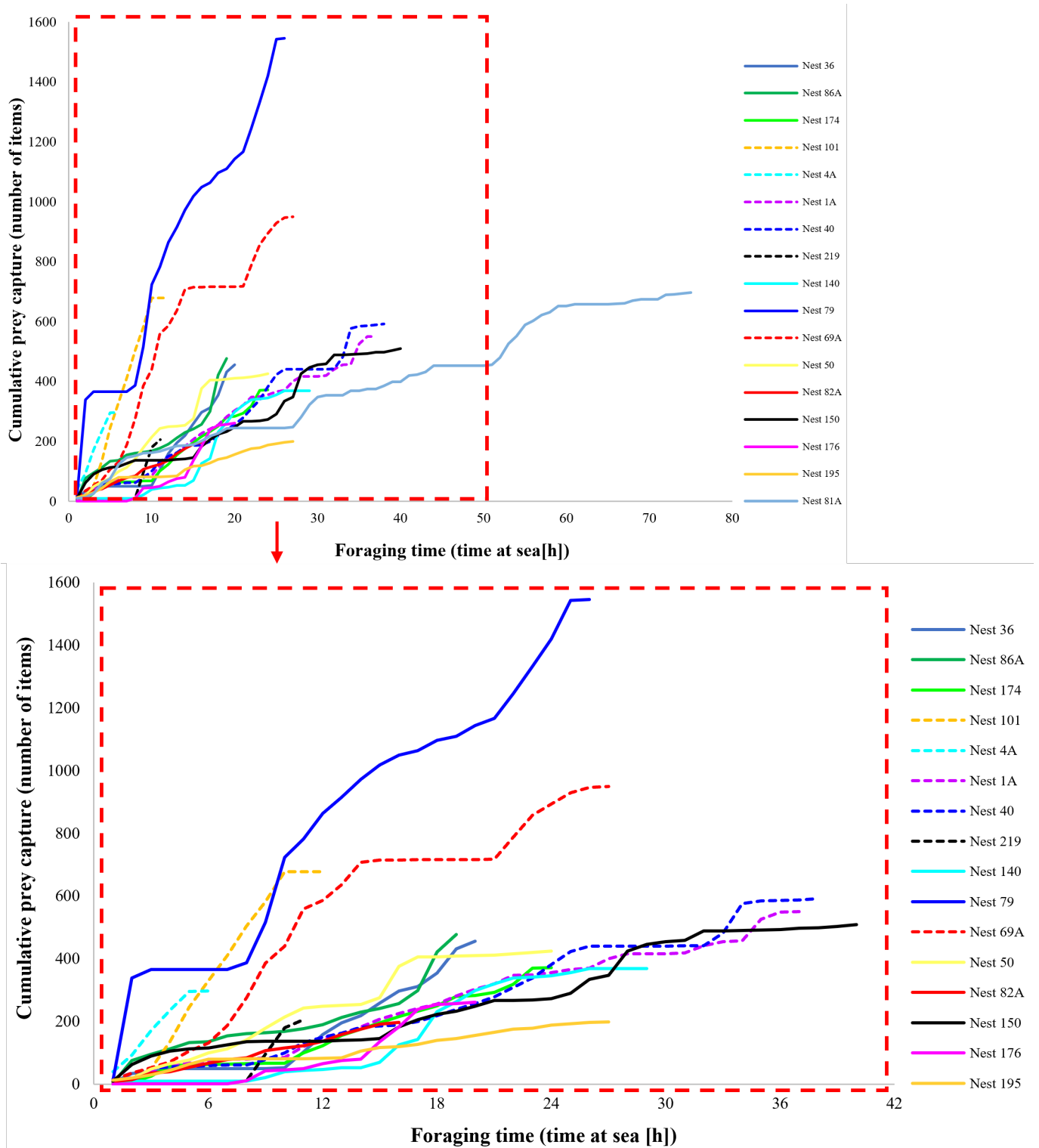


Figure 6. Cumulative putative prey capture of tagged breeding Magellanic Penguins during a single foraging trip in 2016 with corresponding nest ID, excluding trips under six hours. (N = 17).

### 3.3 Effects of CPUE on chick growth

CPUE varied between a minimum of 12 prey items per h (Nest 195, 2016) and a maximum of 120 (Nest 4A, 2016) prey items per h. Linear regression lines for 2015 apparently indicated that as CPUE increased from 18 to 106 prey items caught/h, mean chick growth rate increased slightly from 35 g/day to 38 g/day (Figure 7). In 2016, as CPUE increased from 12 to 120 prey items caught/h, mean growth rate decreased from 62 g/day to 58 g/day (Figure 7). Linear regression lines for nests with one chick apparently indicated that as CPUE increased from 12 to 120 prey items caught/h, mean growth rate decreased from 70 g/day to 40 g/day (Figure 8). For nests with two chicks, as CPUE increased from 18 to 115 prey items caught/h, mean growth rate increased from 38 g/day to 50 g/day (Figure 8). Despite showing an apparent positive relationship in 2015 and for two-chick broods, and a negative relationship in 2016 and for one-chick broods, a linear model showed that CPUE and total catch had no significant effect on mean chick growth rate ( $P = 0.7$ ;  $P = 0.239$ ), but the difference of years and the number of chicks had a significant effect on mean chick growth rate ( $P < 0.001$ ;  $P < 0.001$ ) (Table 3).

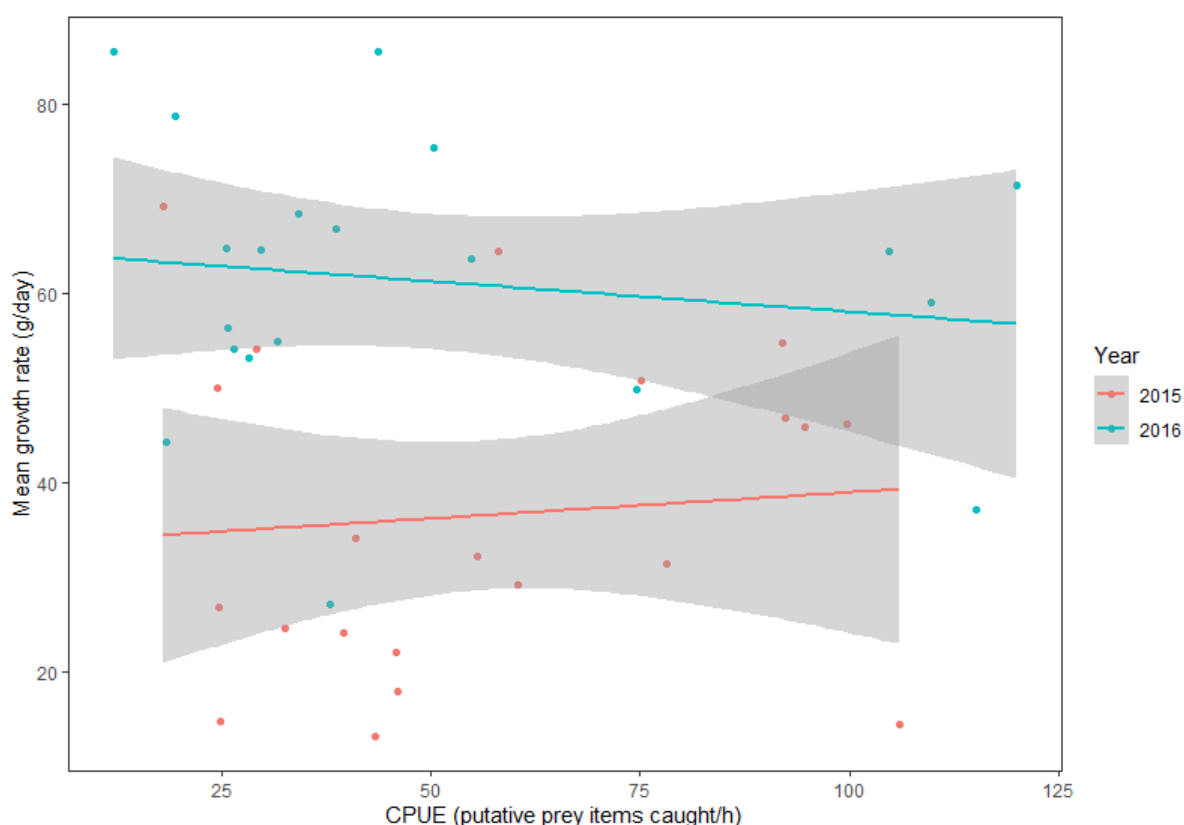


Figure 7. The effect of CPUE (putative prey items caught/h) on mean growth rate (g/day) on Magellanic penguin chicks in 2015 and 2016 with linear regression lines and 95% confidence intervals (2015:  $N = 21$ ; 2016:  $N = 20$ ).

