Individual specialisations in the foraging ecology of seabirds

by

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Submitted in fulfilment of the requirements for the degree of

Doctor of Philosophy

Deakin University.

April, 2017
I am the author of the thesis entitled

**Individual specialisations in the foraging ecology of seabirds**

submitted for the degree of Doctor of Philosophy

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ABSTRACT

Individual specialisations in foraging involve the repetition of specific behaviours or dietary choices over time; they are thought to help individuals mitigate competition and increase foraging efficiency. Even though individual specialisations are now known to be commonly exhibited in natural populations and have the potential to influence ecological processes and foraging dynamics, their drivers and the timescales over which they are maintained are not well understood. Furthermore, quantifying the degree of specialisation is important as even populations considered to be generalists can be made of individual specialists. Lastly, a balance between individual specialisations and behavioural flexibility over different timescales might be necessary for populations to effectively cope with changes in prey availability.

Seabirds are central-place foragers during the breeding season, as they generally nest in colonies, to which they return and in which individuals compete for and have access to the same resources. Three seabird species with different foraging habits were selected and a combination of bio-logging and stable isotope analysis was used to: (i) quantify the degree of individual specialisation in foraging behaviour; (ii) investigate the influence of intrinsic and extrinsic factors on individual specialisations; (iii) determine timescales over which such specialisations are maintained; and (iv) examine whether individual specialisations could be related to mate choice.

Kerguelen shags *Phalacrocorax verrucosus* exhibited short- and medium-term consistency in foraging behaviour and strong long-term dietary specialisations that were not related to morphology or sex but rather seem to match different prey preferences. In this species, mates were more similar in behaviour and diet than expected by chance. Gentoo
penguins *Pygoscelis papua* exhibited low to moderate short-term consistency in foraging metrics at the population level, independently of sex or morphology, and dietary specialisations maintained outside of a single breeding season. In Little penguins *Eudyptula minor*, low to moderate consistency was exhibited in some aspects of their foraging behaviour on a day-to-day basis but was not evident over longer timescales, highlighting the species’ behavioural plasticity.

The findings of the present study, in conjunction with the ones of previous studies, highlight the importance of extrinsic drivers such as ecological opportunity, foraging modes (e.g. benthic vs pelagic) and sites (e.g. polar vs tropical) in determining the degree of individual specialisation. Such drivers are likely to be reinforced by intrinsic factors (e.g. physiological capacity, experience, cognitive and learning capacities). Memory-based foraging, for example, might be used depending on prey availability and diversity, resulting in site fidelity and stereotyped behaviours. In the present work, I highlighted the importance of taking timescales into account when determining the degree of individual specialisations in seabird populations as results on short timescales might not be consistent with those over longer timescales. Furthermore, it seems crucial to develop standardised metrics and analytical methods to use in order to be able to make meaningful comparisons between the degrees of individual specialisation exhibited by different species and between populations of the same species. Lastly, extending the number of species studied to cover a wider range of individual morphological and physiological variations, foraging modes and locations will help ecologists gain a deeper understanding of the drivers of individual specialisations.
Preface

Field work for the present study was done in accordance with the ethical guidelines of the Deakin University Animal Ethics Committee and Animal Welfare Committee (Permit No. B21-2013), as well as of the French Polar Institute Paul-Emile Victor’s Ethics Committee (Program 394). The project was conducted in accordance with the regulations of Parks Victoria and of the Department of Environment, Land, Water and Planning (Wildlife Research Permit No. 10006877).

The core data chapters of this thesis (Chapters 2 to 5) have been published in peer-reviewed journals. Chapter 1 stands as an introduction to the main body of work while Chapter 6 places the main findings of the study in a more general context. I am the primary contributor to all aspects of the work presented in this thesis, with the exception of diet determination for Chapter 2 and the data collection for Chapter 5.

John P.Y. Arnould, Yves Cherel, Charles-André Bost are co-authors on all publications for providing financial and logistical support, contributing to the study designs, and providing equipment, guidance, and editorial advice. Andrew Hoskins provided invaluable insight about statistical analysis for Chapters 2 and 3. Yves Cherel identified prey items in the regurgitates collected on Kerguelen shags. Paco Bustamante, Maud Brault-Favrou and Gaël Guillou contributed to sample preparation and isotopic analysis for Chapters 2, 3 and 4. Selina Kent, Maud Berlincourt, Melanie Wells and Grace Sutton all participated in the collection of the data on Little penguins used in Chapter 5.
Publications arising from this thesis

Chapter 2

Chapter 3

Chapter 4

Chapter 5
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“And she's going on a journey
Always walking down the road
And the water is always calling
"My little child, please come home."

That's when she went away
Away from the light of day

Standing by the riverside
Patiently waiting for the tide
To come along, to come along
The waters going to her feet
And on her body wind so cold and sweet, so cold and sweet”

Awakening – Aurora

I owe my passion for the ocean to my father, Rémi. Ever since I started scuba diving thanks to him, I had sworn to myself I was going to become a marine biologist. I owe my passion for travelling to both my mother, Carole, and my father; they have taken me around the world, helped me experience and respect different cultures and I certainly would not be where I am today if it was not for them. I am proud to have such wonderful and supportive parents and I am grateful for the education I received from them and the rest of my lovely family; they have taught me how to be adventurous and independent, even though they would
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I am also very lucky to have wonderful, dynamic and successful cousins to inspire me, a brother who has fought worse battles than I have, and loving and caring step-mother, grand-mother, aunts and uncles. We did not communicate much during these busy past few years but it was always a pleasure when we did; you are always in my heart and I am looking forward to catching up with you soon hopefully. To the three grandparents I lost just before or during my PhD, I am sorry I have not gotten to say goodbye. You have lived fascinating and at times challenging lives, and inspired me to do the same. You will always be in my heart.

Research is a collaborative exercise and there are many people I could not have carried out my PhD without. I am grateful for my supervisor, John Arnould, for trusting me from the start and helping me get a scholarship to start the project in the first place. He has taught me a lot and made me a better researcher and a tougher person. Thank you, John, for standing by me all these years! Your help along the way has been greatly appreciated and wherever it takes me next, I hope I will make you proud. Thank you to Charly Bost and Yves Cherel for giving me the opportunity to go back to a wild and amazing corner of the world, Kerguelen Islands, and providing advice during the preparation for the fieldwork. I am grateful for your help in Chizé, preparing samples for isotope analysis and determining diet from the regurgitates collected on the island. I wish to thank the French Polar Institute team, including Romuald Bellec and Nina Marchand, for helping with logistics in the Subantarctic. I am very grateful for the help of many field volunteers on Kerguelen Islands, including Ayala Loisel, Martin Delpuech, Joris Laborie, Florian Orgeret, and Elie Gaget, Stéphane
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physically and mentally. It is not always easy to maintain sanity when doing a PhD, and I feel like you have greatly helped in keeping me motivated in the last year.

"I've been staring at the edge of the water
'Long as I can remember, never really knowing why
I wish I could be the perfect daughter
But I come back to the water, no matter how hard I try
Every turn I take, every trail I track
Every path I make, every road leads back
To the place I know, where I cannot go
Where I long to be
See the line where the sky meets the sea? It calls me
And no one knows, how far it goes

If the wind in my sail on the sea stays behind me

One day I'll know, if I go there's just no telling how far I'll go”

Alessia Cara, Moana
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CHAPTER 1

Introduction
Individual specialisations

According to the optimal foraging theory, an individual should select a specific foraging strategy that maximizes its net energy intake per unit of time, and that minimizes other costs, including for example thermoregulation and risks of being predated on (Stephens & Krebs 1986). Foragers would, thus, be expected to adjust their foraging strategies to maximize foraging efficiency (Fretwell & Calver 1969). This is especially true when animals are rearing offspring as foraging effort should be highest because of increased energy requirements (Quillfeldt et al. 2011). Several intrinsic factors (e.g. morphology, physiology) and extrinsic factors (e.g. quality, availability and distribution of prey, the risk of predation and environmental conditions including winds and currents) influence the foraging strategies of individuals (Sargeant 2007, Quillfeldt et al. 2011).

Individuals can vary in prey preference because of different search image formation abilities (Lewis 1986, Bernays & Funk 1999), variations in morphology affecting prey capture rates (Konovalov 1995, Maret & Collins 1997, Estes et al. 2003, Weise et al. 2010), physiological condition that allows individuals to handle or digest specific prey only or limit their distribution to specific water masses (Dawson et al. 1977, Shiels et al. 2011, Dall et al. 2012), limited learning abilities that make it easier to focus on specific prey items (Estes et al. 2003), previous experience with specific prey items (Partridge 1976, dit Durell 2000, McEachern et al. 2006), and different personalities that make them more or less risk averse (Elliott et al. 2010, Patrick et al. 2013). Furthermore, individuals with similar preferences can display different foraging strategies due to social status, mating strategy or microhabitat (Bolnick et al. 2003, Bergmüller & Taborsky 2010). For example, dominant individuals can exclude subordinate individuals from accessing preferred resources (Goss-Custard et al. 1984, Holbrook & Schmitt 1992, Bearhop et al. 2006). All of these factors, in combination
with environmental and prey conditions, affect how an individual selects resources.

An “individual specialist” is defined as an individual whose niche is substantially narrower than its population’s niche for reasons not attributable to its sex, age, or discrete \((a\ priori)\) morphological group (Bolnick et al. 2003); the phrase “individual specialisation” can designate either the overall predominance of individual specialists in a population or the degree to which an individual’s diet or foraging strategy is restricted relative to their population. Individual specialisations in foraging have received growing attention in the past couple of decades (Bolnick et al. 2003, Ceia & Ramos 2015). However, we are still lacking measures for quantifying specialisations (Araújo et al. 2011) and their implications are still poorly understood (Woo et al. 2008). As individual specialisations may have a substantial impact on ecological processes and foraging dynamics, studies going beyond simply testing for their presence should be undertaken to quantify their magnitude using recently proposed indices (Bolnick et al. 2002, Ceia & Ramos 2015). Furthermore, researchers should not stop at documenting the degree of individual specialisations, but should attempt to identify the mechanisms generating inter-individual variation (Bolnick et al. 2003). In some cases apparent individual specialisations are largely a result of sexual or age-related differences in size, experience or dominance but they often occur once sex- and age-effects have been accounted for (Woo et al. 2008).

Since the 1980s, across a wide range of animal taxa, researchers came to realize that some species that are considered ecological generalists and use a wide diversity of resources, are in fact heterogeneous collections of relatively specialised individuals (Bolnick et al. 2002, 2003, McEachern et al. 2006, Bolnick et al. 2007, Araújo et al. 2011) (Figure 1.1). The causes and consequences of individual specialisations are poorly documented (Bolnick et al. 2003, Cook et al. 2007). It is unclear whether or not specialists generally perform better than
generalists although the existence of behavioural-based foraging polymorphisms implies not only that there are benefits of specializing, but also that there exists some mechanism for diversification and maintenance of alternative specialisations within a population over ecological time-scales (Tinker et al. 2009).

The benefits of individual specialisations include the mitigation of competition between conspecifics and the improvement of individual foraging efficiency, including finding, handling, and digesting food, which can lead to a higher reproductive output (Golet et al. 2000, Davoren et al. 2003, Estes et al. 2003, Cook et al. 2006). However, being a specialist, or specialising on specific resources, might also have deleterious effects on individuals such as higher exposure to specific parasites (Konovalov 1995) and limited adaptability, including delay responses to rapid environmental changes (McIntyre et al. 2017). In fact, in short-lived foragers, extreme trophic specialisation such as that exhibited by the sea slug Placida dendritica can prevent individuals from switching to unfamiliar resources (Trowbridge 1991). While individual specialisations in the short-term might allow individuals to forage more efficiently, behavioural flexibility might remain important for them to be able to cope effectively with changes in prey availability and diversity over seasonal, annual and decadal scales (Montevecchi et al. 2009). Northern gannets Sula bassana, for example, are known to integrate a mixed array of flexible and repetitive tactics to engage changes in prey availability driven by dynamic oceanographic conditions, which allows populations to remain stable (Montevecchi et al. 2009).
**Figure 1.1** Number of species, classified by major taxonomic group, in which individual specialisation in diet, foraging behaviour, habitat or other niche axis has been documented.

Total number of species is 189. From Araújo et al. (2011).
Knowledge of the individual consistency of habitat use in long-lived animal species throughout the annual cycle is lacking, despite the fact that such knowledge is fundamental to gain insight into the importance of different foraging habitats, their consequences on individual fitness and on population dynamics (Hoye et al. 2012). In fact, only a few studies have linked the temporal persistence of foraging tactics or locations with long-term dietary specialisations (Bearhop et al. 2006, Cook et al. 2006, Woo et al. 2008, Knudsen et al. 2010). Accurate identification of individual habitat specialisation requires longitudinal records of habitat use, which implies following individuals through time (Bolnick et al. 2002, Newsome et al. 2009). Bolnick et al. (2003) reiterated that determining the timescale over which niche variation persists is important because the temporal consistency of individual specialisation will have implications for both evolution and ecology (see also Araújo et al. (2007)).

Understanding the degree to which individuals differ in their habitat use will help gain insight into their susceptibility to anthropogenic threats and environmental changes; despite this, few studies have attempted to quantify the proportion of specialists in populations, how constant this proportion is over time and how it relates to prey availability and diversity (Bearhop et al. 2006, Ceia et al. 2012). Bolnick et al. (2003) further warned researchers that management plans that aim to protect a species’ resource base by targeting some “average” resource for the population may harm individual specialists.

Seabirds are top predators that are useful as indicators and sentinels of marine ecosystem structure and variability (Furness & Camphuysen 1997, Barrett et al. 2007, Iverson et al. 2007). They face a permanent challenge to find mobile food in large ocean ecosystems (Cook et al. 2013). To understand how they manage such a challenge, gaining insight into their foraging ecology, and particularly into individual foraging behaviour, which has been poorly investigated in marine top predators, is crucial. Central-place foragers such
as seabirds are particularly suited to study individual specialisations because they compete for and have access to the same resources, and encounter the same environmental conditions; thus, differences in behaviour must reflect individual specialisations (Ratcliffe et al. 2013).

**Measures of individual specialisations**

In marine studies, observations of feeding deliveries and conventional dietary techniques such as faeces, pellet, regurgitate and stomach content analysis have been used to obtain information on individuals’ diets (Pierotti & Annett 1991, Ford et al. 1998, Ohizumi et al. 1998, Golet et al. 2000, Simpfendorfer et al. 2001, Carlton & Hodder 2003, Woo et al. 2008, Elliott et al. 2009). Repeated sampling using such techniques, when applied to the same individuals or breeding territories, allows one to detect the presence of individual specialisations (Pierotti & Annett 1991, Watanuki 1992, Annett & Pierotti 1999, Golet et al. 2000, Votier et al. 2004, Woo et al. 2008, Elliott et al. 2009). However, this kind of approach can pose problems as it just provides a ‘snapshot’ picture linked with stochastic sampling effects and, therefore, might not be representative of prey preferences (Byron et al. 1983, Araújo et al. 2007, Barrett et al. 2007, Ceia et al. 2012). Using such conventional dietary techniques and stable isotopes is a complementary approach to infer diet as they represent different integrative histories of feeding (Araújo et al. 2007, Barrett et al. 2007).

Stable isotope ratios have been widely used to estimate the contribution of prey of different trophic positions to predator’s diets (Vander Zanden et al. 2000, Bolnick et al. 2003, Inger & Bearhop 2008). In marine studies, stable isotope ratios of nitrogen and carbon in different tissues have been used to quantify diets, including age- and sex-based dietary segregations and individual differences in foraging habitat and diet (Nisbet et al. 2002,
Matthews & Mazumder 2004, Bearhop et al. 2006, Cherel et al. 2007, Woo et al. 2008, Newsome et al. 2009, Matich et al. 2011, Thomson et al. 2012). The $\delta^{13}$C values in primary producers are reflected throughout the food webs they fuel, and these spatial patterns can allow inferences to be made about the locations in which animals forage, including discrimination between inshore vs offshore and benthic vs pelagic foraging. $\delta^{15}$N, on the other hand, is used as a very effective tracer of prey’s trophic level (Hobson et al. 1994, Barrett et al. 2007, Inger & Bearhop 2008, Cherel et al. 2013).

In seabird studies, researchers have traditionally looked at the correlations in stable isotope values (typically $\delta^{13}$C values and $\delta^{15}$N values, but also $\delta^{34}$S), or more rarely, in Hg concentrations, between different tissues or in the same tissues sampled at different times, in adults or in chicks, to assess the persistence of specific diets through time (Thompson et al. 1991, Bearhop et al. 2000, Bearhop et al. 2006, Quillfeldt et al. 2008b, Votier et al. 2010, Arizaga et al. 2013, Carravieri et al. 2013, Provencher et al. 2013, Granadeiro et al. 2014); the stronger these correlations are, the more similar the diet of the animals is across the periods sampled. Most commonly, the correlation in those values between blood and feathers are reported (Bearhop et al. 2000, Bearhop et al. 2006, Quillfeldt et al. 2008a, Carravieri et al. 2013, Granadeiro et al. 2014), but tissues sampled can also include muscle (Thompson et al. 1991, Provencher et al. 2013). The rationale is that those different tissues integrate different periods of information, due to their different isotope turn-overs and the fact that certain components, such as the keratin in feathers, are inert after synthesis (Cherel et al. 2008). Blood is a metabolically active tissue that integrates a period of weeks before sampling, whereas feathers reflect the diet at the time they were grown as feathers are metabolically inert after they are grown (Cherel et al. 2000). In comparison, muscle has a turn-over of approximately one month (Hobson & Clark 1992). Importantly, validating stable isotope
analysis by bio-logging studies is the most powerful approach to detect individual specialisations (Cherel et al. 2013).

Stable isotopes provide information on prospected habitats, trophic levels and feeding ecology but remain imprecise for the identification of small-scale spatial use, such as microhabitats for example (Bailleul et al. 2010). Bio-logging, which refers to the deployment of autonomous recording tags on free-living animals (Ropert-Coudert et al. 2012), allows researchers to gather different kinds of information, and helps obtain a fine-scale representation of foraging behaviour and allows the identification of foraging sites (Kernaléguen et al. 2015a). Advances in technology leading to the miniaturisation of loggers now allow us to implement a sampling strategy involving the use of a combination of different loggers, and to use data loggers on smaller species than in the past, with minimal impact on the birds’ behaviour (Naito 2004, Ropert-Coudert et al. 2009b). In marine animals, data loggers used to assess behavioural consistency include Very-High-Frequency (VHF) radio transmitters (e.g. Watanuki et al. (2003), Tinker et al. (2008)), Global-Positioning-System (GPS) loggers (e.g. Votier et al. (2010), Baylis et al. (2015a)), Global-Location-Sensing (GLS) data loggers (e.g. McFarlane Tranquilla et al. (2014), Yamamoto et al. (2014), Chilvers (2008), McIntyre et al. (2017)), Time-Depth-Recorders (TDR) loggers (e.g. Cook et al. (2006), Tinker et al. (2007), Ratcliffe et al. (2013)), and video cameras (e.g. Watanuki et al. (2008), Kernaléguen et al. (2015b)). The deployment of these kinds of data recorders allows researchers to obtain metrics representative of the animals’ foraging behaviour, such as the commonly used maximum distances reached and total distances travelled, bearings to most distal points, and trip durations for each trip, and dive depths and durations for each dive (Soanes et al. 2013, Harris et al. 2014, Patrick et al. 2014, Oppel et al. 2015). In seabird studies, several methods use these metrics to get an estimate of individual consistency.
Study species

Three study species were included in the present thesis, to cover species with different foraging ecology and diets. Kerguelen shags are benthic foraging seabirds that fly from the colonies to their foraging sites (Cook et al. 2013). Gentoo and Little penguins are divers only. Gentoo penguins are known to exhibit high flexibility in foraging behaviour and diet, across and within breeding locations, and can dive benthically or pelagically (Woehler 1995, Lescroël & Bost 2005, Miller et al. 2009, Cook et al. 2013). Lastly, Little penguins have the most restricted foraging range and feed on pelagic prey items of relatively limited diversity (Reilly 1974, Cullen et al. 1992, Hoskins et al. 2008, Saraux et al. 2011).

Flexibility in feeding habits has been reported for various species of cormorants, and it has been argued that this flexibility plays an important role in maximizing their food intake (Grémillet et al. 1998, Punta et al. 2003). The birds included in the “blue-eyed shag complex”, a group of 13 species of foot-propelled pursuit-divers, are indeed known to display high flexibility in diving behaviour, prey choice, proportion of benthic versus pelagic dives, and furthermore exhibit differences between sexes and individuals (Cook et al. 2006, Quillfeldt et al. 2011, Ratcliffe et al. 2013). Their morphology implies high flight costs and they exhibit poor flight performance but remarkable diving capacities (Grémillet et al. 2003, Tremblay et al. 2005, Watanabe et al. 2011). In addition, because of their wettable plumage, the amount of time they can spend in the water is limited (Grémillet et al. 2005).

The Kerguelen shag Phalacrocorax verrucosus (Cabanis 1875) is a member of the “blue-eyed shag” group (Van Tets 1969, Siegel-Causey 1988) and is endemic to the Kerguelen Archipelago, where the most recent estimate of the number of breeding pairs is 7000 (Weimerskirch et al. 1989). Observations suggest that Kerguelen shags prey mainly on
benthic animals, including nototheniid fishes (Watanabe et al. 2011, Cook et al. 2013) and exhibit plasticity in their foraging tactics (Lescroël & Bost 2005). Being resident and long-lived benthic foragers, individual shags should learn to apply efficient foraging tactics throughout their lifetime, thus increasing their individual efficiency when foraging under situations of competition or food limitation (Estes et al. 2003). In this context, it is interesting to test whether individuals are, indeed, capable of elaborating a foraging strategy, in the sense of applying a particular foraging pattern (Cook et al. 2006). Benthic divers offer an excellent opportunity for studying individual specialisation, as they are thought to be able to use features of the seafloor to navigate back to areas where they have previously been successful (Cook et al. 2006, 2007, Mattern et al. 2007). The competition those coastal, benthic foraging birds face is likely to be extreme, and easy to document; despite this, the way they avoid such competition has not been explained yet (Quintana et al. 2011).

Gentoo penguins *Pygoscelis papua* are one of the most widespread penguin species and breed in Antarctic and subantarctic regions (Williams 1995). They display a high degree of plasticity in their life-history strategies (Bost & Jouventin 1990), and they are considered opportunistic foragers that can display both benthic and pelagic foraging (Woehler 1995, Lescroël & Bost 2005, Miller et al. 2009). However, some studies revealed that Gentoo penguins might not forage as opportunistic as previously considered (Croxall et al. 1988, Clausen et al. 2005, Polito et al. 2015). This is consistent with the view that populations that are considered generalists can actually be comprised of specialised individuals (Loxdale et al. 2011, Matich et al. 2011, Layman & Allgeier 2012, Fodrie et al. 2015).

On Kerguelen Islands, one of their major breeding sites with 40 000 breeding pairs (Bost & Jouventin 1990), the species shows some degree of behavioural flexibility when it comes to foraging and exhibits large inter-individual variations in foraging and morphology.
(Lescroël & Bost 2005, Cook et al. 2013). Furthermore, in their review of the ecology of Gentoo penguins, Bost and Jouventin (1990) emphasized the fact that they exhibit a relatively high variability in factors such as biometry, population size, timing of laying, diet, growth rate, foraging range and breeding success, in the northern part of their range, including Kerguelen. At this location, their diet is composed mainly of neritic fish and crustaceans but exhibit important spatial and seasonal variations (Lescroël et al. 2004). Gentoo penguins, like blue-eyed shags, have been suggested to partially be able to compensate for different prey availabilities and cope with changes in environmental conditions thanks to their high plasticity in both diet and foraging tactics, which allows them to maintain a relatively constant breeding success (Miller et al. 2009, Quillfeldt et al. 2011). Because Gentoo penguins are inshore foragers, they are believed to be dependent on local resources more closely than other penguin species that feed offshore and are able to escape local food shortages by extending their foraging ranges (Bost & Jouventin 1990).

The Little penguin *Eudyptula minor*, the smallest of the penguin species, breeds around the mainland and offshore islands of New Zealand and southern Australia (Reilly 1974) and has been shown to be in decline in parts of its range (Bool et al. 2007, Overeem & Wallis 2007). It is a diurnal, shallow-diving forager, which has the smallest foraging range among seabirds during the breeding season (Reilly 1974, Gales et al. 1990, Collins et al. 1999, Dann & Norman 2006, Ropert-Coudert et al. 2006). Little penguins rely mostly on small pelagic schooling prey such as Clupeiformes (Reilly 1974, Stahel et al. 1987, Hobday 1991, Cullen et al. 1992, Chiaradia et al. 2007b, Hoskins et al. 2008, Saraux et al. 2011). Because of their short foraging range, and the fact that their food supply is very unpredictable (Hoskins et al. 2008, Kowalczyk et al. 2015), Little penguins also represent useful models to investigate differences in behavioural consistency. Like Gentoo penguins, they are generally
considered generalists (Bool et al. 2007, Deagle et al. 2010, Chiaradia et al. 2012).