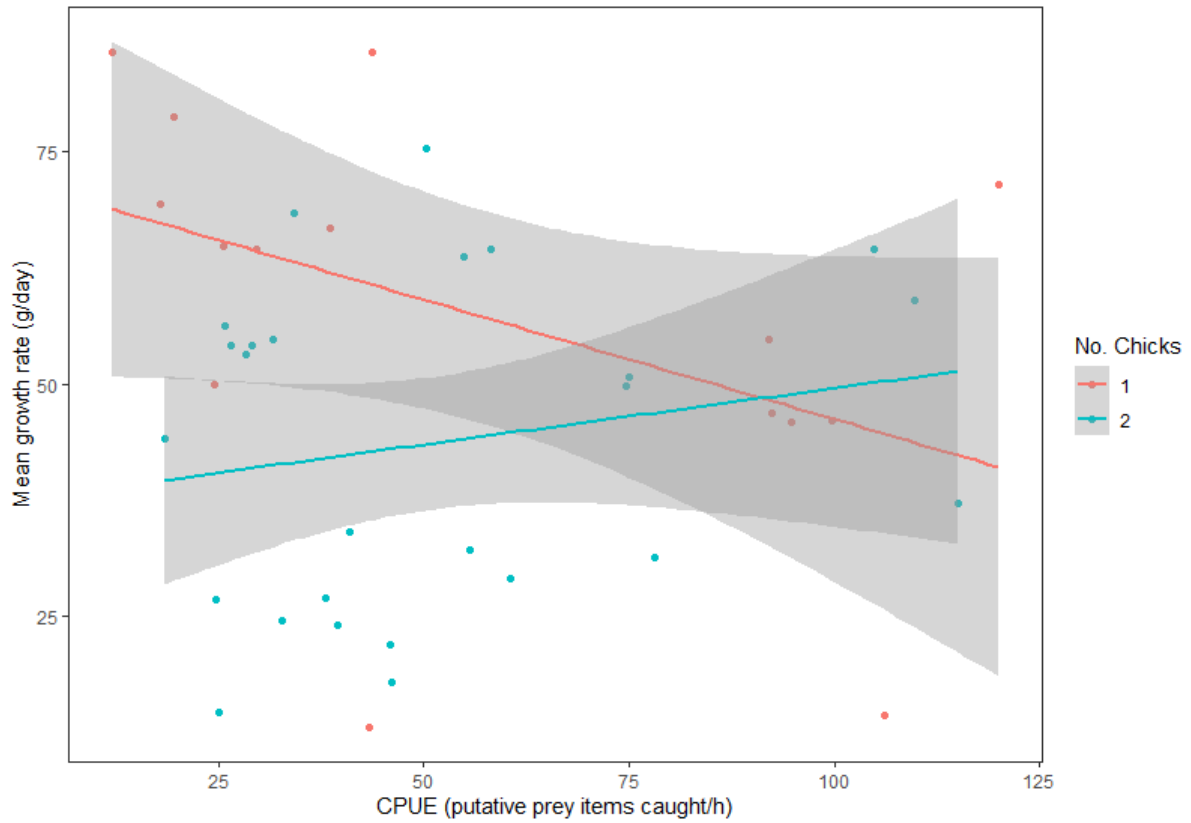


Figure 8. The effect of CPUE (putative prey items caught/h) on mean growth rate (g/day) of Magellanic penguin chicks between nests with one- and two-chick broods with linear regression lines and 95% confidence intervals. (One chick: N = 15; Two chicks: N = 26).

Table 3. ANOVA output of the linear model to examine the effects of CPUE, year, number of chicks and total catch on Magellanic penguin chick mean growth rate (g/day), excluding trips under six hours.

| <b>Factor</b> | <b>d.f.</b> | <b>F-value</b> | <b>P-value</b> |
|---------------|-------------|----------------|----------------|
| CPUE          | 1           | 0.229          | 0.636          |
| Year          | 1           | 27.327         | <0.001         |
| No. Chicks    | 1           | 11.642         | <0.01          |
| Total catch   | 1           | 1.438          | 0.239          |
| Residuals     | 32          |                |                |

## 4 Discussion

### 4.1 Effects of brood size, year and CPUE on chick growth rate

The major significant finding, that there was a difference in growth rates between both one- and two-chick broods is expected and has been documented many times in the literature for seabird species in general (Ricklefs, 1990; Robinson and Hamer, 2000; Spaans, 1971) and penguins in particular (Heezik and Davis, 1990; Meyer et al., 1997; Wagner and Boersma, 2019). The conventional explanation is simply that, when food is limited, the more young have to be fed, the less food there is per individual (Lack, 1947; Meyer et al., 1997). Indeed, there is a whole sub-field of research that looks at the causes and consequences of brood reduction linked to this (Forbes and Mock, 1996; Lack, 1947; Ploger, 1997; Royle and Hamer, 1998). Certainly, the results of my study indicate that food is limiting to some degree, otherwise there would have been no growth rate differences between one- and two-chick broods.

The foraging trips of penguins in both years is consistent with Ashmole's halo hypothesis (Ashmole, 1963). The hypothesis states that large seabird colonies deplete their food resources in the vicinity of their breeding colonies first, before venturing further to find more prey. This would explain why when the birds left the colony, only a few caught prey immediately, such as Nest 79 in 2016, which caught 320 items of prey within the first two hours of the foraging trip, whereas most penguins (2015: 70%; 2016: 82%) took six hours to catch less than 200 items of prey, a seemingly low amount (Figure 6). Although the patchy nature of the prey of seabirds that feed on aggregating species (Clode, 1993; Ramírez et al., 2014; Wilson, 2003) means that there is always a chance that even individuals travelling through/over Ashmole's halo might be 'lucky' enough to find a patch (Wilson et al., 2018b), models have shown that several seabird species (murre, puffins, shearwaters and petrels) have increased foraging ranges as their colony size increases (Gaston et al., 2007). All this provides evidence for Ashmole's halo and helps explain the foraging success patterns that I observed. Having said that, once my study birds began capturing prey, it was clear that there were still great differences in the rate at which the birds acquired putative prey over the course of the foraging trip, both within and between years (Figure 5 & 6). Although there was no significant difference in the actual medians of total putative prey catch between the years ( $P = 0.648$ ), there was greater visible variability within 2015 (Figure 5). This could clarify why-the overall mean ( $\pm$  SE) chick growth rate was almost twice as high in 2016 as in 2015 ( $61.2 \pm 3.35$  g/day vs  $36.5 \pm 3.69$  g/day), which would be difficult to explain if not in terms of prey capture variability.

There was no significant relationship between CPUE and Magellanic penguin chick growth rates and no obvious relationship with foraging duration, possibly due to the considerable inter-individual variability of these three metrics (Table 3; Appendix 1) (Ropert-Coudert et al., 2004). This suggests that perhaps neither (or both) chick growth rates and my derivation for CPUE are appropriate simple proxies for foraging success and thus prey availability in Magellanic penguins (see limitations).

#### **4.2 CPUE in relation to parent foraging ability and prey abundance**

Variability in CPUE would imply variability in prey abundance or at least the rate at which prey is encountered or accumulated. Variability in CPUE can translate to day-to-day variation in how much food chicks receive, with high variability in food delivery not being conducive to rapid, sustained growth (Boersma et al., 1990; Piatt et al., 2007; Weimerskirch et al., 2001). In the case of penguins, for example, both provisioning adults can incur periods of low food abundance, during which chicks starve but then, suddenly, from one day to the next, arrive back at the nest with much food in rapid successions, satiating the brood's ability to process the food (Wilson et al., 1989). This effectively alternates periods of starvation with over-feeding. Thus, variation *per se* may cause low and even decreased growth rates even if mean/median amounts show no differences in the amount of food brought back.

When competition for food is high (e.g. due to low prey availability), seabirds may feed closer to the colony on lower quality prey (Forero et al., 2002b) or alternatively expand their foraging range to acquire the normal higher quality prey (Burke and Montevecchi, 2009; Kitaysky et al., 2000; Monaghan et al., 1992). The difference in prey qualities (Jackson and Ryan, 1986; Wilson et al., 1985), and the ease with which they can be acquired makes understanding foraging 'success', either in terms of CPUE or brood growth, difficult to standardise. Although some birds' CPUEs may have been higher in 2015 due to shorter trips and a higher prey count, they may have caught less nutritious prey than birds which ventured further, stayed out longer, and caught less prey. As squid has a lower energy content than fish (Cherel and Ridoux, 1992; Herling et al., 2005), Magellanic penguins chicks that feed on a higher quality diet (anchovy, hake) have a better body condition at fledging than chicks fed on a lower quality diet of squid (Forero et al., 2002b; Heath and Randall, 1985). As a result, birds with a high CPUE in 2015 may have had chicks exhibiting a lower overall growth rate due to them being fed lower quality prey. Conversely, birds that chose to undergo longer foraging trips in order to obtain higher quality prey, could have incurred lower growth rates due to lower rates of provisioning (Burke and Montevecchi, 2009; Horswill et al., 2017). In short, the

general variability in 2015 may have been due to low prey availability, with different penguins' strategies affecting chick growths variously. However, with the information available it is impossible to say what really happened.

In 2015, 55% of the birds and 29% of the birds in 2016 had at least one period lasting more than three hours where no prey was ingested, causing a plateau (Figure 5 & 6). This is not necessarily due to poor foraging success. Nesting penguins must feed both themselves and their chicks (Ballard et al., 2010; Booth and McQuaid, 2013). Most birds eat for themselves first, then pause to digest the food, before beginning to acquire prey for their chicks by delaying digestion in their stomachs so that they can transfer it to their chicks when they return to the colony (Boersma et al., 2009; Kirkwood and Robertson, 1997). When seabirds, including penguins, are exposed to prey abundance that is critically low, they tend to focus on keeping themselves alive and/or keep one chick alive while sacrificing the other in order to continue reproducing in the future when food availability is more stable (Croll et al., 2006; Furness and Monaghan, 2012; Lack, 1954). This could explain why a greater proportion of birds encountered more plateaus (periods of digestion) and why the growth rate of chicks in 2015 was lower than in 2016: i.e. because penguins in 2015 prioritised feeding themselves over their chicks due to reduced prey availability.