Furthermore, like in other seabird species, parental investment strategies are not necessarily set at the beginning of the breeding season in Little penguins but, instead, depend on environmental conditions (Saraux et al. 2011). However, it has been suggested that the species exhibits, like other seabirds, foraging site fidelity and display individual specialisations as they target specific depth ranges (Ropert-Coudert et al. 2003, Kowalczyk et al. 2014). As in other species, Little penguins appear to be more specialised when density of prey is higher (Perriman et al. 2000, Woo et al. 2008, Chiaradia et al. 2010).

**Aims of the thesis and thesis structure**

Using the three coastal seabird species mentioned above, the objectives of this thesis were to: 1) determine the degree of individual specialisation displayed by each population studied; 2) determine whether there is a link between mate choice and individual specialisations; 3) explore the intrinsic (e.g. sex, morphology, species) and extrinsic drivers (e.g. site, breeding stage or year) of individual specialisations; and 4) identify timescales over which individual specialisations are maintained. The central chapters of this thesis represent specific studies that have been published in peer-reviewed scientific journals. Specifically,

- Chapter 2 quantifies the degree of behavioural individual specialisations displayed in benthically foraging Kerguelen shags from trip to trip and stage to stage, and reports on long-term dietary specialisations; it assesses the importance of different intrinsic and extrinsic drivers;
- Chapter 3 documents the mate similarity in behaviour, behavioural consistency, spatial overlap and in diet in Kerguelen shags;
• Chapter 4 provides a documented example of short-term behavioural specialisations and long-term dietary specialisations in a species considered opportunistic, the Gentoo penguin, and explores the influence of various intrinsic and extrinsic drivers on the level of individual specialisation;

• Chapter 5 quantifies the degree of behavioural consistency individual Little penguins display, assesses timescales over which such consistency is maintained and investigate the influence of intrinsic and extrinsic drivers of individual consistency.
CHAPTER 2

Combined bio-logging and stable isotopes reveal individual specialisations in a benthic coastal seabird, the Kerguelen shag

A version of this chapter has been published as:

Abstract

Individual specialisations, which involve the repetition of specific behaviours or dietary choices over time, have been suggested to benefit animals by avoiding competition with conspecifics and increasing individual foraging efficiency. Among seabirds, resident and benthic species are thought to be good models to study inter-individual variation as they repetitively exploit the same environment. I investigated foraging behaviour, isotopic niche and diet in the Kerguelen shag *Phalacrocorax verrucosus* during both the incubation and chick-rearing periods for the same individuals to determine the effect of sex, breeding stage, body mass and morphometrics on mean foraging metrics and their consistency. There were large differences between individuals in foraging behaviour and consistency, with strong individual specialisations in dive depths and heading from the colony. Stable isotopes revealed specialisations in feeding strategies, across multiple temporal scales. Specifically, individuals showed medium term specialisations in feeding strategies during the breeding season, as well as long-term consistency. A clustering analysis revealed 4 different foraging strategies displaying significantly different δ^{15}N values and body masses. There were no sex or stage biases to clusters and individuals in different clusters did not differ in their morphology. Importantly, the results suggest that the different strategies emphasized were related to individual prey preferences rather than intrinsic characteristics.
Introduction

According to the optimal foraging theory, an individual should select a specific foraging strategy that maximizes its net energy intake per unit of time while minimizing other costs such as predation risk (Stephens & Krebs 1986). Foragers would be expected to maximize foraging efficiency even more when provisioning young as foraging effort is increased to meet the energy requirements of the offspring (Hamel & Côté 2009). Individual specialisations have been suggested as a way to avoid competition with conspecifics and to increase individual foraging efficiency (including prey finding, handling, and digesting) (Estes et al. 2003). They have been linked with greater body condition, fitness or reproductive output in some species (Annett & Pierotti 1999, Patrick & Weimerskirch 2014a).

Individual specialisations in foraging involve the repetition of specific behaviours or dietary choices over time, and have been, until recently, poorly investigated (Bolnick et al. 2003, Estes et al. 2003, Cook et al. 2006). Individual specialists can be defined as “individuals whose niche is substantially narrower than their population’s niche for reasons not attributable to their sex, age or discrete morphological group” (Bolnick et al. 2003). It is of importance to identify the mechanisms generating inter-individual variation and study the wider implications of variation in foraging behaviour if we are to understand trophic relationships between the animals and their environment (Bolnick et al. 2003, Baylis et al. 2015b, Ceia & Ramos 2015, Kernaléguen et al. 2015a). In addition, these variations in foraging behaviour may have substantial impacts on ecological processes and foraging dynamics (Ceia & Ramos 2015).

Individual specialisations are reported across a wide range of taxonomic groups.
including molluscs, crustaceans, insects, fishes, reptiles, amphibians, birds and mammals (Bolnick et al. 2003). Consistency in animal behaviour and niche has also been reported in a wide range of contexts: mate choice (Godin & Dugatkin 1995, Forstmeier & Birkhead 2004); nesting behaviour (Janzen & Morjan 2001); wintering strategies (McFarlane Tranquilla et al. 2014); feeding strategies (Werner & Sherry 1987); space use (Estes et al. 2003); trophic levels (Beaudoin et al. 1999, Ceia et al. 2012); responses to environmental variables (Patrick et al. 2014); and boldness (Verbeek et al. 1994).

Determining the temporal consistency of individual specialisations requires longitudinal studies involving repeated observations on individuals over time (Bolnick et al. 2003). Seabirds generally nest in colonies and are central-place foragers during the breeding season and, therefore, offer the possibility for such longitudinal studies. Indeed, many seabirds can be accessed repetitively throughout the breeding season and also across years as they display a high level of nest fidelity. In addition, collecting data from multiple members of the same colony allows the level of variation in diet and behaviour between individuals that arises from specialisation to be determined as animals have access to the same resources and are exposed to the same environmental conditions (Ratcliffe et al. 2013).

Cormorants are inshore feeders, foot-propelled pursuit-divers, feeding on a wide range of inshore benthic or pelagic prey in a limited ecological niche (Wanless et al. 1992, Grémillet et al. 1998, Cook et al. 2013). Their body plan implies high flight and diving costs (Grémillet et al. 2003, Watanabe et al. 2011). In addition, because they are air-breathers and have a wettable plumage, the amount of time they can spend diving is limited (Grémillet et al. 2005). The Kerguelen shag Phalacrocorax verrucosus (Cabanis 1875), is a member of the 13 species so-called blue-eyed shag complex (Van Tets 1976, Siegel-Causey 1988), which represents one of the main top predators to feed on the fish community in the coastal areas of
the Antarctic and subantarctic territories (Casaux & Barrera-Oro 2006).

Flexibility in feeding habits has been reported for various species of cormorants, and it has been argued that this flexibility plays an important role in maximizing their food intake (Grémillet et al. 1998). For example, species in the “blue-eyed shag complex” can exhibit a high intra- and inter-individual variation in diving behaviour and prey choice, as well as inter-individual and inter-sexual differences (Cook et al. 2006, 2007, Quillfeldt et al. 2011). Species in this group can display strong individual specialisations that can be maintained across years (Bearhop et al. 2006, Cook et al. 2006, Harris et al. 2014, Harris et al. 2016). These philopatric, mostly benthic foraging birds are well suited to answer such questions as they are long-lived species, repetitively breed and forage in the same locations. Kerguelen shags show dietary specialisations (Bearhop et al. 2006, Cook et al. 2013), but the consistency in their space use and diving behaviour has not been investigated in detail.

The aims of the present study were to (1) quantify and identify the factors influencing consistency in diving behaviour, space use, and diet in Kerguelen shags at different temporal scales, as well as to (2) study the links between foraging behaviour, consistency in foraging, diet, and morphometry. Different complementary approaches, representing different timescales, have been used to do so as no single timescale may provide a complete and accurate picture of the level of individual specialisation (Kernaléguen et al. 2015b). Snapshot methods such as regurgitate analysis provide essential diet information, while stable isotope analysis on tissues with different turnovers allow to examine the diets and foraging habitats across longer timescales, and GPS/TDR provide a fine-scale representation of foraging behaviour and allow the identification to foraging sites (Kernaléguen et al. 2015a).
Materials and methods

Instrumentation

Field work was conducted at the Pointe Suzanne Kerguelen shag colony (49°26′S, 70°26′E), Kerguelen Islands, southern Indian Ocean, during the 2014/15 breeding season. This study was approved by the ethics committee of the French Polar Institute (Program IPEV 394, resp. C.A. Bost) and therefore meets ethics guidelines. All animals in this study were cared for in accordance with its guidelines. Sampling occurred during 2 sessions. During the first session, a total of 20 individuals (both partners from 10 nests) were instrumented with GPS data loggers (I-gotU GT120, Mobile Action, Taiwan; 44.5 x 28.5 x 13.0 mm, 22 g in air corresponding to ca. 1 % of mean body mass) for 3 to 6 d at the end of incubation/early chick rearing (26 November-2014 to 10 December -2014; hereafter incubation), when chicks were no older than 1 wk. During the second session, a total of 22 birds (both partners from 11 nests) were instrumented for 3 to 12 d during late chick rearing (6 January -2015 to 18 –January -2015; hereafter chick-rearing), of which 10 birds had previously been sampled and were deployed only with GPS data loggers while the remaining 12 individuals were equipped both with GPS data loggers and time-depth recorders (TDR, LAT1800S, Lotek Wireless Inc.; 36.0 x 11.0 x 7.2 mm, 4.8 g in air corresponding to ca. 0.2 % of mean body mass). All chick-rearing instrumented birds had a single chick, except for 1 nest, which had 2 chicks at the beginning of deployments but lost 1 of them within a few days. GPS loggers were programmed to sample positions every 1 min at incubation and every 2 min in chick-rearing. The TDR units were set to record depth and temperature at 1 s intervals.

Individuals were captured at the colony using a noose attached to a fishing pole,
weighed in a cloth bag using a suspension scale (± 25 g, Pesola AG Baar, Switzerland), and banded with an individually numbered coloured plastic ring on 1 leg and an individually numbered metal ring on the other for identification. The GPS loggers, removed from their housings and encased in heat shrink plastic for waterproofing, and the dive recorders were attached to the back feathers using waterproof tape (Tesa 4651, Quickborn str 24, Hamburg 20253, Germany) and cyanoacrylate glue (Loctite 401, Prism, Instant Adhesive, Hempstead, Hertfordshire, HP2 4RQ UK).

Individuals were recaptured 3 to 18 d later using the methods previously described. The data loggers were removed and individuals were weighed again and morphometric measurements (bill length, bill width, head length, wing length and tarsus length) were taken with a vernier caliper and metal ruler (± 0.05 and 1 mm, respectively). In addition, 3 to 6 dorsal dark contour feathers from between the wings were plucked and a blood sample (0.5 to 1.5 ml) was obtained by venipuncture of a tarsal vein. Spontaneous regurgitations during handling were collected for later analysis of prey remains. Handling times ranged 15 to 20 min during which the bird’s head was covered with a hood to reduce stress.

Due to battery malfunction or flooding of loggers, GPS positions were obtained from only 36 deployments (29 different birds in total), each of which comprised 3 to 18 trips. Out of these deployments, 15 were carried out during incubation, and 21 during the chick-rearing period. 7 birds were used during both breeding stages, at an approximately one-month interval.