### **4.3 Using chick growth rate as an indicator of prey availability**

This evidence of the varying level of parental quality could be why there was no significant link between CPUE and chick growth rate, and why using chick growth rate as an indicator of prey availability could be naïve. In the first instance, seabird prey can be abundant but inaccessible: For example, Patagonian sprat (*Sprattus fuegensis*) is concentrated within the first 5 m of the water column at night and descends deeper into the water column at dawn where it is found within a few meters of the seabed (Sánchez et al., 1995), while anchovies form compact shoals at different depths during the day (Hansen et al. 2001; Gudmundsson and Gamberale 1972), and scatter close to the water surface at night (Hansen and Madirolas, 1996). This variable distribution with respect to depth has consequences for the energy invested to acquire prey in air-breathing predators operating from the surface depending on when they forage, with birds taking deeper prey having to pay more energy to commute between the surface and depths where prey are found (Peters et al., 1998). Thus, prey can be plentiful, but energetically expensive to exploit.

Secondly, the birds might travel north but prey could be more available in the south and *vice versa*. One presumes that the term 'abundance' refers to 'within the foraging area of the

birds' but the birds might not travel in the right direction. Anchovy is typically located north of 44°S whereas sprat is located south of 50°S (Frere et al., 1996) and Magellanic penguins are known to exclusively consume anchovy in the north (Frere et al., 1996; Sclaro et al., 1999; Sclaro and Badano, 1986) and sprat in the south (Clausen and Pütz, 2002; Forero et al., 2002a; Frere et al., 1996; Sclaro et al., 1999). Prey densities can be higher in the south resulting in shorter foraging trips (Wilson et al., 2005), but whether the birds decide to forage for their preferred but less abundant prey of anchovy, or more abundant sprat may depend on individual choice. In this, it is notable that there is good evidence that colonial seabirds carry out group-based foraging trips (Götmark et al., 1986; McInnes et al., 2017; Sutton et al., 2015), so if the first early departed bird(s) travels in the direction of the less abundant prey, this might set a precedent for birds leaving later.

Finally, varying school size of seabird's prey (pelagic fish) can affect the likelihood that they will be encountered. Large schools of fish have a lower surface area to volume ratio than smaller schools, so the mean surface area exposed to predators of individual fish decreases as the school size expands, lowering the predator-prey encounter rate (The Selfish Herd Hypothesis - Hamilton 1971) (Cushing and Jones, 1968). So, one would suggest that smaller schools are more beneficial to foraging birds. However, small schools of fish at depth are harder to be relocated than a larger school after the penguin has resurfaced to breathe (Wilson and Wilson, 1990), so that birds may have to travel further to relocate another fish school once they have surfaced to breath. Therefore, predator-prey encounter rates can be highly variable, depending on whether the birds get 'lucky' by either quickly finding a large school or several patches of small schools or unlucky by taking longer to find a large school or being unable to relocate smaller schools (Wilson, 1985; Wilson and Wilson, 1990). Thus, prey may be abundant but difficult to find according to school size. In short, the expectation that there should be a link between chick growth and prey abundance is naïve due to the varying factors mentioned.

#### **4.4 Limitations/considerations of the data**

The current study's findings are subject to several limitations. The dive metrics used in the algorithm to determine a PPCE was based on extensive research carried out by Del Caño et al (2021) and Wilson et al (2010) to determine that prey capture events are carried out when the VeDBA value is greater than 0.4 g and depth greater than 2 m. However, there is a chance that the algorithm could be marking behaviour as a prey capture event with these criteria when no prey capture occurred. For example, a penguin could be fleeing from a predator at high speeds

which could cause the algorithm to determine this as a prey capture event or there is a chance that the penguin might have failed to secure fish during its prey capture attempt. Therefore, the values for prey capture should be taken as an assumed/attempted prey capture event and not an actual prey capture event, with values presented possibly being overestimates.

Only one foraging trip from one parent was recorded throughout the study which is not enough to summarise the events during the chick growth weighing period of up to 25 days. During this time, each parent typically undergoes an average of four to five foraging trips each, eight to ten trips in total (Miller et al., 2009; Stokes and Boersma, 1999; Williams and Rothery, 1990) which means that the data available only covers a small portion of what typically occurs during that time frame. This assumes that the unrecorded foraging trips and those of the other parent are similar. However, as shown, there is high variability between tagged penguins, so this is unlikely to be the case. As a result, this limitation is likely to have skewed the study's results.

The size and species of prey were not recorded and therefore were assumed to be constant. Magellanic penguins are monomorphic and typically only eat anchovies, although there is a possibility that on some occasions (as discussed), penguins could have caught different species or sizes of prey depending on the availability of their preferred prey. This means that some penguins could have caught fewer prey but of larger sizes (e.g. squid), resulting in a lower CPUE, which could be no different to birds catching more, but smaller prey, resulting in a higher CPUE.

The data from the foraging trips may not have matched the measurements of chick growth because not enough of them were recorded. For example, the chick in Nest 107 (2015) had a very low growth rate and began to lose weight from 28/11/2015 to 10/12/2015, but the foraging trip recorded is from 12/12/2015, during which the parent caught 1161 items of prey and had a CPUE of 106, one of the highest in 2015, resulting in the chick weighing 120 g more on 13/12/2015 than the previous weigh in on 10/12/2015. This shows that, based on the data from the foraging trip, the parent could have found a good patch of prey or was simply a better forager than the other parent which was previously feeding the chick. However, due to previous measurements, the mean growth weight was 14 g/day, indicating that a high CPUE had no effect on growth rate. This demonstrates that the relationship between CPUE and chick growth rate could have been misrepresented by only recording one foraging trip.

Finally, the data loggers attached to the penguins could have affected its foraging ability as it has been documented in the past (Saraux et al., 2011). Externally placed tags can cause penguins to perform almost twice as many shallow dives (Ropert-Coudert et al., 2000) and



encounter longer foraging trips (Taylor et al., 2001) than birds without external tags. Although the tags were attached and shaped to minimise hydrodynamic drag, it could have still affected the birds foraging performance, and since this was not measured it is unknown on the effects the tag had on the penguin.

Nevertheless, this study's attempt was a useful one and has covered a wide range of topics, adding to the evidence linking foraging success, prey availability and chick growth in Magellanic penguins. In the future, and to improve the listed limitations, both parents should be tagged for at least three foraging trips each so that an average can be calculated to get a better representation of foraging ability. Having foraging trip data for both parents from the beginning, middle, and end of the chick growth measurement period would allow for a better comparison and determination of a link between foraging success and chick growth. As well as this, to find out more about prey capture and whether or not a successful prey capture event has taken place, video cameras (Del Caño et al., 2021) should be attached to the foraging birds in tandem with tri-axial acceleration tags to show if the birds have caught anything and what they have caught in terms of prey size and type.

## **5 Conclusion**

This study has shown that there is high inter-individual variability between chick growth rates and CPUE and why there was no relationship between the two. The difference of growth rates between both the years and within one- and two-chick broods demonstrated the varying foraging success, prey abundance and encounter between individuals. Variability can be caused by the size and species of prey penguins catch during a foraging trip, whether the birds choose to feed for themselves or their chicks, inaccessible prey, travelling in the wrong direction or the varying school size of their prey and whether they are 'lucky' enough to find one big prey patch or numerous smaller patches of prey. Variability of food delivery on a day-to-day basis can cause low and even decreased growth rates even if mean/median amounts show no difference in food delivery. This does not mean that chick growth rate cannot be used as a proxy for food abundance, but it should be used with careful consideration alongside CPUE, which has been measured for a substantial amount of the chick growth phase, with cameras as well as tags to determine the size and species of the prey.

## 6 Appendices

### Appendix 1: Table 4

Table 4. Outcome of the Spearman's rank correlation coefficient between total time underwater (h) and total time at sea (h) with CPUE (putative prey caught/h), with and without the outlier (Nest 81A)

| <b>Spearman's rank correlation coefficient</b>  | <b>P-value</b> | <b>R<sup>2</sup></b> |
|---|----------------|----------------------|
| Total time underwater x CPUE                    | 0.027          | - 0.36               |
| Total time underwater x CPUE (without Nest 81A) | 0.059          | - 0.32               |
| Total time at sea x CPUE                        | 0.161          | - 0.24               |
| Total time at sea x CPUE (without Nest 81A)     | 0.230          | - 0.19               |

## Appendix 2: Correlation Coefficient R script (Figure 2)

```
# Correlation coefficient
install.packages("ggplot2")
library("ggplot2")

# Attach data and check if variables are correct
attach(correlation_coefficient)
str(correlation_coefficient)

#####

# Scatter graph
p1 <- ggplot(correlation_coefficient, aes(x = CPUE_vedba, y = CPUE_time)) +
  geom_point(shape = 16) + geom_smooth(method = lm) +
  xlab(expression(paste("Summed VeDBA (", italic("g"), ")"))) +
  ylab("Total time underwater (h)") + coord_cartesian(xlim=c(0.001, 0.007)) +
  scale_x_continuous(breaks = seq(0.001, 0.007, 0.001)) +
  coord_cartesian(ylim=c(0, 150)) + scale_y_continuous(breaks = seq(0, 150, 25))
p1 + theme_bw() + theme(panel.grid.major = element_blank(),
  panel.grid.minor = element_blank()) +
  theme(axis.text = element_text(size=14)) +
  theme(axis.title = element_text(size=18))

#####

# Correlation Coefficient
# Check assumptions
shapiro.test(CPUE_vedba)
shapiro.test(CPUE_time)

# CPUE_time assumptions not met so non-parametric correlation test will be used
cor1 <- cor.test(CPUE_time, CPUE_vedba, method = "spearman")
cor1

#####

detach(correlation_coefficient)
```

### Appendix 3: Chick growth histogram R script (Figure 4)

```
# Chick growth histogram
# Install required packages
install.packages("ggplot2")
library(ggplot2)
# Attach data and check if variables are correct
attach(chick_growth_histogram)
str(chick_growth_histogram)
# change year into a factor
chick_growth_histogram$Year<- factor(chick_growth_histogram$Year,
                                     levels = c("2015", "2016"))
#####
# Histogram
p1 <- ggplot(chick_growth_histogram, aes (x = growth_rate)) +
  geom_histogram(aes(fill = Year), binwidth = 5,
                colour = "black", show.legend = FALSE) +
  facet_grid(Year ~ .) + labs(x = "Growth rate (g/day)", y = "Frequency") +
  theme_classic()
p1
#####
detach(chick_growth_histogram)
```

## Appendix 4: R script for main statistical analysis, including correlation coefficient (Appendix 1)

```
# Chick growth and foraging success data analysis

# Install required packages

install.packages("boot")

install.packages("ggplot2")

install.packages("tidyverse")

install.packages("dplyr")

library(ggplot2)

library(tidyverse)

library(dplyr)

require(boot)

# Attach the data and check if variables are correct

attach(combined_chick)

str(combined_chick)

# Nest 79, 150 and 174 in 2016 changed name to 79A 150A and 174A due to

# duplicated names in 2015

# Change variables into factors

combined_chick$no_chicks<- factor(combined_chick$no_chicks,

                                levels = c("1", "2"))

combined_chick$year<- factor(combined_chick$year, levels = c("2015", "2016"))

combined_chick$nest<-factor(combined_chick$nest)

#####

# Difference between GR and no. chicks with year interaction
```

```

# Violin plot with +/- SD

p1 <- ggplot(combined_chick, aes(x = no_chicks, y = mean_growth_rate)) +
  xlab("No. Chicks") + ylab("Mean growth rate (g/day)") + labs(fill = "Year")

p1 + geom_violin(aes(fill = year), trim = FALSE,
  position = position_dodge(0.9))+ geom_boxplot(aes(fill = year),
  width = 0.15, position = position_dodge(0.9)) + theme_bw() +
  theme(panel.grid.major = element_blank(), panel.grid.minor = element_blank())

# Stats for boxplot in violin plot to find median values

stats.1 <- boxplot(mean_growth_rate ~ no_chicks + year)

stats.1

# Mean, SD, SE of data

stats.2 <- combined_chick %>% group_by(no_chicks, year) %>%
  summarise(mean = mean(mean_growth_rate), sd = sd(mean_growth_rate), n = n(),
  se = sd/sqrt(n))

stats.2

stats.3 <- combined_chick %>% group_by(year) %>%
  summarise(mean = mean(mean_growth_rate), sd = sd(mean_growth_rate), n = n(),
  se = sd/sqrt(n))

stats.3

# Check assumptions

YearChick <- interaction(no_chicks, year)

bartlett.test(mean_growth_rate ~ YearChick)

```

```

# Assumptions met

# Two-way ANOVA
m1 <- aov(mean_growth_rate ~ no_chicks*year)
summary(m1)
m2 = update(m1,~.-no_chicks:year)
summary(m2)

# Check to see which model is the better fit
AIC(m1, m2)

# Both models are very similar
# Check residuals
shapiro.test(m1$residuals)
hist(m1$residuals)
shapiro.test(m2$residuals)
hist(m2$residuals)

# Doesn't deviate from normal distribution
#####

# If CPUE has a significant effect on growth rate

# Scatter graph for both years with trend line and 95% confidence intervals
p2 <- ggplot(combined_chick, aes(x = cpue, y = mean_growth_rate,
    colour = year)) + geom_point(shape = 16) + geom_smooth(method=lm) +
    xlab("CPUE (putative prey items caught/h)") + ylab("Mean growth rate (g/day)")
p2 + labs(col="Year")+ theme_bw() + theme(panel.grid.major = element_blank(),

```

```

panel.grid.minor = element_blank())

# Scatter graph for no. chicks with trend line and 95% confidence intervals
p3 <- ggplot(combined_chick, aes(x = cpue, y = mean_growth_rate,
  colour = no_chicks)) + geom_point(shape = 16) + geom_smooth(method=lm) +
  xlab("CPUE (putative prey items caught/h)") + ylab("Mean growth rate (g/day)")
p3 + labs(col="No. Chicks")+ theme_bw() +
  theme(panel.grid.major = element_blank(), panel.grid.minor = element_blank())

# Linear model to show the effects of CPUE, year, no. chicks and total catch on
# mean growth rate
m3 <- lm(mean_growth_rate ~ cpue*year*no_chicks*total_catch)
summary(m3)

# Deletion of non-significant interaction terms
m3A = update(m3, ~ .-cpue:year:no_chicks:total_catch)
summary(m3A)
m3B = update(m3A, ~ .-year:no_chicks:total_catch)
summary(m3B)
m3C=update(m3B, ~ .-cpue:no_chicks:total_catch)
summary(m3C)
m3D=update(m3C, ~ .-cpue:year:total_catch)
summary(m3D)
m3E=update(m3D, ~ .-cpue:year:no_chicks)
summary(m3E)

```



```

m3F=update(m3E,~ .-no_chicks:total_catch)
summary(m3F)
m3G=update(m3F,~ .-year:total_catch)
summary(m3G)
m3H=update(m3G,~ .-cpue:total_catch)
summary(m3H)
m3I=update(m3H,~ .-year:no_chicks)
summary(m3I)
m3J=update(m3I,~ .-cpue:no_chicks)
summary(m3J)
m3K=update(m3J,~ .-cpue:year)
summary(m3K)
# Check which model is the better fit
AIC(m3, m3A, m3B, m3C, m3D, m3E, m3F, m3G, m3H, m3I, m3J, m3K)
# All models are similar

# Final reduced model
m4 <- lm(mean_growth_rate ~ cpue + year + no_chicks + total_catch)
summary(m4)
anova(m4)

# Check residuals
shapiro.test(m4$residuals)
hist(m4$residuals)

```

```
#####
```

```
# The relationship between CPUE and total time underwater
```

```
# Plot data
```

```
p4 <- ggplot(combined_chick, aes(x = ttu, y = cpue)) +  
  geom_point(shape = 16) + geom_smooth(method = lm) +  
  xlab("Total time underwater (h)") +  
  ylab("CPUE (putative prey items/h)")  
p4 + theme_bw() + theme(panel.grid.major = element_blank(),  
  panel.grid.minor = element_blank()) +  
  theme(axis.text = element_text(size=14)) +  
  theme(axis.title = element_text(size=18))
```

```
# Check assumptions
```

```
shapiro.test(cpue)
```

```
shapiro.test(ttu)
```

```
# Assumptions not met
```

```
# Correlation coefficient
```

```
cor1 <- cor.test(ttu, cpue, method = "spearman", use = "complete.obs")
```

```
cor1
```

```
# Test without 81A (outlier)
```

```
test <- combined_chick[-c(39),]
```

```

p5 <- ggplot(test, aes(x = ttu, y = cpue)) +
  geom_point(shape = 16) + geom_smooth(method = lm) +
  xlab("Total time underwater (h)") +
  ylab("CPUE (putative prey items/h)")

p5 + theme_bw() + theme(panel.grid.major = element_blank(),
  panel.grid.minor = element_blank()) +
  theme(axis.text = element_text(size=14)) +
  theme(axis.title = element_text(size=18))

# Correlation coefficient
cor2 <- cor.test(test$ttu, test$cpue, method = "spearman", use = "complete.obs")

cor2

#####

# The relationship between CPUE and total time at sea

# Plot data

p6 <- ggplot(combined_chick, aes(x = tta, y = cpue)) +
  geom_point(shape = 16) + geom_smooth(method = lm) +
  xlab("Total time at sea (h)") +
  ylab("CPUE (putative prey items/h)")

p6 + theme_bw() + theme(panel.grid.major = element_blank(),
  panel.grid.minor = element_blank()) +
  theme(axis.text = element_text(size=14)) +
  theme(axis.title = element_text(size=18))

```

```

# Check assumptions

shapiro.test(cpue)

shapiro.test(ttas)

# Assumptions not met

# Correlation coefficient

cor3 <- cor.test(ttas, cpue, method = "spearman", use = "complete.obs")

cor3

# Test without 81A (outlier)

test2 <- combined_chick[-c(39),]

p7 <- ggplot(test2, aes(x = ttas, y = cpue)) +
  geom_point(shape = 16) + geom_smooth(method = lm) +
  xlab("Total time at sea (h)") +
  ylab("CPUE (putative prey items/h)")

p7 + theme_bw() + theme(panel.grid.major = element_blank(),
  panel.grid.minor = element_blank()) +
  theme(axis.text = element_text(size=14)) +
  theme(axis.title = element_text(size=18))

# Correlation coefficient

cor4 <- cor.test(test2$ttas, test2$cpue, method = "spearman",

```

```
use = "complete.obs")
```

```
cor4
```

```
#####
```

```
detach(combined_chick)
```

```
#####
```