*Isotopic and dietary analyses*

The isotopic method was validated in the southern Indian Ocean, with δ¹³C values of
seabirds indicating their foraging habitats (Cherel & Hobson 2007, Jaeger et al. 2010), and their δ^{15}N values increasing with trophic level (Cherel et al. 2010). Isotopic values (details in (Cherel et al. 2008)) were measured on whole blood (hereafter blood) and contour feathers of shags. The rationale is that the 2 complementary tissues integrate different periods of information, due to different turnover times. Blood is a metabolic active tissue that integrates a period of weeks before sampling, whereas feathers reflect the diet at the time they were grown, because keratin is inert after synthesis. Here, blood and feathers collected during the breeding period reflect the breeding period itself and the previous post-breeding moulting period that took place almost 1 yr before the study, respectively. In the laboratory, blood samples were freeze-dried and powdered. Lipid extraction was not necessary as the C:N mass ratio was < 3.5 for all blood samples (Cherel et al. 2005b). A single contour feather per bird was cleaned of surface lipids and contaminants using a 2:1 chloroform: methanol bath, air-dried and cut into small pieces. Nitrogen and carbon isotopic ratios were measured with a continuous-flow isotope-ratio mass spectrometer (Thermo Scientific Delta V Advantage) coupled to an elemental analyser (Thermo Scientific Flash EA 1112). Results are presented in the usual δ notation relative to Vienna PeeDee Belemnite for carbon and atmospheric N\textsubscript{2} for nitrogen. Replicate measurements of internal laboratory standards (acetanilide) indicated measurement errors < 0.15 ‰ for both δ^{13}C and δ^{15}N. Blood isotopic values were obtained from 32 individuals and feather values from 31 individuals (including 9 shags that were sampled twice, at incubation and then in chick-rearing; 12 of those individuals had GPS and TDR data over consecutive trips and 15 of those had GPS data only over consecutive trips).

Regurgitate samples were stored frozen until processing in the laboratory. They were first defrosted and the fresh and accumulated fractions were weighed separately. The fresh fraction was sorted into different prey categories (annelids, cephalopods and fish) that were
weighed separately. Items were identified to species level when possible, according to Duhamel et al. (2005) for fish, and to a reference collection, i.e. bones and otoliths for fish, chitinized beaks for cephalopods and jaws for annelids. Standard length (SL) was measured in the few intact fishes. Otherwise, otoliths were measured (precision ± 0.01 mm) and SL estimated from allometric equations (Hecht & Cooper 1986, Williams & McEldowney 1990).

Data processing and statistical analyses

All data analyses were conducted in the R Statistical Environment version 3.2.0 (R Core Team 2015). GPS records for each individual were visually inspected and individual trips were determined. On average, GPS points during foraging trips were obtained every 3.1 minutes for GPS loggers set to record every min, and every 3.8 minutes for the ones set to record every 2 min. The diveMove package was used to apply a speed filter to the GPS data to remove erroneous locations with a threshold of 18 m·s⁻¹, and obtain summaries of diving metrics from TDR records (only dives deeper than 1 m were considered). Means of diving behaviour metrics and coefficients of variation (CV) per individual were calculated for dive duration, depth, and sum of vertical distance.

GPS records were linearly interpolated to the 1 s intervals in the adehabitatLT package (Calenge 2006) to provide spatial information for the dive records. Furthermore, the packages trip (Sumner 2013) and sp (Pebesma & Bivand 2015) were used to obtain summaries of at-sea movements and to calculate the number of grid cells used (1x1 km grid cells) per trip. Means and CVs per individual and per stage were calculated. Heading for each trip was calculated as the angle between the colony and the most distal point of the tracks, and standard deviation in heading was calculated for each individual using the circular
An index of consistency in space use was calculated for each animal within each stage. For each trip the number of grid cells used by the individuals were identified. The number of shared grid cells for each pair of trips (e.g. trip 1 and trip 2, trip 2 and trip 3, trip 1 and trip 3 etc.) was determined and the average of these calculated. This number was then divided by the average number of grid cells used per trip. To assess whether spatial information alone could reflect consistency in foraging locations, this index was compared for the GPS derived tracks and the dive locations alone. There was a significant positive correlation between the consistency index calculated from GPS data alone and diving locations obtained using GPS and TDR ($R^2 = 0.74$, $P < 0.001$). Therefore, it was considered that consistency in spatial space use was representative of consistency in foraging space use. Different grid cell sizes were used to calculate the index of consistency in space use (from 0.5 x 0.5 km to 5 x 5 km) to check the influence of grid cell size on my estimate of spatial consistency. Indices obtained, regardless of cell grid sizes, were highly correlated.

In order to investigate the factors influencing dive behaviour, spatial use and consistency in foraging behaviour, linear mixed effects models were fitted, using the nlme package (Pinheiro et al. 2014). For all models, backward-stepwise model selection was used to select the most parsimonious model (Ratcliffe et al. 2013). First, the most appropriate random effects structure was identified with the restricted maximum likelihood (REML); then the best fixed effects structure was determined using maximum likelihood (ML) before refitted the selected model with REML to estimate the model parameters.

As maximum depths, total vertical distances and dive durations were correlated, I used maximum depths as a representative explanatory variable to investigate the drivers of
diving behaviour. Specifically, maximum depth was used as a response variable, sex or mass as explanatory variables, trip nested within individuals nested within pairs as random effects, and a power variance structure. To investigate the effect of sex on dive behaviour consistency, I selected the coefficient of variation in maximum depth as explanatory variable, as this metric was correlated with the coefficients of variation for total vertical distances and for dive durations. The model included sex as an explanatory variable, and individual as a random effect. In order to quantify how specialised shags were in diving behaviour, I used a variance component analysis to calculate the variance, standard deviation and proportion of total variance occurring at the levels of individual, and trip within individual using the R package \textit{ape} (Paradis et al. 2004) following (Ratcliffe et al. 2013). An estimate of individual specialisation is given by the proportion of variance explained by the individual variance component (Bolnick et al. 2003, Dingemanse & Dochtermann 2013, Ratcliffe et al. 2013).

To understand the influence of sex and stage on spatial metrics, total distance travelled was used as an explanatory variable as it was correlated with maximum distance and trip duration; sex, stage and their interaction were used as explanatory variables, individual was used as a random effect and a sex and stage identity variance structure was applied. Heading to most distal point was included as the response variable in a second similar model, except with individual nested within pair as a random effect. To understand the effects of morphology on these 2 metrics, the least correlated morphometrics (i.e head length, wing length and mass at deployment) were used as explanatory variables in models containing individual as a random effects and a power variance structure.

To look at whether sex and stage influenced the consistency in spatial use, I used the coefficient of variation in total distance as a response variable. Indeed, this metric was correlated with the coefficients of variation in maximum distance and trip duration, with the
standard deviation in heading and with the index of spatial use consistency. The model included sex, stage and their interaction as fixed effects, individual as a random effect, and a sex and stage identity variance structure. In order to quantify how specialised shags were in spatial use, I used a variance component analysis as described above. This was not done separately for each sex, however, because no difference in spatial use consistency was detected between sexes.

In order to identify differences in foraging strategies, an agglomerative hierarchical clustering analysis with Euclidean distance and Ward’s linkage criterion (Kaufman & Rousseeuw 1990) was performed on mean and CVs of trip spatial metrics for each individual within stages. The function “HCPC” of the FactoMineR package was used to determine the appropriate number of clusters (Lê et al. 2008). Data on diving behaviour were not included in this clustering analysis as only a third of individuals were instrumented with a TDR and only in a single breeding stage. Linear mixed effects models were used to determine if cluster affiliation had a significant impact on mass and isotopic values. Null models (including no fixed factors and individual nested within breeding stages as random factors) were compared with models additionally including cluster number as a fixed factor. Significant differences between both models fitted by maximum likelihood indicated that clusters varied significantly in terms of the response variable of interest. Post hoc Tukey HSD multiple comparison tests were then conducted to determine more specifically which clusters differed in the multcomp package (Bretz et al. 2002).

To look at the effect of sex and stage on stable isotopes, linear mixed models were used with blood δ^{13}C or blood δ^{15}N values as response variables. In the first case and second case, the random effects were individual and individual nested within pair, respectively. In order to assess dietary specialisations, linear mixed effects models were used, with either the
isotope values during chick-rearing as response variables and the isotope values during incubation as explanatory variables, or feather isotope values as response variables and blood values (averaged between samples when repeat samples were obtained) as explanatory variables. Pair was included as a random effects in those 4 models. Unless stated otherwise, values presented are means ± SE.

Results

Foraging behaviour and its consistency

4 to 10 trips per individual were obtained (n = 76 trips) from birds equipped with both GPS and TDR during the chick-rearing period. A total of 5679 dives were recorded with individuals displaying large variations in the means and CV of diving behaviour (Table S2.1). There was a trend for males to dive deeper than females and be less consistent in their maximum depths (Figure 2.1). However, a sex effect on maximum depth could not be detected (LME: P = 0.10, df = 1, F = 3.93). Dive depths increased with mass at a rate of 41.0 ± 11.24 m·kg$^{-1}$ (LME: P = 0.01, df = 1, F = 13.31). Sex influenced the CV in maximum dive depths, with CV being higher by 0.13 ± 0.05 in males compared to females (LME: P = 0.02, df = 1, F = 7.90). There was substantial inter-individual variation in space use but, in general, all animals tended to dive at the section of the foraging trip most distant from the colony (Figure 2.2).
Figure 2.1 Boxplots of maximum dive depths, dive durations for all dives, and vertical distance travelled for all trips of individual male and female Kerguelen shags instrumented from the Pointe Suzanne colony, Kerguelen Islands (n = 6 males and 6 females).
Figure 2.2 Individual tracks and dive locations for all trips of individual Kerguelen shags instrumented during the chick-rearing period at the Pointe Suzanne colony, Kerguelen Islands (n = 12).
There were strong differences between individuals in mean trip metrics (Figure 2.2, Table S2.2). Kerguelen shags were sexually dimorphic (Table S2.3). Overall, sex and breeding stage did not influence individual foraging behaviour and consistency in a predictable manner (Table 2.1). The best model to explain total distances travelled, however, only included stage as an explanatory variable, with total distances travelled $6.32 \pm 2.21$ km higher at incubation, compared to chick-rearing (LME: $P = 0.005$, df = 1, $F = 8.22$). In contrast, heading to most distal point was not explained by sex or breeding stage as the best model to explain heading did not include either sex or stage. In terms of morphology and mass, mass best explained total distance, which increased with bird mass at a rate of $16.45 \pm 7.47$ m·kg$^{-1}$ (LME: $P = 0.03$, df = 1, $F = 4.85$), while heading to most distal point was not influenced by mass, wing length or head length. Sex and stage did not influence the CV for total distances travelled. In addition, birds instrumented during both incubation and chick-rearing used the same foraging areas (Figure 2.3), suggesting individuals displayed consistent behaviours over the whole breeding season.

*Foraging strategies, diet and specialisation*

The shags instrumented in this study displayed strong degrees of individual specialisations (Table 2.2). Males were less specialized than females in diving behaviour (maximum depths: proportion of variance explained by individual component = 41.7 and 85.1 % respectively). Specialisations in spatial use were also high (proportion of variance explained by individual component = 84.5 and 72.7 %, for total distances travelled and headings to most distal point, respectively) (Table 2.2).
Table 2.1 Summary of trip metrics for Kerguelen shags instrumented at the Pointe Suzanne colony, Kerguelen Islands, separated by sex and breeding stage (values are means ± SD).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Females</th>
<th>Males</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Incubation (n = 8, 35 trips)</td>
<td>Incubation (n = 7, 48 trips)</td>
</tr>
<tr>
<td>Trip duration (h)</td>
<td>5.9 ± 1.8</td>
<td>5.4 ± 2.9</td>
</tr>
<tr>
<td>Maximum distance (km)</td>
<td>10.2 ± 6.5</td>
<td>9.5 ± 8.0</td>
</tr>
<tr>
<td>Total distance (km)</td>
<td>26.6 ± 14.0</td>
<td>25.0 ± 19.5</td>
</tr>
<tr>
<td>Heading (°)</td>
<td>47.6 ± 0.2</td>
<td>75.4 ± 0.4</td>
</tr>
<tr>
<td>Index of space use consistency</td>
<td>0.6 ± 0.1</td>
<td>0.4 ± 0.2</td>
</tr>
</tbody>
</table>
Figure 2.3 Tracks for Kerguelen shags instrumented at the Pointe Suzanne colony, Kerguelen Islands during the incubation and chick-rearing periods (subset of 3 representative birds).
Table 2.2 Variance component analysis of Kerguelen shag dive depths, total distances travelled and headings to most distal point.