## Appendix 5: Mean, Standard Deviation and Standard Error values for parent foraging ability (Figure 5 & 6) and t-test / Mann-Whitney test R script

```
# Sd for cumualtive data - parent foraging ability
# Download required packages
install.packages("dplyr")
library(dplyr)
# Attach data and check if variables are correct
attach(cumulative_stats)
str(cumulative_stats)
# Change variables into factors
cumulative_stats$year<- factor(cumulative_stats$year,
                              levels = c("2015", "2016"))
cumulative_stats$nest<-factor(cumulative_stats$nest)
#####
# SD and mean of total foraging time without nest 81A for 2016
# Get rid of 81A from dataset
cumulative_stats_1 <- cumulative_stats[-c(36),]
# stats
cumulative_stats_1 %>% summarise(mean = mean(total_foraging_time),
                                sd = sd(total_foraging_time))

# SD and mean of total foraging time with 81A
cumulative_stats %>% summarise(mean = mean(total_foraging_time),
                                sd = sd(total_foraging_time))

# Mean total putative catch & SD
cumulative_stats %>% group_by(year) %>% summarise(mean = mean(total_catch),
                                                  sd = sd(total_catch))
```

```

#####
# two-sample t test on total catch between years
m1 <- t.test(total_catch ~ year)
m1
# Normality test on data
shapiro.test(total_catch)
# Data does not follow normal distribution so carry out non-parametric
# alternative - 2-sample Mann-Whitney U-test
m2 <- wilcox.test(total_catch ~ year)
m2
#####
# Median values for each year
stats <- boxplot(total_catch ~ year)
stats
#####
detach(cumulative_stats)

```

## 7 References

- Ainley, D.G., Ballard, G., Dugger, K.M., Harvey, H.T., 2006. Competition Among Penguins And Cetaceans Reveals Trophic Cascades In The Western Ross Sea, Antarctica. *Ecology* 87, 2080–2093. <https://doi.org/10.1890/0012-9658>
- Aleman, D., Iribarne, O.O., Acha, E.M., 2013. Effects of a large-scale and offshore marine protected area on the demersal fish assemblage in the Southwest Atlantic. *ICES J. Mar. Sci.* 70, 123–134. <https://doi.org/10.1093/icesjms/fss166>
- Ancel, A., Cristofari, R., Trathan, P.N., Gilbert, C., Fretwell, P.T., Beaulieu, M., 2017. Looking for new emperor penguin colonies? Filling the gaps. *Glob. Ecol. Conserv.* 9, 171–179. <https://doi.org/10.1016/J.GECCO.2017.01.003>
- Andersen, R., Gaillard, J.-M., Linnell, J.D.C., Duncan, P., 2000. Factors affecting maternal care in an income breeder, the European roe deer. *J. Anim. Ecol.* 69, 672–682. <https://doi.org/10.1046/J.1365-2656.2000.00425.X>
- Angelier, F., Weimerskirch, H., Dano, S., Chastel, O., 2007. Age, experience and reproductive performance in a long-lived bird: A hormonal perspective. *Behav. Ecol. Sociobiol.* 61, 611–621. <https://doi.org/10.1007/s00265-006-0290-1>
- Ashmole, N.P., 1963. The Regulation of Numbers of Tropical Oceanic Birds. *Ibis (Lond. 1859)*. 103b, 458–473. <https://doi.org/10.1111/j.1474-919X.1963.tb06766.x>
- Ballard, G., Dugger, K.M., Nur, N., Ainley, D.G., 2010. Foraging strategies of Adélie penguins: adjusting body condition to cope with environmental variability. *Mar. Ecol. Prog. Ser.* 405, 287–302. <https://doi.org/10.3354/MEPS08514>
- Bannerot, S.P., Austin, C.B., 1983. Using Frequency Distributions of Catch per Unit Effort to Measure Fish-Stock Abundance. *Trans. Am. Fish. Soc.* 112, 608–617.
- BirdLife International. 2020. *Spheniscus magellanicus*. *The IUCN Red List of Threatened Species* 2020: e.T22697822A157428850. <https://dx.doi.org/10.2305/IUCN.UK.2020-3.RLTS.T22697822A157428850.en>
- Boersma, P.D., Frere, E., Kane, O., Pozzi, L.M., Pütz, K., Raya Rey, A., Rebstock, G.A., Simeone, A., Smith, J., Van Buren, A., Yorio, P., Garcia Borboroglu, P., 2013. Magellanic Penguin (*Spheniscus magellanicus*), in: Garcia Borboroglu, P., Boersma, P.D. (Eds.), *Penguins. Natural History and Conservation*. University of Washington Press, Seattle, Washington, USA, pp. 233–263.



- Boersma, P.D., Rebstock, G.A., Frere, E., Moore, S.E., 2009. Following the fish: penguins and productivity in the South Atlantic. *Ecol. Monogr.* 79, 59–76.  
<https://doi.org/10.1890/06-0419.1>
- Boersma, P.D., Stokes, D.L., Yorio, P.M., 1990. Reproductive Variability and Historical Change of Magellanic Penguins (*Spheniscus magellanicus*) at Punta Tombo, Argentina, in: Davis, L., Darby, J. (Eds.), *Penguin Biology*. Academic Press Inc, San Diego, California, pp. 15–43.
- Booth, J.M., McQuaid, C.D., 2013. Northern rockhopper penguins prioritise future reproduction over chick provisioning. *Mar. Ecol. Prog. Ser.* 486, 289–304.  
<https://doi.org/10.3354/meps10371>
- Boyd, I.L., 2003. State-dependent fertility in pinnipeds: contrasting capital and income breeders, *Func Ecol.* 14, 623–630. <https://doi.org/10.1046/j.1365-2435.2000.t01-1-00463.x>
- Burke, C.M., Montevecchi, W.A., 2009. The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. *J. Zool.* 278, 354–361.  
<https://doi.org/10.1111/j.1469-7998.2009.00584.x>
- Carroll, G., Harcourt, R., Pitcher, B.J., Slip, D., Jonsen, I., 2018. Recent prey capture experience and dynamic habitat quality mediate short-term foraging site fidelity in a seabird. *Proc. R. Soc. B Biol. Sci.* 285, 1–8. <https://doi.org/10.1098/rspb.2018.0788>
- Cavallo, C., Chiaradia, A., Deagle, B.E., Hays, G.C., Jarman, S., McInnes, J.C., Ropert-Coudert, Y., Sánchez, S., Reina, R.D., 2020. Quantifying prey availability using the foraging plasticity of a marine predator, the little penguin. *Funct. Ecol.* 34, 1626–1639.  
<https://doi.org/10.1111/1365-2435.13605>
- Chastel, O., Weimerskirch, H., Jouventin, P., 1995. Body Condition and Seabird Reproductive Performance: A Study of Three Petrel Species. *Ecology* 76, 2240–2246.  
<https://doi.org/10.2307/1941698>
- Cherel, Y., Ridoux, V., 1992. Prey species and nutritive value of food fed during summer to King Penguin *Aptenodytes patagonica* chicks at Possession Island, Crozet Archipelago. *Ibis (Lond. 1859)*. 134, 118–127. <https://doi.org/10.1111/j.1474-919X.1992.tb08388.x>
- Clausen, A.P., Pütz, K., 2002. Recent trends in diet composition and productivity of gentoo, magellanic and rockhopper penguins in the Falkland Islands, in: *Aquatic Conservation: Marine and Freshwater Ecosystems*. John Wiley & Sons, Ltd, pp. 51–61.  
<https://doi.org/10.1002/aqc.476>

- Clode, D., 1993. Colonially breeding seabirds: Predators or prey? *Trends Ecol. Evol.* 8, 336-338. [https://doi.org/10.1016/0169-5347\(93\)90242-H](https://doi.org/10.1016/0169-5347(93)90242-H)
- Crawford, R. J. M., Barham, P.J., Underhill, L.G., Shannon, L.J., Coetzee, J.C., Dyer, B.M., Leshoro, T. M., Upfold, L., 2006. The influence of food availability on breeding success of African penguins *Spheniscus demersus* at Robben Island, South Africa. *Biol. Conserv.* 132, 119–125. <https://doi.org/10.1016/j.biocon.2006.03.019>
- Crocker, D.E., Williams, J.D., Costa, D.P., Le Boeuf, B.J., 2001. Maternal Traits And Reproductive Effort In Northern Elephant Seals. *Ecology* 82, 3541–3555. <https://doi.org/10.1890/0012-9658>
- Croll, D.A., Demer, D.A., Hewitt, R.P., Jansen, J.K., Goebel, M.E., Tershy, B.R., 2006. Effects of variability in prey abundance on reproduction and foraging in chinstrap penguins (*Pygoscelis antarctica*). *J. Zool.* 269, 506–513. <https://doi.org/10.1111/j.1469-7998.2006.00090.x>
- Cushing, D.H., Jones, F.R.H., 1968. Why do fish school? *Nature* 218, 918–920. <https://doi.org/10.1038/218918b0>
- Davis, L.S., Renner, M., 2010. Penguins. A & C Black Publishers Ltd, Soho, London, England, pp. 55-56.
- Del Caño, M., Quintana, F., Yoda, K., Dell’Omo, G., Blanco, G.S., Gómez-Laich, A., 2021. Fine-scale body and head movements allow to determine prey capture events in the Magellanic Penguin (*Spheniscus magellanicus*). *Mar. Biol.* 168, 84. <https://doi.org/10.1007/s00227-021-03892-1>
- Drent, R.H., Daan, S., 1980. The Prudent Parent: Energetic Adjustments in Avian Breeding. *Ardea* 68, 225–252. <https://doi.org/10.5253/arde.v68.p225>
- Falabella V., Tamini L., García Borboroglu P., Frere E., Seco Pon J.P., S.C.A., Stanworth A., Suazo C., C.C., 2019. Report of the IUCN Regional Red List First Workshop for Species of the Patagonian Sea: SeaBirds. Forum for the Conservation of the Patagonian Sea.
- Fernandez, S.J., Yorio, P., Ciancio, J.E., 2019. Diet composition of expanding breeding populations of the Magellanic Penguin. *Mar. Biol. Res.* 15, 84–96. <https://doi.org/10.1080/17451000.2019.1596286>
- Forbes, L.S., Mock, D.W., 1996. Food, information and avian brood reduction. *Ecoscience* 3, 45–53. <https://doi.org/10.1080/11956860.1996.11682314>
- Forero, M.G., Hobson, K.A., Bortolotti, G.R., Donázar, J.A., Bertellotti, M., Blanco, G., 2002a. Food resource utilisation by the Magellanic penguin evaluated through stable-

- isotope analysis: Segregation by sex and age and influence on offspring quality. *Mar. Ecol. Prog. Ser.* 234, 289–299. <https://doi.org/10.3354/meps234289>
- Forero, M.G., Tella, J.L., Hobson, K.A., Bertellotti, M., Blanco, G., 2002b. Conspecific food competition explains variability in colony size: A test in Magellanic Penguins. *Ecology* 83, 3466–3475. [https://doi.org/10.1890/0012-9658\(2002\)083\[3466:CFCEVI\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[3466:CFCEVI]2.0.CO;2)
- Frere, E., Gandini, P., Lichtschein, V., 1996. Variación latitudinal en la dieta del Pingüino de Magallanes (*Spheniscus magellanicus*) en la costa Patagónica, Argentina. *Ornitol. Neotrop.* 7, 35–41.
- Furness, R., Monaghan, P., 2012. Regulation of populations: the theories, in: *Seabird Ecology*. Springer Science and Business Media, New York.
- Gandini, P.A., Frere, E., Pettovello, A.D., Cedrola, P. V., 1999. Interaction between Magellanic Penguins and Shrimp Fisheries in Patagonia, Argentina. *Condor* 101, 783–789. <https://doi.org/10.2307/1370065>
- Gaston, A., Ydenberg, R., Smith, G., 2007. Ashmole’s halo population regulation in seabirds. *Mar. Ornithol.* 35, 119–126.
- Gillespie, M.J., Haring, V.R., McColl, K.A., Monaghan, P., Donald, J.A., Nicholas, K.R., Moore, R.J., Crowley, T.M., 2011. Histological and global gene expression analysis of the “lactating” pigeon crop. *BMC Genomics* 12, 1–9. <https://doi.org/10.1186/1471-2164-12-452>
- Giordano, M., Groothuis, T.G.G., Tschirren, B., 2014. Interactions between prenatal maternal effects and post hatching conditions in a wild bird population. *Behav. Ecol.* 25, 1459–1466. <https://doi.org/10.1093/beheco/aru149>
- Gleiss, A.C., Wilson, R.P., Shepard, E.L.C., 2011. Making overall dynamic body acceleration work: On the theory of acceleration as a proxy for energy expenditure. *Methods Ecol. Evol.* 2, 23–33 <https://doi.org/10.1111/j.2041-210X.2010.00057.x>
- Gosztonyi, A., 1984. La alimentación del pingüino Magallánico (*Spheniscus magellanicus*) en las adyacencias de Punta Tombo, Chubut, Argentina. *Cent. Nac. Patagon.* 95, 1–9.
- Götmark, F., Winkler, D.W., Andersson, M., 1986. Flock-feeding on fish schools increases individual success in gulls. *Nature* 319, 589–591. <https://doi.org/10.1038/319589a0>
- Grémillet, D., 1997. Catch per unit effort, foraging efficiency, and parental investment in breeding great cormorants (*Phalacrocorax carbo carbo*). *ICES. J. Mari. Sci.* 54, 635–644. <https://doi.org/10.1006/jmsc.1997.0250>
- Gudmundsson, T., Gamberale, A., 1972. Observaciones sobre existencias aprovechables de

- anchoita frente a la costa bonaerense, 1969-1970-1971. Publ. Proy. Desarr. Pesq., Mar del Plata. 40, pp. 31.
- Hamilton, W.D., 1971. Geometry for the selfish herd. *J. Theor. Biol.* 31, 295–311.  
[https://doi.org/10.1016/0022-5193\(71\)90189-5](https://doi.org/10.1016/0022-5193(71)90189-5)
- Hansen, J.E., Madirolas, A., 1996. Distribución, evaluación acústica y estructura poblacional de la anchoíta. Resultados de las campañas del año 1993. *Rev Invest Des Pesq* 10, 5–21.
- Hansen, J.E., Martos, P., Madirolas, A., 2001. Relationship between spatial distribution of the Patagonian stock of Argentine anchovy, *Engraulis anchoita*, and sea temperatures during late spring to early summer. *Fish. Oceanogr.* 10, 193–206.  
<https://doi.org/10.1046/j.1365-2419.2001.00166.x>
- Heath, R.G.M., Randall, R.M., 1985. Growth of Jackass penguin chicks (*Spheniscus demersus*) hand reared on different diets. *J. Zool.* 205, 91–105.  
<https://doi.org/10.1111/j.1469-7998.1985.tb05615.x>
- Heezik, Y., Davis, L., 1990. Effects of food variability on growth rates, fledging sizes and reproductive success in the Yellow-eyed Penguin *Megadyptes antipodes*. *Ibis (Lond. 1859)*. 132, 354–365. <https://doi.org/10.1111/j.1474-919X.1990.tb01055.x>
- Hennicke, J.C., Culik, B.M., 2005. Foraging performance and reproductive success of Humboldt penguins in relation to prey availability. *Mar. Ecol. Prog. Ser.* 296, 173–181.  
<https://doi.org/10.3354/meps296173>
- Herling, C., Culik, B.M., Hennicke, J.C., 2005. Diet of the Humboldt penguin (*Spheniscus humboldti*) in northern and southern Chile. *Mar. Biol.* 147, 13–25.  
<https://doi.org/10.1007/S00227-004-1547-8>
- Horswill, C., Trathan, P.N., Ratcliffe, N., 2017. Linking extreme interannual changes in prey availability to foraging behaviour and breeding investment in a marine predator, the macaroni penguin. *PLoS One* 12, e0184114.  
<https://doi.org/10.1371/journal.pone.0184114>
- Houston, A.I., Stephens, P.A., Boyd, I.L., Harding, K.C., Mcnamara, J.M., 2006. Capital or income breeding? A theoretical model of female reproductive strategies. *Behav. Ecol.* 18, 241–250. <https://doi.org/10.1093/beheco/arl080>
- Hull, C.L., Hindell, M., Le Mar, K., Scofield, P., Wilson, J., Lea, M.A., 2004. The breeding biology and factors affecting reproductive success in rockhopper penguins *Eudyptes chrysocome* at Macquarie Island. *Polar Biol.* 27, 711–720.  
<https://doi.org/10.1007/s00300-004-0643-z>

- Green, J. A., Boyd, I. L., Woakes, A.J., Green, C.J., Butler, P.J., 2007. Feeding, fasting and foraging success during chick rearing in macaroni penguins. *Mar. Ecol. Prog. Ser.* 346, 299–312.
- Jackson, S., Ryan, P., 1986. Differential Digestion Rates of Prey by White-Chinned Petrels (*Procellaria aequinoctialis*). *Auk* 103, 617–619. <https://doi.org/10.1093/auk/103.3.617>
- Jönsson, K.I., 1997. Capital and Income Breeding as Alternative Tactics of Resource Use in Reproduction. *Oikos* 78, 57. <https://doi.org/10.2307/3545800>
- Kirkwood, R., Robertson, G., 1997. Seasonal change in the foraging ecology of emperor penguins on the Mawson Coast, Antarctica. *Mar. Ecol. Prog. Ser.* 156, 205–223. <https://doi.org/10.3354/meps156205>
- Kitaysky, A.S., Hunt, G., Flint, E.N., Rubega, M.A., Decker, M.B., 2000. Resource allocation in breeding seabirds: responses to fluctuations in their food supply. *Mar. Ecol. Prog. Ser.* 206, 283–296. <https://doi.org/10.3354/MEPS206283>
- Irvine, L. G., Clarke, J. R., Kerry., K. R., 2000. Low breeding success of the Adelie Penguin at Bechervaise Island in the 1998/99 season. *CCAMLR Sci.* 7, 151–167.
- Lack, D., 1954. *The Natural Regulation of Animal Numbers*, 1st ed. Oxford University Press, Oxford, London.
- Lack, D., 1947. The Significance of Clutch-size. *Ibis (Lond. 1859)*. 89, 302–352. <https://doi.org/10.1111/j.1474-919X.1947.tb04155.x>
- Lecomte, V.J., Sorci, G., Cornet, S., Jaeger, A., Faivre, B., Arnoux, E., Gaillard, M., Trouvé, C., Besson, D., Chastel, O., Weimerskirch, H., 2010. Patterns of aging in the long-lived wandering albatross. *Proc. Natl. Acad. Sci. U. S. A.* 107, 6370–6375. <https://doi.org/10.1073/pnas.0911181107>
- Lourdais, O., Lориoux, S., DeNardo, D.F., 2015. Structural and Performance Costs of Reproduction in a Pure Capital Breeder, the Children’s Python *Antaresia childreni*. *Physiol. Biochem. Zool.* 86, 176–183. <https://doi.org/10.1086/669127>
- Luo, Y., Wang, X., Ma, Y., Li, X., 2017. The biological function of pigeon crop milk and the regulation of its production. *Yi Chuan* 39, 1158–1167. <https://doi.org/10.16288/J.YCZZ.17-132>
- Madsen, T., Shine, R., 1999. The adjustment of reproductive threshold to prey abundance in a capital breeder. *J. Anim. Ecol.* 68, 571–580. <https://doi.org/10.1046/J.1365-2656.1999.00306.X>