<table>
<thead>
<tr>
<th>Variance component</th>
<th>Males</th>
<th></th>
<th>Females</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>σ²</td>
<td>Σ</td>
<td>σ²%</td>
<td>σ²</td>
<td>Σ</td>
</tr>
<tr>
<td>Maximum depths (n = 6 males, n = 6 females)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Individual</td>
<td>127.6</td>
<td>11.3</td>
<td>41.7</td>
<td>163.0</td>
</tr>
<tr>
<td>Trip</td>
<td>171.6</td>
<td>13.1</td>
<td>56.1</td>
<td>27.5</td>
</tr>
<tr>
<td>Residual variation</td>
<td>6.6</td>
<td>2.6</td>
<td>0.02</td>
<td>1.1</td>
</tr>
<tr>
<td>Males (n = 14), females (n = 15)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total distance travelled</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Individual</td>
<td>137.9</td>
<td>11.7</td>
<td>84.5</td>
<td></td>
</tr>
<tr>
<td>Stage</td>
<td>24.9</td>
<td>5.0</td>
<td>15.3</td>
<td></td>
</tr>
<tr>
<td>Dive</td>
<td>0.4</td>
<td>0.6</td>
<td>0.002</td>
<td></td>
</tr>
<tr>
<td>Heading to most distal point</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Individual</td>
<td>1482.1</td>
<td>38.5</td>
<td>72.7</td>
<td></td>
</tr>
<tr>
<td>Stage</td>
<td>0.0</td>
<td>0.01</td>
<td>0.0</td>
<td></td>
</tr>
<tr>
<td>Trip</td>
<td>556.1</td>
<td>23.6</td>
<td>0.3</td>
<td></td>
</tr>
</tbody>
</table>
Results of the clustering analysis incorporating the means of space use variables and their CVs grouped individuals into 4 clusters corresponding to different foraging strategies (Figure 2.4). Each strategy differed in mean heading, consistency in space use, standard deviation in heading and total distance travelled (Table 2.3). Individuals from clusters 1 and 2 (n = 15 and 10, respectively) exploited foraging areas to the east and to the north, north-east of the colony, respectively. These 2 clusters had the highest total distances travelled and indices of space use consistency. Individuals from cluster 3 (n = 2) showed intermediate travelled distances and foraged to the south, south-east of the colony. Individuals from cluster 4 (n = 2) foraged very close to the colony, to the north or south. Both clusters 3 and 4 had individuals that were much more consistent in their space use compared to the remaining clusters. Due to small sample size in each cluster, I could not test whether clusters differed in diving behaviour.

Individuals instrumented in both breeding stages were always classified in the same cluster confirming the existence of stereotyped behaviours at one-month interval. There were no sex or breeding stage biases to clusters. Lastly, members of different clusters did not vary significantly in morphology. Importantly, there were differences in body mass between clusters, with individuals from cluster 2 being significantly heavier (but not structurally larger) than individuals from all other clusters (LME: df = 3, F = 3.97, P = 0.02). A small sample size and unequal representation of individuals in each cluster, prevented us from testing whether clusters differed in foraging success (mass gains of adults during deployment at incubation or mass gains of chicks during chick-rearing).
Figure 2.4 Successive tracks of all individuals in each cluster (for definition, see text) for Kerguelen shags instrumented at the Pointe Suzanne colony, Kerguelen Islands.

Cluster 1 (n = 15 individuals), cluster 2 (n = 10 individuals), cluster 3 (n = 2 individuals), cluster 4 (n = 2 individuals).
Table 2.3 Differences in space use metrics, mass and blood δ\textsuperscript{15}N values between clusters identified for Kerguelen shags instrumented at the Pointe Suzanne colony, Kerguelen Islands (means ± SE).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Cluster 1</th>
<th>Cluster 2</th>
<th>Cluster 3</th>
<th>Cluster 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total distance (km)</td>
<td>45.4 ± 5.4</td>
<td>33.5 ± 4.7</td>
<td>16.4 ± 7.6</td>
<td>2.1 ± 0.5</td>
</tr>
<tr>
<td>Mean heading (°)</td>
<td>35.6 ± 2.4</td>
<td>82.2 ± 4.0</td>
<td>155.0 ± 5.7</td>
<td>-21.2 ± 9.5</td>
</tr>
<tr>
<td>Index of space use consistency</td>
<td>0.61 ± 0.0</td>
<td>0.36 ± 0.1</td>
<td>0.72 ± 0.1</td>
<td>0.57 ± 0.0</td>
</tr>
<tr>
<td>Standard deviation in heading</td>
<td>0.17 ± 0.0</td>
<td>0.46 ± 0.1</td>
<td>0.08 ± 0.0</td>
<td>0.78 ± 0.6</td>
</tr>
<tr>
<td>Mean mass (kg)</td>
<td>2.2 ± 0.0</td>
<td>2.4 ± 0.1</td>
<td>2.1 ± 0.1</td>
<td>2.0 ± 0.1</td>
</tr>
<tr>
<td>Blood δ\textsuperscript{15}N (‰)</td>
<td>15.0 ± 0.2</td>
<td>14.1 ± 0.3</td>
<td>13.9 ± 0.6</td>
<td>16.1 ± 0.8</td>
</tr>
</tbody>
</table>
Blood $\delta^{13}$C and $\delta^{15}$N values averaged $-16.3 \pm 1.3$ and $14.6 \pm 1.0 \%$, respectively ($\text{C:N mass ratio: } 3.39 \pm 0.04, n = 41$). Large ranges in blood isotopic values reflected foraging variation between individuals during breeding (Table S2.4), with differences between the lowest and highest values amounting to 5.5 and 3.8 % in $\delta^{13}$C and $\delta^{15}$N, respectively. Blood $\delta^{13}$C and $\delta^{15}$N values during incubation and chick-rearing (sampling at 32 to 44 days interval) were highly significantly positively correlated ($90 \pm 9 \%$ for $\delta^{13}$C, df = 1, $F = 102.75$ and $93 \pm 6 \%$ for $\delta^{15}$N, df = 1, $F = 246.94$, respectively; Figure 2.5). Blood $\delta^{13}$C values were influenced neither by sex nor breeding stage. Stage was the only variable to significantly influence blood $\delta^{15}$N values, which were $0.56 \pm 0.07 \%$ higher during incubation (LME: breeding stage, $P < 0.001$, df = 1, $F = 59.93$). Mass was the only morphometric measurement influencing $\delta^{13}$C and $\delta^{15}$N values (LME: $P = 0.04$, df = 1, $F = 6.92$, and $P = 0.016$, df = 1, $F = 11.07$, respectively), with increasing values for heavier individuals (increase at a rate of 1.23 % kg$^{-1}$ for both $\delta^{13}$C and $\delta^{15}$N). There were significant differences in blood $\delta^{15}$N values amongst the 4 clusters (LME: df = 3, $F = 8.85$, $P < 0.001$) (Table 2.3). Post-hoc tests detected significant differences between clusters: individuals from cluster 1 had higher blood $\delta^{15}$N values than those from clusters 2 and 3, and lower values than those in cluster 4; in addition, individuals from cluster 4 had higher blood $\delta^{15}$N values than those in clusters 2 and 3. Feather $\delta^{13}$C and $\delta^{15}$N values averaged $-15.2 \pm 1.4$ and $15.3 \pm 1.2 \%$ ($\text{C:N mass ratio: } 3.20 \pm 0.05, n = 32$). Large ranges in feather isotopic values were also observed, with differences between the lowest and highest values amounting to 6.7 and 3.9 % in $\delta^{13}$C and $\delta^{15}$N, respectively. Importantly, both $\delta^{13}$C and $\delta^{15}$N values in blood and feathers were highly significantly positively correlated ($92 \pm 1 \%$ for $\delta^{13}$C, df = 1, $F = 79.25$ and $84 \pm 1\%$ for $\delta^{15}$N, df = 1, $F = 37.24$, respectively; Figure 2.5).

A total of 26 dietary samples were opportunistically collected, with a mean fresh mass
amounting to 85 ± 43 g. Identified prey were benthic organisms including 9 fish and 1 octopus species, the remaining identifiable prey items being errant polychaetes (Table 2.4). Overall the diet was dominated by *Notothenia cyanobrancha*, with *Lepidonotothen mizops* and *Harpagifer kerguelensis/spinosus* ranking second and third, respectively. Prey diversity was low with 85% of samples containing 1 to 3 prey species (maximum 7), but the dominant prey in samples differed between individuals. Repeat samples were obtained from 7 individuals; in 3 of them, the dominant prey remained consistent between the incubation and chick-rearing periods.

**Discussion**

Using complementary methods corresponding to different timescales (bio-logging, stable isotopes (Kernaléguen et al. 2015b)), the present study showed strong individual specialisations in a resident, benthic predator over different timescales (consecutive trips within a breeding stage, between stages of a single breeding season, and between the breeding and interbreeding periods). Importantly, 4 clusters were identified, corresponding to different strategies in terms of mean space use metrics and consistency, and related to differences in body masses and trophic levels.
Figure 2.5 Medium- and long-term specialisations in Kerguelen shags sampled at the Pointe Suzanne colony, Kerguelen Islands, as shown by the correlations between incubation and chick-rearing blood δ$^{13}$C and δ$^{15}$N values, and between blood and feather δ$^{13}$C and δ$^{15}$N values, respectively (n = 10 and 30, respectively). (●) males, (Δ) females.
Table 2.4 Prey items found in regurgitate samples from Kerguelen shags.

<table>
<thead>
<tr>
<th>Prey species</th>
<th>Prey group</th>
<th>Number of prey items</th>
<th>Proportion of prey items (%)</th>
<th>Number of individuals associated with each prey item</th>
<th>Proportion of individuals associated with each prey item (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Muraenolepis marmoratus</td>
<td>fish</td>
<td>2</td>
<td>0.9</td>
<td>2</td>
<td>7.7</td>
</tr>
<tr>
<td>Zanclorhynchus spinosus</td>
<td>fish</td>
<td>1</td>
<td>0.5</td>
<td>1</td>
<td>3.8</td>
</tr>
<tr>
<td>Gobionotothen acuta</td>
<td>fish</td>
<td>3</td>
<td>1.4</td>
<td>1</td>
<td>3.8</td>
</tr>
<tr>
<td>Lepidonotothen mizops</td>
<td>fish</td>
<td>32</td>
<td>14.4</td>
<td>6</td>
<td>23.1</td>
</tr>
<tr>
<td>Notothenia cyanobrancha</td>
<td>fish</td>
<td>92</td>
<td>41.4</td>
<td>21</td>
<td>80.8</td>
</tr>
<tr>
<td>Notothenia rossii</td>
<td>fish</td>
<td>1</td>
<td>0.5</td>
<td>1</td>
<td>3.8</td>
</tr>
<tr>
<td>Paranotothenia magellanaica</td>
<td>fish</td>
<td>14</td>
<td>6.3</td>
<td>10</td>
<td>38.5</td>
</tr>
<tr>
<td>Nototheniidae sp.</td>
<td>fish</td>
<td>3</td>
<td>1.4</td>
<td>3</td>
<td>11.5</td>
</tr>
<tr>
<td>Harpagifer kerguelensis/spinosus</td>
<td>fish</td>
<td>54</td>
<td>24.3</td>
<td>11</td>
<td>42.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>----------------</td>
<td>-----</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td><strong>Channichthys rhinoceratus</strong></td>
<td>fish</td>
<td>1</td>
<td>0.5</td>
<td>1</td>
<td>3.8</td>
</tr>
<tr>
<td>Undetermined fish</td>
<td>fish</td>
<td>1</td>
<td>0.5</td>
<td>1</td>
<td>3.8</td>
</tr>
<tr>
<td>Polynoidae sp.</td>
<td>annelid</td>
<td>13</td>
<td>5.9</td>
<td>9</td>
<td>34.6</td>
</tr>
<tr>
<td><strong>Benthoctopus thielei</strong></td>
<td>cephalopod</td>
<td>5</td>
<td>2.3</td>
<td>4</td>
<td>15.4</td>
</tr>
</tbody>
</table>
Sexual dimorphism in birds is known to relate to differential niche utilization (Selander 1966). Kerguelen shags are sexually dimorphic and are temporally segregated with females foraging earlier in the day than males, and with males diving significantly deeper than females at some colonies (Cook et al. 2013); these patterns appear to be widespread in the blue-eyed shag complex (Kato et al. 2000, Casaux & Barrera-Oro 2006, Michalik et al. 2012, Harris et al. 2013, Harris et al. 2014). No differences in means for maximum dive depth, distances travelled and headings were found between sexes in the present study. Thus, differential niche utilization might be driven more by individual specialisations than sex in Kerguelen shags, although sex still influenced some aspects of behavioural consistency. Male and female shags in my study also lacked differences in both their $\delta^{13}$C and $\delta^{15}$N values, suggesting that males and females had similar habitats and diets, respectively.

Male and female Kerguelen shags in the present study did not differ in mean maximum dive depths, which contradicts other studies performed on species of the blue-eyed shag complex (Kato et al. 2000, Casaux & Barrera-Oro 2006, Cook et al. 2007, Quintana et al. 2011, Ratcliffe et al. 2013). The small sample size for birds equipped with dive recorders and the large inter- and intra-individual variation in depths in males might have been responsible for the lack of statistical significance in regards to the influence of sex on dive depths. The difference in consistency in maximum depths between males and females, however, is in line with values reported in Kato et al. (2000) and Ratcliffe et al. (2013), who proposed differential degrees of individual specialisation within sexes as a mechanism for vertical niche partitioning. Harris et al. did not report differences in consistency between sexes in the depth of area-restricted search (ARS) areas but identified differences in consistency in other aspects of the foraging behaviour of the Imperial shags they instrumented; indeed females were more consistent in the maximum distances reached from
the colony and the shore (Harris et al. 2014). They suggested that these differences might be linked with sexual dimorphism, which constrains one sex more than the other and reduces their behavioural plasticity.

True individual specialisations (i.e. independent of sex, (Bolnick et al. 2003)) were emphasized in the present study. Individuals were indeed very repeatable in their headings to foraging zones, total distances travelled, and in dive depths, especially for females for which dive depth was the variable showing the highest repeatability. Fidelity of shags to a restricted diving depth range has been reported in other studies and was suggested to occur as a result of fidelity to specific food patches (Kato et al. 2000, Cook et al. 2006, Bolnick et al. 2011, Ratcliffe et al. 2013), which is consistent with that observed in some individuals in the present study. Individuals sampled at incubation and a month later during the chick-rearing period were markedly consistent in their space use, exploiting the same foraging areas in both periods. The percentages of variance explained by the individual component reported in the present study are similar to those in Harris et al. (2016) (e.g. 91 % for maximum distances from the colony, 76 % for depth of ARS), indicating those foraging metrics might show high repeatability within species of the blue-eyed shag complex.

The Kerguelen shags in the present study exhibited consistent feeding strategies, as indicated by stable isotope values, between stages within the breeding season but also between the breeding and inter-breeding periods. Other species from the blue-eyed shag complex show dietary specialisations that can be maintained over long timescales, consistent with the ability of some animals to adopt long-term behavioural strategies (Estes et al. 2003, Bearhop et al. 2006, Ratcliffe et al. 2013, Harris et al. 2014).

A large number of seabird species have been shown to exhibit significant consistency
in foraging strategies (Ceia & Ramos 2015). However, a significant degree of foraging consistency within a population does not necessarily mean that all individuals are consistent (Ceia et al. 2012). In my study, there were indeed differences in the behaviours exhibited by birds and in their consistency, which could not be explained by sex or breeding stage. Individuals tended to repetitively forage in the same areas and search for prey at the terminal part of their track in relatively restricted areas (Harris et al. 2014, Patrick et al. 2014). This suggests they deliberately re-visited the same areas and, hence, that food patches exploited were localised and predictable in time and space (Cook et al. 2013, Harris et al. 2014).

Similar to other species of the blue-eyed shag complex, Kerguelen shags are benthic divers and seafloor characteristics or bathymetric features could provide them with cues to memorize the location and quality of distinct foraging areas (Cook et al. 2006, 2007, Woo et al. 2008). Alternatively, as shown in Northern gannets *Morus bassanus*, individuals might be responding differentially to environmental variables that are good proxies for prey type and abundance (Patrick & Weimerskirch 2014a). Returning to known profitable areas could reduce search time, and increase the efficiency of prey localization and capture as a result of experience (Cook et al. 2006). Lastly, individual specialisations could be an important mechanism to reduce intra-specific competition for predators with a restricted foraging range, such as Kerguelen shags and other species of the blue-eyed shag complex, needing to feed their offspring at regular intervals (Lack 1968, Bolnick et al. 2003, Ceia et al. 2012, Harris et al. 2014, Patrick et al. 2014, Kernaléguen et al. 2015a).

Rather than being explained by sex or stage, foraging strategies corresponding to different types of behaviours and levels of consistency were associated with prey of different trophic levels. Such dietary specialisations have been reported in Kerguelen and South Georgian shags *P. georgianus* (Bearhop et al. 2006) and have been matched to specialisation
in foraging behaviour (Woo et al. 2008, Harris et al. 2014, Harris et al. 2016). If prey types determine spatial use in these inshore divers, it is logical that they consistently prospect areas of similar characteristics (e.g. in terms of substrate or water depth), making them more consistent (Harris et al. 2014). If preferred prey items have different ecological niches, individuals might differ in their consistency when exploiting specific prey.

Individual morphology did not appear to influence isotopic niche and there were no significant differences in morphometric measurements between the observed foraging strategies, confirming the existence of true specialisations (i.e. independent of discrete morphological groups, (Bolnick et al. 2003)). As there were no sex or breeding stage biases to foraging strategies, what drives individual prey preferences still remains unknown. Some studies have shown benefits of individual specialisations (e.g. better reproductive output, (Watanuki 1992, Annett & Pierotti 1999, Furness et al. 2006, Patrick & Weimerskirch 2014a); body condition and survival, (Furness et al. 2006)), while others failed to do so in various contexts (e.g. survival and reproductive fitness, (Woo et al. 2008); body condition, (Ceia et al. 2012)). In the present study, there were some differences in body mass between individuals displaying the 4 identified foraging strategies, although these results should be interpreted with caution due to my small sample size. It was not possible to ascertain whether the different strategies were a consequence of body mass variation (e.g. potential physiological advantages in flying or diving (Witter & Cuthill 1993)) or the differences in mass a consequence of the strategies employed (i.e. variation in strategy profitability); it seems, however, more likely for body mass to influence individual consistency than *vice versa* in birds that exhibit determinate growth. Heavier birds, such as birds from clusters 1 and 2, tended to fly farther, potentially indicating they were bringing back larger food loads, consistent with the optimal foraging theory. I suggest that the strategies identified arise as the
best compromise for specific individuals given their intrinsic characteristics to respond to the variability of coastal resources (Bost et al. 1992).

In summary, the results of the present study have demonstrated strong individual specialisations in space use and diet across multiple temporal scales in a benthic forager, the Kerguelen shag, consistent with patterns reported for different species of the blue-eyed shag complex. Within the population, different foraging strategies could be highlighted and were associated with different levels of behavioural consistency and dietary choices. Sex, breeding stage and body measurements did not influence individual strategies. I show here the usefulness of using a combination of approaches – merging spatial, behavioural and dietary analyses – to investigate the links between foraging behaviour, its consistency and diet in individuals, which is essential to understand and accurately characterise ecological processes (Kernaléguen et al. 2015b). Future studies should investigate if such links are maintained in years of different environmental conditions and prey availabilities and whether age/experience influences consistency and individual specialisation. Furthermore, whether individual strategies confer specific advantages in terms of immediate foraging success and overall fitness should be determined.
Supporting documentation

**Table S2.1** Summary of dive metrics.

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<tr>
<th>Bird number</th>
<th>Sex</th>
<th>Maximum depth (m)</th>
<th>Vertical distance travelled (m)</th>
<th>Dive duration (s)</th>
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</thead>
<tbody>
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<td>Mean ± SD</td>
<td>CV</td>
<td>Mean ± SD</td>
<td>CV</td>
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<td>55.1 ± 23.3</td>
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<td>22.6 ± 3.7</td>
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Table S2.2 Summary of spatial use metrics.

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CHAPTER 3

Mate similarity in foraging Kerguelen shags: a combined bio-logging and stable isotope investigation

A version of this chapter has been published as:

Abstract

Similarity or dissimilarity between 2 individuals that have formed a pair to breed can occur in morphology, behaviour and diet. Such patterns influence partners’ cooperation when rearing their offspring, consequently influencing reproductive success. They may confer different benefits, depending on species and contexts. However, the extent to which breeding partners are similar in morphology, behaviour, and diet is poorly documented. Furthermore, the relationship between behavioural consistency and mate choice is particularly poorly understood. To investigate these issues, Kerguelen shags *Phalacrocorax verrucosus*, which are monogamous with high mate fidelity across years, were studied. Partners were equipped with GPS and diving behaviour loggers. Feather and blood samples were analysed for stable isotopes (δ^{13}C, a proxy of foraging habitat, and δ^{15}N, a proxy of diet/trophic position). Generalized linear mixed effects models and permutation tests were used to investigate pair similarity in morphology, foraging behaviour, behavioural consistency, overlap in foraging areas, and diets/foraging habitats. Mates were found not to exhibit size-assortative mating, but were more similar in foraging behaviour. They did not show assortative or disassortative mating based of foraging behavioural consistency. Furthermore, they followed more similar bearings and overlapped more in foraging areas. In accordance with this, partners were more similar in δ^{15}N. Given the lack of assortative mating by morphology, the similarity in behaviour could be due to individuals selecting mates with similar foraging abilities, linked with individual quality, and/or subsequently using information gained regarding their partners’ foraging strategies (e.g. local enhancement). This could help partners increase their foraging efficiency and reproductive success.
Introduction

Similarity in behavioural traits within breeding pairs can have important, long-lasting effects on reproductive success and fitness in species with biparental care, probably because of reduced sexual conflict over the provision of parental investment associated with choosing a partner with compatible provisioning rules (Schuett et al. 2011). This allows mates to enhance their cooperation and coordination in the provision of care, essential in species with biparental care and associated with improved reproductive performance, including offspring growth and survival (Spoon et al. 2006, Schuett et al. 2010, 2011, Rangassamy et al. 2015). Disassortative mating with respect to the partners’ recognition cues may, however, lead to reduced inbreeding (Holman et al. 2013). In terms of personality, disassortative mating can lead to the production of offspring of intermediate personality, associated with lower variance in survival in the long-term and higher life expectancy (Dingemanse et al. 2004, Schuett et al. 2010). Risk partitioning has been shown to increase the fitness of both partners; while one parent could adopt a risk-averse strategy to provide enough food to ensure that the chicks reach fledging, the other partner might provide the extra bulk for improved post-fledging survival through a risk-adverse strategy (Elliott et al. 2010). In contrast, combinations of dissimilar behavioural traits within pairs could result in unstable and disharmonious conditions, generating high stress levels that have the potential to negatively influence reproduction (Von Holst 1998, Rangassamy et al. 2015). In general, the extent of mate similarity in behaviour is poorly investigated (Schuett et al. 2010).

Empirical evidence suggests that mate similarity or dissimilarity confer different advantages and are selected for in different species or environmental conditions in a non-mutually exclusive way (Dingemanse et al. 2004, Schuett et al. 2010). In the Dumpling squid *Euprymna tasmanica*, mates showing similar levels of boldness had higher probabilities of
reproducing successfully, which might result from either behavioural mate preference or genetic compatibility between partners (Sinn et al. 2006). Similarly, in some bird species, highly behaviourally compatible pair members had higher reproductive success potentially as a result of better cooperation of individuals of similar behavioural traits (Both et al. 2005, Spoon et al. 2006). In contrast, Thick-billed murre *Uria lomvia* pairs exhibited a higher reproductive success when they were constituted of one risk-averse and one risk-prone partners (Elliott et al. 2010). Similarly, in animals with distinct foraging territories such as raptors, overall feeding rates become higher when mates adopt different foraging strategies (Andersson & Norberg 1981).

Behavioural consistency could also be used to assess the quality of potential mates, and, therefore, influence mate choice (Byers 2007, Botero et al. 2009, de Kort et al. 2009). Consistency in behaviour can signal predictability and, as such, can provide benefits to partners in many aspects of their social life (Schuett et al. 2010). Consistency could also be an indicator of quality and it has been suggested that consistency could be generated by sexual selection if individuals tend to preferentially choose mates that are consistent or individuals outperform competitors when they consistent (Dall et al. 2004). Assortative mating in terms of behavioural consistency could be important to enhance behavioural coordination within breeding pairs, leading to increased reproductive success (Spoon et al. 2006). In contrast, in cases in which pairs constituted of a risk-prone and a risk-averse mate have a better reproductive success, disassortative mating by behavioural consistency might be preferable; risk-prone individuals might indeed be more inclined to explore new environments (Dingemanse et al. 2003, Bremner-Harrison et al. 2004), and therefore exhibit lower behavioural consistency, compared to their risk-averse mates. Data on assortment in terms of behavioural consistency is lacking, but studies in Zebra finches *Taeniopygia guttata*
suggest that pairs comprised of partners that differ in behavioural consistency raise offspring in poorer condition (Schuett et al. 2010, 2011).