- McInnes, A.M., McGeorge, C., Ginsberg, S., Pichegru, L., Pistorius, P.A., 2017. Group foraging increases foraging efficiency in a piscivorous diver, the African penguin. *R. Soc. Open Sci.* 4, 170918. <https://doi.org/10.1098/RSOS.170918>
- Meyer, W.R., Bengtson, J.L., Jansen, J.K., Russell, R.W., 1997. Relationships between brood size and parental provisioning performance in chinstrap penguins during the chick guard phase. *Polar Biol.* 1997 173 17, 228–234. <https://doi.org/10.1007/S003000050126>
- Miller, A.K., Karnovsky, N.J., Trivelpiece, W.Z., 2009. Flexible foraging strategies of gentoo penguins *Pygoscelis papua* over 5 years in the South Shetland Islands, Antarctica. *Mar. Biol.* 156, 2527–2537. <https://doi.org/10.1007/s00227-009-1277-z>
- Monaghan, P., Uttley, J.D., Burns, M.D., 1992. Effect of changes in food availability on reproductive effort in Arctic terns *Sterna paradisaea*. *Ardea* 80, 71–81.
- Olsson, O., 1997. Clutch Abandonment: A State-Dependent Decision in King Penguins. *J. Avian Biol.* 28, 264. <https://doi.org/10.2307/3676979>
- Oosthuizen, W.C., Postma, M., Altwegg, R., Nevoux, M., Pradel, R., Bester, M.N., Bruyn, P.J.N. de, 2019. Individual heterogeneity in life-history trade-offs with age at first reproduction in capital breeding elephant seals. *Popul. Ecol.* 61, 421–435. <https://doi.org/10.1002/1438-390X.12015>
- Orians, G.H., Pearson, N.E., 1979. On the theory of central place foraging. In: Horn, D.J., Mitchell, R.D., Stairs, G.R. (eds) *Analysis of ecological systems*. Ohio State University Press, Columbus, OH, pp. 154–177.
- Otley, H.M., Clausen, A.P., Christie, D.J., Pütz, K., 2004. Aspects of breeding biology of the Magellanic Penguin in the Falkland Islands. *Waterbirds.* 27(4), 396-405. [https://doi.org/10.1675/1524-4695\(2004\)027\[0396:AOTBBO\]2.0.CO;2](https://doi.org/10.1675/1524-4695(2004)027[0396:AOTBBO]2.0.CO;2)
- Peters, G., Wilson, R.P., Scolaro, J.A., Laurenti, S., Upton, J., Galleli, H., 1998. The diving behavior of Magellanic Penguins at Punta Norte, Peninsula Valdés, Argentina. *Colon. Waterbirds* 21, 1–10. <https://doi.org/10.2307/1521725>
- Petersen, S.L., Ryan, P.G., Gremillet, D., 2006. Is food availability limiting African Penguins *Spheniscus demersus* at Boulders? A comparison of foraging effort at mainland and island colonies. *Ibis (Lond. 1859).* 148, 14–26. <https://doi.org/10.1111/j.1474-919X.2006.00459.x>
- Piatt, J.F., Harding, A.M.A., Shultz, M., Speckman, S.G., Van Pelt, T.I., Drew, G.S., Kettle, A.B., 2007. Seabirds as indicators of marine food supplies: Cairns revisited. *Mar. Ecol. Prog. Ser.* 352, 221–234. <https://doi.org/10.3354/meps07078>

- Ploger, B.J., 1997. Does brood reduction provide nestling survivors with a food bonus? *Anim. Behav.* 54, 1063–1076. <https://doi.org/10.1006/anbe.1997.0503>
- R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Ramírez, F., Afán, I., Hobson, K.A., Bertellotti, M., Blanco, G., Forero, M.G., 2014. Natural and anthropogenic factors affecting the feeding ecology of a top marine predator, the Magellanic penguin. *Ecosphere* 5, 1–21. <https://doi.org/10.1890/ES13-00297.1>
- Ricklefs, R.E., 1990. Seabird Life Histories and the Marine Environment: Some Speculations. *Colon. Waterbirds* 13, 1. <https://doi.org/10.2307/1521414>
- Ricklefs, R.E., 1967. A Graphical Method of Fitting Equations to Growth Curves. *Ecology* 48, 978–983. <https://doi.org/10.2307/1934545>
- Robinson, J.A., Hamer, K.C., 2000. Brood size and food provisioning in Common Terns *Sterna hirundo* and Arctic Terns *S. paradisaea*: Consequences for chick growth. *Ardea* 88, 51–60.
- Roff, D.D., 2002. Life History Evolution. Sinauer Associates, Sunderland, Massachusetts, USA.
- Robert-Coudert, Y., Bost, C.A., Handrich, Y., Bevan, R.M., Butler, P.J., Woakes, A.J., Le Maho, Y., 2000. Impact of externally attached loggers on the diving behaviour of the king penguin. *Physiol. Biochem. Zool.* 73, 438–445. <https://doi.org/10.1086/317743>
- Robert-Coudert, Y., Wilson, R.P., Daunt, F., Kato, A., 2004. Patterns of energy acquisition by a central place forager: Benefits of alternating short and long foraging trips. *Behav. Ecol.* 15, 824–830. <https://doi.org/10.1093/beheco/arh086>
- Royle, N.J., Hamer, K.C., 1998. Hatching Asynchrony and Sibling Size Hierarchies in Gulls: Effects on Parental Investment Decisions, Brood Reduction and Reproductive Success. *J. Avian Biol.* 29, 266. <https://doi.org/10.2307/3677109>
- Sainmont, J., Andersen, K.H., Varpe, Ø., Visser, A.W., 2015. Capital versus Income Breeding in a Seasonal Environment. *Am. Nat.* 184, 466–476. <https://doi.org/10.1086/677926>
- Salihoglu, B., Fraser, W.R., Hofmann, E.E., 2001. Factors affecting fledging weight of adélie penguin (*Pygoscelis adeliae*) chicks: A modeling study. *Polar Biol.* 24, 328–337. <https://doi.org/10.1007/s0030000000215>
- Sánchez, R.P., Remeslo, A., Madirolas, A., de Ciechowski, J.D., 1995. Distribution and abundance of post-larvae and juveniles of the Patagonian sprat, *Sprattus fuegensis*, and

- related hydrographic conditions. *Fish. Res.* 23, 47–81. [https://doi.org/10.1016/0165-7836\(94\)00339-X](https://doi.org/10.1016/0165-7836(94)00339-X)
- Saraux, C., Friess, B., Le Maho, Y., Le Bohec, C., 2012. Chick-provisioning strategies used by king penguins to adapt to a multiseasonal breeding cycle. *Anim. Behav.* 84, 675–683. <https://doi.org/10.1016/J.ANBEHAV.2012.06.024>
- Saraux, C., Le Bohec, C., Durant, J.M., Viblanc, V.A., Gauthier-Clerc, M., Beaune, D., Park, Y.H., Yoccoz, N.G., Stenseth, N.C., Le Maho, Y., 2011. Reliability of flipper-banded penguins as indicators of climate change. *Nature* 469, 203–208. <https://doi.org/10.1038/nature09630>
- Scolaro, J.A., Badano, L.A., 1986. Diet of the Magellanic penguin *Spheniscus magellanicus* during the chick-rearing period at Punta Clara, Argentina. *Mar. Ornithol.* 13, 91–97.
- Scolaro, J.A., Wilson, R.P., Laurenti, S., Kierspel, M., Gallelli, H., Upton, J.A., 1999. Feeding preferences of the Magellanic Penguin over its breeding range in Argentina. *Waterbirds* 22, 104–110. <https://doi.org/10.2307/1521999>
- Shepard, E.L.C., Wilson, R.P., Quintana, F., Laich, A.G., Liebsch, N., Albareda, D.A., Halsey, L.G., Gleiss, A., Morgan, D.T., Myers, A.E., Newman, C., Macdonald, D.W., 2008. Identification of animal movement patterns using tri-axial accelerometry. *Endanger. Species Res.* 10, 47–60. <https://doi.org/10.3354/ESR00084>
- Sherley, R.B., Underhill, L.G., Barham, B.J., Barham, P.J., Coetzee, J.C., Crawford, R.J.M., Dyer, B.M., Leshoro, T.M., Upfold, L., 2013. Influence of local and regional prey availability on breeding performance of African penguins *Spheniscus demersus*. *Mar. Ecol. Prog. Ser.* 473, 291–301. <https://doi.org/10.3354/MEPS10070>
- Simeone, A., Wilson, R.P., 2003. In-depth studies of Magellanic penguin (*Spheniscus magellanicus*) foraging: can we estimate prey consumption by perturbations in the dive profile? *Mar. Biol.* 143, 825–831. <https://doi.org/10.1007/S00227-003-1114-8>
- Skewgar, E., Boersma, P.D., Harris, G., Caille, G., 2007. Anchovy fishery threat to Patagonian ecosystem. *Science* 315, 45. <https://doi.org/10.1126/science.1135767>
- Skewgar, E., Boersma, P.D., Simeone, A., 2014. Winter migration of magellanic penguins (*Spheniscus magellanicus*) along the southeastern pacific. *Waterbirds* 37, 203–209. <https://doi.org/10.1675/063.037.0208>
- Spaans, A., 1971. On the Feeding Ecology of the Herring Gull *Larus Argentatus* Pont. In the Northern Part of the Netherlands. *Ardea* 59, 75–188.