Mate similarity or dissimilarity can also be influenced by sexual dimorphism and size-assortative mating. Sexual size dimorphism is widespread in animal taxa, and species exhibiting dimorphism are known to exhibit differences in behaviour and diet (Andersson & Norberg 1981, Camilleri & Shine 1990, Magurran & Garcia 2000, Marcelli et al. 2003, Isaac 2005, Weimerskirch et al. 2006). For example, male and female European polecats *Mustela putorius* forage at different times of the day (Marcelli et al. 2003) and some snake species exhibit dimorphism leading to dietary divergence between males and females (Camilleri & Shine 1990). Hence, sexual dimorphism would be expected to influence mate similarity and lead to a higher mate dissimilarity in behaviour and/or diet within dimorphic species (Andersson & Norberg 1981, Elliott et al. 2010) in comparison to monomorphic species. However, when size-assortative mating occurs, such dissimilarity is likely to be reduced as mates are then more similar in morphology and, therefore, expected to be more similar in behaviour as well in comparison to non-mated individuals. The interplay between dimorphism, size assortative mating, and mate similarity in behaviour and diet has rarely been investigated.

Seabirds are generally socially monogamous, exhibit biparental care and show high mate-fidelity (Bried & Jouventin 2002). As such, seabird partners establish specific foraging strategies in order to enhance their reproductive success through, for example, better coordination of provisioning behaviour (Davis 1988, Shoji et al. 2011, Thiebot et al. 2015). Despite the potentially long-lasting and important consequences of pair similarity on reproductive success, only 2 studies, to the best of my knowledge, have focused on identifying pair similarity in the diet and behaviour of seabirds. They showed that partners do
not necessarily show similar food preferences (Harris et al. 2016), and that similarity in partners’ diets can lead to a decline in chick growth rates and fledglings produced (Watanuki 1992). To fill these knowledge gaps, testing the pair similarity in key traits affecting offspring provisioning and condition, such as in foraging metrics and behavioural consistency during the breeding season, is needed, particularly in dimorphic species in which males and females are expected to differ in behaviour and diet.

Kerguelen shags *Phalacrocorax verrucosus* are suited for investigations of relationships in the behaviour, consistency in foraging and diet of partners within a breeding pair. Individuals exhibit strong specialisation in such traits that can be maintained over the long-term, regardless of their sex, and therefore could be used by individuals to evaluate the quality of potential mates (Bearhop et al. 2006, Cook et al. 2006, Camprasse et al. 2017a). They are long-lived, resident, and benthic foraging seabirds, and individuals repetitively exploit the same foraging areas (Camprasse et al. 2017a). In addition, both parents often exhibit high nest fidelity, mate retention, and share incubation and chick-rearing duties (Aebischer et al. 1995, Sapoznikow & Quintana, 2008, C.A. Bost, pers. obs.). Kerguelen shags exhibit sexual dimorphism, with males being larger and heavier than females, as well as specialisations in feeding times with females foraging in the morning, and males foraging in the afternoon (Cook et al. 2013); these patterns might be expected to lead to mates exhibiting differences in behaviour, which makes Kerguelen shags interesting models to investigate the interplay between sexual dimorphism, size-assortative mating, and pair similarity.

In the present study, the similarity in foraging behaviour and morphology within pairs of Kerguelen shags was examined through the use of morphometric measurements and the combination of stable isotope dietary analysis and bio-logging techniques. My aim was to
determine if: (1) individuals exhibit size-assortative or -disassortative mating; (2) the foraging (diving and spatial use) effort of partners was more or less similar compared to non-mated birds; (3) the consistency in foraging behaviour of partners was more or less similar compared to non-mated birds; (4) partners overlapped more or less than non-mated birds in foraging locations; and (5) partners exhibited more similar or dissimilar diets/foraging habitats compared to non-mated birds.

**Materials and methods**

*Instrumentation*

Field work was conducted at Pointe Suzanne (49°26’S, 70°26’E), Kerguelen Islands, southern Indian Ocean, during the 2014/15 breeding season. Sampling occurred during 2 sessions. First, a total of 20 Kerguelen shag *Phalacrocorax verrucosus* individuals (both partners from 10 nests) were equipped with GPS data loggers (I-gotU GT120, Mobile Action; 44.5 x 28.5 x 13 mm, 12 g in air corresponding to ca. 0.5% of mean body mass) for 3 to 6 d at the end of incubation/early chick rearing period (26 November to 10 December, hereafter “incubation/early chick-rearing”), when chicks were no older than 1 wk. During this session, nest checks every 2 or 3 d allowed me to determine the age of the chicks. Second, a total of 22 birds (both partners from 11 nests, including 6 new nests and 5 nests used during the first deployment session) were equipped for 3 to 12 d during the late chick rearing period (6 to 18 January, hereafter “late chick-rearing”), of which the 10 previously sampled birds were deployed with GPS data loggers while the remaining 12 individuals were equipped both with GPS data loggers and time-depth recorders (TDR, LAT1800S, Lotek Wireless; 36 x 11 x 7.2 mm, 4.8 g in air corresponding to ca. 0.2% of mean body mass). During this second session,
chicks were ca. 30 to 40 d old, except for 1 pair that had a chick ca. 10 to 15 d old. Monitoring of the nests could not be conducted at all times but a high proportion of observed change-overs (75.8%) occurred after females came back from their morning trips, after which they tended to stay at the colony for the day (E.C.M. Camprasse, pers. obs.), and therefore chicks were still in the presence of a parent most of the time. All but 1 brood had a single chick at deployment. This unique brood, however, lost their second chick immediately after deployment. While no quantitative data was collected on the rest of the population, this low number of chicks per brood was a general pattern within the colony compared to the maximum of 3 chicks that Kerguelen shag pairs can raise during a single breeding season (C.A. Bost, pers. obs.). In conjunction with poor breeding success in sympatrically breeding Gentoo penguins Pygoscelis papua at the time of the study, such a pattern seems indicative of unfavourable environmental conditions (Camprasse et al. 2017b).

Individuals were captured at the colony using a noose attached to a fishing pole, weighed in a cloth bag using a suspension scale (± 25 g, Pesola), and banded with an individually numbered coloured plastic ring on one leg and an individually numbered metal ring on the other leg for identification. The data loggers, encased in heat shrink plastic for waterproofing, were attached to the back feathers using waterproof tape (Tesa 4651) and cyanoacrylate glue (Loctite 401). Handling times ranged from 15 to 20 min during which the bird’s head was covered with a hood to reduce stress. Females tended to forage in the morning while males foraged mostly during the afternoon (Cook et al. 2013). Whenever possible, I took advantage of this difference in schedule to deploy data loggers before the birds left the colony.

Individuals were gently recaptured 3 to 18 d later as previously described. The data loggers were removed and individuals were weighed again and morphometric measurements
(bill length, bill width, head length, wing length, and tarsus length) were taken using a vernier calliper (± 0.05 mm), or ruler (± 1 mm) (except for 1 bird for which I obtained mass but not morphometric measurements). In addition, 3 to 6 dorsal dark contour feathers were plucked and a blood sample (0.5 to 1.5 ml) was collected by venipuncture of a tarsal vein.

GPS loggers were programmed to sample position at 1 min intervals during incubation/early chick-rearing and at 2 min intervals during the chick-rearing period. The TDR units were set to record depth at 1 sec intervals.

GPS data were obtained for only 17 of the 20 individuals equipped during the first round of deployments due to logger failure, resulting in 7 pairs with spatial data for both partners at this stage. During the second deployment session, spatial data were obtained for 21 out of 22 individuals, and thus 10 pairs had complete data for both members. Out of these 10 pairs, 6 pairs were from new nests and 4 pairs were from those that were deployed with loggers during incubation; out of these 4, 2 had complete data from the first deployment session. This resulted in a total number of 15 different pairs with data on both members. For 13 of those pairs, both members have data on more than one trip and could be used to evaluate consistency in spatial use.

Isotopic analyses

The measurement of ratios of stable isotopes of carbon (¹³C/¹²C) and nitrogen (¹⁵N/¹⁴N) is a powerful tool to investigate the food and feeding ecology of consumers (Cherel et al. 2005a). More specifically, δ¹³C and δ¹⁵N values of seabirds are considered to be proxies of their foraging habitats, and diets/trophic position, respectively (Cherel & Hobson 2007). Overall, δ¹³C values decrease along a latitudinal gradient (Cherel & Hobson 2007, Jaeger et
al. 2010) and δ\textsuperscript{15}N values increase with trophic level (Cherel et al. 2010). δ\textsuperscript{13}C enrichment also occurs for inshore or benthic species as opposed to offshore and pelagic ones (Hobson et al. 1994). Isotopic values (details in Cherel et al. (2008)) were measured on whole blood (hereafter “blood”) and contour feathers (hereafter “feathers”) of the studied shags. The rationale is that the 2 complementary tissues integrate different periods of information. Blood is a metabolically active tissue that covers a period of weeks before sampling, whereas feathers, a metabolically inert tissue, reflect the foraging ecology at the time they were grown. In other species from the blue-eyed shag complex, such as the Antarctic shags P. bransfieldensis, contour feathers are replaced in March, immediately after breeding (Bernstein & Maxson 1981). Here, blood and feathers collected during the breeding period reflect the breeding period itself and the previous post-breeding moulting period that took place almost 1 yr before the study, respectively.

In the laboratory, blood samples were freeze-dried and powdered. Lipid extraction was not necessary as the C:N mass ratio was < 3.5 for all blood samples (Cherel et al. 2005b). A single contour feather per bird was cleaned of surface lipids and contaminants using a 2:1 chloroform: methanol bath, air-dried, and cut into small pieces. Nitrogen and carbon isotopic ratios were measured with a continuous-flow isotope-ratio mass spectrometer (Thermo Scientific Delta V Advantage) coupled to an elemental analyser (Thermo Scientific Flash EA 1112). Results are presented in the usual δ notation relative to Vienna PeeDee Belemnite for carbon and atmospheric N\textsubscript{2} for nitrogen. Replicate measurements of internal laboratory standards (acetanilide and peptone) indicated measurement errors < 0.15 ‰ for both δ\textsuperscript{13}C and δ\textsuperscript{15}N. Isotopic values were obtained for both members of 15 pairs.
Data processing

All data processing and analyses were conducted in the R Statistical Environment, version 3.2 (R Core Team 2015). GPS records were visually inspected and individual trips were determined. The diveMove package (Luque 2007) was used to apply a speed filter on the GPS data to remove erroneous locations and obtain summaries of diving metrics from TDR records (only dives > 1 m were considered in analyses). As dive depths (i.e. depths at the deepest part of a dive) were not normally distributed within individuals, the mode of dive depths instead of the mean was recorded for each trip. The means of dive durations and the sum of vertical distance travelled per trip was also calculated. These values were used to calculate a mean of means (or means of modes) and coefficients of variation (CVs) across foraging trips for each individual. The packages trip (Sumner 2013) and sp (Pebesma & Bivand 2015) were used to obtain foraging metrics for each trip (bearings, total distances travelled, maximum distances and trip durations). Bearing for each trip was calculated as the angle between the colony and the most distal point of the tracks and standard deviation in bearing was calculated for each individual using the circular package (Agostinelli & Lund 2011). Means and CVs for all metrics were obtained per individual and per stage, except bearings, for which SD was calculated.

Kernel home ranges for each trip of each individual were determined and their overlap calculated in the adehabitatHR package (Calenge 2006). Because Kerguelen shags tend to fly to their foraging grounds and dive predominantly at the most distal part of their trip (Camprasse et al. 2017a), and because I wanted to know whether sexes or partners forage in the same locations, only core foraging area (50% home range) was calculated. Each trip for each male within each breeding stage was compared to each trip for each female sampled within the same stage by calculating the overlap in core foraging area between these 2 trips.
with the “kerneloverlap” function in the *adehabitatHR* package using the Bhattacharyya’s affinity (Fieberg & Kochanny 2005).

An index of spatial use consistency was calculated for each animal within each stage. For each pair of trips within a deployment, a kernel overlap was calculated (e.g. for a bird with 3 trips, 3 overlap values were obtained, between Trip 1 and Trip 2, Trip 2 and Trip 3 and Trip 1 and Trip 3), as describe above for the overlap between males and females. The average of these numbers was obtained and used as an index of consistency for each individual within each stage.