- Stephens, P.A., Boyd, I.L., Mcnamara, J.M., Houston, A.I., 2009. Capital breeding and income breeding: Their meaning, measurement, and worth. *Ecology* 90, 2057–2067. <https://doi.org/10.1890/08-1369.1>
- Stokes, D.L., Boersma, P.D., 1999. Where breeding magellanic penguins *Spheniscus magellanicus* forage: Satellite telemetry results and their implications for penguin conservation. *Mar. Ornithol.* 27, 63–65.
- Sutton, G.J., Hoskins, A.J., Arnould, J.P.Y., 2015. Benefits of Group Foraging Depend on Prey Type in a Small Marine Predator, the Little Penguin. *PLoS One* 10, e0144297. <https://doi.org/10.1371/JOURNAL.PONE.0144297>
- Takahashi, A., Watanuki, Y., Sato, K., Kato, A., Arai, N., Nishikawa, J., Naito, Y., 2003. Parental foraging effort and offspring growth in Adélie Penguins: Does working hard improve reproductive success? *Funct. Ecol.* 17, 590–597. <https://doi.org/10.1046/j.1365-2435.2003.00772.x>
- Taylor, S.S., Leonard, M.L., Boness, D.J., Majluf, P., 2001. Foraging trip duration increases for Humboldt Penguins tagged with recording devices. *J. Avian Biol.* 32, 369–372. <https://doi.org/10.1111/j.0908-8857.2001.320413.x>
- Thaxter, C.B., Lascelles, B., Sugar, K., Cook, A.S.C.P., Roos, S., Bolton, M., Langston, R.H.W., Burton, N.H.K., 2012. Seabird foraging ranges as a preliminary tool for identifying candidate Marine Protected Areas. *Biol. Conserv.* 156, 53–61. <https://doi.org/10.1016/J.BIOCON.2011.12.009>
- Tjørve, K.M.C., Tjørve, E., 2010. Shapes and functions of bird-growth models: How to characterise chick postnatal growth. *Zoology* 113, 326–333. <https://doi.org/10.1016/j.zool.2010.05.003>
- Trivelpiece, W.Z., Hinke, J.T., Miller, A.K., Reiss, C.S., Trivelpiece, S.G., Watters, G.M., 2011. Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proc. Natl. Acad. Sci.* 108, 7625–7628. <https://doi.org/10.1073/PNAS.1016560108>
- Vaz-dos-Santos, A.M., Rossi-Wongtschowski, C.L.D.B., de Figueiredo, J.L., Ávila-da-Silva, A.O., 2010. Threatened fishes of the world: *Merluccius hubbsi* Marini, 1933 (*Merlucciidae*). *Environ. Biol. Fishes* 87, 349–350. <https://doi.org/10.1007/s10641-010-9608-y>
- Wagner, E.L., Boersma, P.D., 2019. Food allocation and feeding behaviours of Magellanic penguin, *Spheniscus magellanicus*, adults and chicks. *Anim. Behav.* 148, 161–168. <https://doi.org/10.1016/j.anbehav.2018.12.008>

- Wanless, S., Harris, M.P., Redman, P., Speakman, J.R., 2005. Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Mar. Ecol. Prog. Ser.* 294, 1–8. <https://doi.org/10.3354/MEPS294001>
- Weimerskirch, H., 2007. Are seabirds foraging for unpredictable resources? *Deep. Res. II* 54, 211–223. <https://doi.org/10.1016/j.dsr2.2006.11.013>
- Weimerskirch, H., Zimmermann, L., Prince, P.A., 2001. Influence of environmental variability on breeding effort in a long-lived seabird, the yellow-nosed albatross. *Behav. Ecol.* 12, 22–30. <https://doi.org/10.1093/oxfordjournals.beheco.a000374>
- Williams, T.D., Croxall, J.P., 1990. Is Chick Fledging Weight a Good Index of Food Availability in Seabird Populations? *Oikos* 59, 414–416. <https://doi.org/10.2307/3545154>
- Williams, T.D., Rothery, P., 1990. Factors Affecting Variation in Foraging and Activity Patterns of Gentoo Penguins (*Pygoscelis papua*) During the Breeding Season at Bird Island, South Georgia. *J. Appl. Ecol.* 27, 1042. <https://doi.org/10.2307/2404394>
- Wilson, R.P., 2003. Penguins predict their performance. *Mar. Ecol. Prog. Ser.* 249, 305–310. <https://doi.org/10.3354/meps249305>
- Wilson, R.P., 1992. Environmental monitoring with seabirds: Do we need additional technology? *South African J. Mar. Sci.* 12, 919–926. <https://doi.org/10.2989/02577619209504752>
- Wilson, R.P., 1985. The Jackass Penguin (*Spheniscus demersus*) as a pelagic predator. *Mar. Ecol. Prog. Ser.* 25, 219–227. <https://doi.org/10.3354/meps025219>
- Wilson, R.P., Börger, L., Holton, M.D., Scantlebury, D.M., Gómez-Laich, A., Quintana, F., Rosell, F., Graf, P.M., Williams, H., Gunner, R., Hopkins, L., Marks, N., Geraldini, N.R., Duarte, C.M., Scott, R., Strano, M.S., Robotka, H., Eizaguirre, C., Fahlman, A., Shepard, E.L.C., 2020. Estimates for energy expenditure in free-living animals using acceleration proxies: A reappraisal. *J Anim Ecol* 89, 161–172. <https://doi.org/10.1111/1365-2656.13040>
- Wilson, R.P., Cock, G.D. La, Wilson, M. P., Mollagee, F., 1985. Differential Digestion of Fish and Squid in Jackass Penguins *Spheniscus demersus*. *Ornis Scand.* 16, 77. <https://doi.org/10.2307/3676580>
- Wilson, R.P., Holton, M.D., di Virgilio, A., Williams, H., Shepard, E.L.C., Lambertucci, S., Quintana, F., Sala, J.E., Balaji, B., Lee, E.S., Srivastava, M., Scantlebury, D.M., Duarte, C.M., 2018a. Give the machine a hand: A Boolean time-based decision-tree template for

- rapidly finding animal behaviours in multisensor data. *Methods Ecol. Evol.* 9, 2206–2215. <https://doi.org/10.1111/2041-210X.13069>
- Wilson, R.P., Neate, A., Holton, M.D., Shepard, E.L.C., Scantlebury, D.M., Lambertucci, S.A., di Virgilio, A., Crooks, E., Mulvenna, C., Marks, N., 2018b. Luck in Food Finding Affects Individual Performance and Population Trajectories. *Curr. Biol.* 28, 3871–3877.e5. <https://doi.org/10.1016/J.CUB.2018.10.034>
- Wilson, R.P., Pütz, K., Peters, G., Culik, B., Scolaro, J.A., Charrassin, J.B., Ropert-Coudert, Y., 1997. Long-Term Attachment of Transmitting and Recording Devices to Penguins and Other Seabirds. *Wildl. Soc. Bull.* 25, 101–106.
- Wilson, R.P., Ropert-Coudert, Y., Kato, A., 2002. Rush and grab strategies in foraging marine endotherms: the case for haste in penguins. *Anim. Behav.* 63, 85–95. <https://doi.org/10.1006/ANBE.2001.1883>
- Wilson, R.P., Ryan, P.G., Wilson, M.P., 1989. Sharing food in the stomachs of seabirds between adults and chicks-A case for delayed gastric emptying. *Comp. Biochem. Physiol.* 94, 461–466. [https://doi.org/10.1016/0300-9629\(89\)90121-7](https://doi.org/10.1016/0300-9629(89)90121-7)
- Wilson, R.P., Scolaro, J.A., Grémillet, D., Kierspel, M.A.M., Laurenti, S., Upton, J., Gallelli, H., Quintana, F., Frere, E., Müller, G., Straten, M.T., Zimmer, I., 2005. How do magellanic penguins cope with variability in their access to prey? *Ecol. Monogr.* 75, 379–401. <https://doi.org/10.1890/04-1238>
- Wilson, R.P., Shepard, E.L.C., Laich, A.G., Frere, E., Quintana, F., 2010. Pedalling downhill and freewheeling up; a penguin perspective on foraging. *Aquat. Biol.* 8, 193–202. <https://doi.org/10.3354/AB00230>
- Wilson, R.P., White, C.R., Quintana, F., Halsey, L.G., Liebsch, N., Martin, G.R., Butler, P.J., 2006. Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *J. Anim. Ecol.* 75, 1081–1090. <https://doi.org/10.1111/j.1365-2656.2006.01127.x>
- Wilson, R.P., Wilson, M.P., 1990. Foraging Ecology of Breeding Speniscus Penguins, in: Davis, L., Darby, J. (Eds.), *Penguin Biology*. Academic Press Inc, San Diego, California, pp. 181–203.