*Data analyses*

Linear mixed effects models were used to confirm sexual dimorphism in mass in study birds, as mass data was obtained both at incubation/early chick-rearing and in late chick-rearing for some birds, and always both at deployment and retrieval. Dimorphism in size was checked using only 1 of the morphometrics obtained (tarsus length, as the other ones were correlated) using linear regression as single measurements were obtained. When looking at pair similarity, 2 kinds of analyses were run depending on the structure of the data: when a single observation per individual was available, permutation tests were run, and when multiple observations were available (i.e. one observation per trip on multiple consecutive trips), generalized linear mixed models (GLMMs) with crossed random effects were used. p-values < 0.05 were considered significant for all tests. Specifically, a significant p-value for the permutation tests or binomial GLMM meant that partners were more similar or dissimilar than expected by chance and summarizing the data for “true pairs” and “false pairs” gave the direction of the effect.
To investigate any potential correlations in morphology in partners, a principal component analysis (PCA) was run on masses at deployment and retrieval and on the 5 body measurements. The Euclidean distances for all possible combinations of males and females were calculated from the scores obtained thanks to the PCA for each individual. Euclidean distances were used as a way to examine the pattern of similarities in the body size and mass of individuals in the sample (Wojczulanis-Jakubas et al. 2011). Permutation tests were carried out in the *permute* package (Simpson 2014) on the matrix containing the Euclidean distances and whether they came from actual paired individuals (value of 1) or not (value of 0) with the null hypothesis being that partners were not more similar than expected by chance.

Permutation tests (10 000 iterations) randomly assigned each Euclidean distance to a type of pairing. Permutational p-values were used and they are defined as the proportion of randomized values as extreme or more extreme than the observed value (Manly 1991).

The 3 dive-level variables that were extracted from the TDR data (dive duration, maximum depth, and vertical distance) were correlated, so we only considered maximum depth in the analysis (maximum depths and trip duration: Spearman’s rho = 0.93, p < 0.0001, maximum depths and sums of vertical distances: Spearman’s rho = 0.36, p = 0.05). Maximum depths were used in modelling as representative of habitat selection in the vertical dimension. The absolute values of the differences in maximum depth between males and females were used to investigate the similarity or dissimilarity between paired males and females within the chick-rearing stage, because I was not specifically interested in which sex had the higher value, but just in the distance between them. I estimated the probability of pairs constituting true pairs using logistic regression using a generalized linear mixed-effects modelling framework (GLMM, “glmer” in the *lme4* package (Bates et al. 2011), with a binomial distribution and logit link). Best models were selected based on their Akaike’s information
criteria. For the diving behaviour model, differences between males and females in maximum dive depths were used as explanatory variables, while the individual bird ID was used as a crossed random effect with males crossed with females of each possible pair (with 1 being “true pair” and 0 being “false pair”). Total distance travelled, maximum distance and trip duration were highly correlated (total distances and trip duration: Spearman’s rho=0.60, P<0.0001, total distances and maximum distances: Spearman’s rho=0.96, P<0.0001). Therefore, only total distance travelled was included in the analysis of pair similarity or dissimilarity in spatial use. As such, to investigate whether partners exhibited a similar spatial use, a model similar to the one described above included the absolute values of the differences in total distances between males and females for each possible pairs and for each stage. In the final model, these differences, stage and their interaction were used as explanatory variables.

To determine if partners were more similar or dissimilar than non-mated birds in consistency, classical multidimensional scaling was applied and the Euclidean distances for all possible combinations of males and females were calculated separately for each stage. Pairing was indicated (with 1 being “true pair” and 0 being “false pair”). Permutation tests were performed and permutational p-values were obtained, as described above, for dive behaviour consistency and spatial use consistency, respectively. For the former, Euclidean distances were calculated from the coefficients of variation in maximum depth, dive duration and sum of vertical distance travelled; in this case, all 3 variables were used as their coefficients of correlation were not correlated. For the latter, the variables included in the calculation of the Euclidean distances were the following, uncorrelated measures of consistency: the indices of spatial use consistency, standard deviations in bearing, and coefficients of variation in trip duration, total and maximum distances.
To examine whether partners of the same nest overlapped more or less than birds from different nests, 2 tests were run: 1 with bearings, and 1 with the kernel overlap values. In both cases, the probability of pairs constituting true pairs was analysed by logistic regression using a generalized linear mixed-effects model (GLMM with a binomial distribution and logit link). The absolute values of the differences between bearings in true and randomised pairs, and the overlap values between males’ and females’ trips, stage, and their interaction were used as explanatory variables in 2 different models, while individual bird ID was used as a crossed random effect with males crossed with females of each possible pairing.

To investigate whether partners had a more similar or dissimilar diet/trophic level compared to non-mated birds, the Euclidean distances for all possible combinations of males and females were calculated, separately for each stage, either for δ¹³C and δ¹⁵N values combined, for δ¹³C values only, or for δ¹⁵N values only, in blood and feathers. Permutation tests were carried out on the matrices containing the Euclidean distances and whether they came from actual paired individuals.

Results

Equipped Kerguelen shags were sexually dimorphic (Table 3.1). Males were 0.29 ± 0.06 (means ± SD) kg heavier than their partners ($t_{30} = 4.60, p < 0.001$) and had tarsus lengths 2.60 ± 0.65 mm ($t_{29} = 3.97, p < 0.001$) greater than females. Partners were not more similar or dissimilar to each other in morphological traits and body mass than expected by chance. Indeed, permutation tests indicated no significant differences between paired individuals and the rest of the individuals sampled (permutational $p = 0.18$).
Table 3.1 Morphometric measurements (mean ± SD; min-max) of all Kerguelen shags equipped at the Pointe Suzanne colony, Kerguelen Islands.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Females (n = 14)</th>
<th>Males (n = 15)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body mass (kg)</td>
<td>2.1 ± 0.2 (1.9 – 2.6)</td>
<td>2.4 ± 0.2 (2.0 – 2.8)</td>
</tr>
<tr>
<td>Head length (mm)</td>
<td>132.1 ± 6.9 (124.5 – 149.0)</td>
<td>133.6 ± 4.4 (125.5 – 142.0)</td>
</tr>
<tr>
<td>Tarsus length (mm)</td>
<td>63.6 ± 1.5 (60.9 – 66.2)</td>
<td>66.1 ± 2.9 (61.4 – 69.2)</td>
</tr>
<tr>
<td>Beak width (mm)</td>
<td>13.2 ± 1.4 (11.9 – 16.9)</td>
<td>14.0 ± 1.0 (12.7 – 15.7)</td>
</tr>
<tr>
<td>Culmen length (mm)</td>
<td>50.3 ± 1.7 (47.3 – 52.6)</td>
<td>52.4 ± 3.8 (40.9 – 56.6)</td>
</tr>
<tr>
<td>Wing length (mm)</td>
<td>272.0 ± 7.4 (252.0 – 282.0)</td>
<td>278.9 ± 27.9 (183.0 – 295.0)</td>
</tr>
</tbody>
</table>
Diving data were obtained for all 12 birds equipped with TDR during late chick-rearing. Males tended to dive deeper and be more variable in dive depths than females (Figure 3.1, Table S3.1) as shown in Camprasse et al. (2017a). The difference in maximum depth between mates was lower than for non-mated birds (binomial GLMM: $\chi^2 = 68.34$, df = 1, $p < 0.0001$); on average mates differed in depths by $17.1 \pm 0.9$ m, as opposed to $27.6 \pm 0.5$ m in non-mated birds. Males and females did not differ in trip metrics, including trip durations, maximum distances, total distances, and bearings (Table 3.2 & S3.2). Partners were more similar in spatial use than expected by chance. Indeed, the differences in total distances travelled were smaller in true pairs compared to randomised pairs (binomial GLMM: $\chi^2 = 26.14$, df = 1, $p < 0.0001$). Further, there was a significant effect of stage on the differences in total distances (binomial GLMM: $\chi^2 = 7.74$, df = 1, $p = 0.005$), and a significant interaction between pairing and stage (binomial GLMM: $\chi^2 = 24.90$, df = 1, $p < 0.0001$). Specifically, mates differed in total distances travelled by $14.95 \pm 0.80$ km at incubation/early chick-rearing, and $16.38 \pm 0.71$ km in late chick-rearing; in contrast, the differences in total distances for non-paired birds did not significantly change between incubation/early chick-rearing ($19.80 \pm 0.36$ km) and in late chick-rearing ($19.61 \pm 0.25$ km).

Within pairs, no specific pattern was observed in terms of the consistency of males and females, both in terms of diving behaviour (Figure 3.1) and spatial use. Paired birds were not more similar or dissimilar in consistency in maximum depth, dive duration, and sum of vertical distance (permutational $p = 0.14$). Lastly, paired birds were not more similar or dissimilar in spatial use consistency (consistency index, SD in bearing, CV in maximum distance, total distance and trip duration) compared to non-paired birds (permutational $p = 0.51$).
Table 3.2 Summary of trip metrics for Kerguelen shags instrumented at the Pointe Suzanne colony, Kerguelen Islands, separated by sex and breeding stage (means ± SD).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Females</th>
<th>Males</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Incubation (n = 8, 35 trips)</td>
<td>Chick-rearing (n = 10, 61 trips)</td>
<td>Incubation (n =7, 48 trips) Chick-rearing (n =11, 90 trips)</td>
</tr>
<tr>
<td>Trip duration (h)</td>
<td>5.9 ± 1.8</td>
<td>6.1 ± 3.1</td>
<td>5.4 ± 2.9</td>
</tr>
<tr>
<td>Maximum distance (km)</td>
<td>10.2 ± 6.5</td>
<td>9.0 ± 6.7</td>
<td>9.5 ± 8.0</td>
</tr>
<tr>
<td>Total distance (km)</td>
<td>26.6 ± 14.0</td>
<td>22.7 ± 15.2</td>
<td>25.0 ± 19.5</td>
</tr>
<tr>
<td>Bearing (°)</td>
<td>47.6 ± 0.2</td>
<td>60.8 ± 0.4</td>
<td>75.4 ± 0.4</td>
</tr>
<tr>
<td>Index of consistency</td>
<td>0.6 ± 0.1</td>
<td>0.5 ± 0.2</td>
<td>0.4 ± 0.2</td>
</tr>
</tbody>
</table>
Figure 3.1 Dive distributions in relation to dive depth for pairs of Kerguelen shags *Phalacrocorax verrucosus* equipped at the Pointe Suzanne colony, Kerguelen Islands
Males always departed after their mates came back from their morning foraging trips during incubation/early chick-rearing, and did so 75.8% of the time during late chick-rearing. Within pairs, males and females followed similar bearings to their foraging areas (binomial GLMM: $\chi^2 = 187.14$, df = 1, $p < 0.0001$) (Figure 3.2) and there was a significant effect of stage on those differences in bearings (binomial GLMM: $\chi^2 = 32.36$, df = 1, $P < 0.0001$), but no interaction between pairing and the differences in bearings (binomial GLMM: $\chi^2 = 2.60$, df = 1, $P = 0.11$). Mates differed in bearings by $41.8 \pm 2.9$ ° at incubation/early chick-rearing, and $52.0 \pm 2.2$ ° in late chick-rearing; in contrast, the differences in bearings for non-paired birds were $55.7 \pm 1.0$ ° at incubation/early chick-rearing, and $70.7 \pm 0.8$ ° in late chick-rearing. Overall, paired birds overlapped significantly more than non-paired birds (binomial GLMM: $\chi^2 = 159.05$, df = 1, $p < 0.0001$) and overlap was not affected by stage (binomial GLMM: $\chi^2 = 1.60$, df = 1, $p = 0.21$). The mean overlap was $14.5 \pm 0.6\%$ for paired birds and $9.8 \pm 0.2\%$ for non-paired birds.

There were large inter-individual differences in both $\delta^{13}$C and $\delta^{15}$N values of the sampled Kerguelen shags (difference: 5.5 and 3.8 ‰, respectively) (Table S3.3, Figure S3.1). Blood $\delta^{13}$C values ranged from -19.97 to -14.44 and $\delta^{15}$N values ranged from 12.88 to 16.68. There were no differences in blood isotopic values between sexes, thus confirming that males and females had similar foraging habitats ($\delta^{13}$C) and diet/trophic levels ($\delta^{15}$N) during breeding. When taking into account both blood $\delta^{13}$C and $\delta^{15}$N values, partners were not more similar or dissimilar than expected by chance for both stages (permutational $p = 0.43$ and $p = 0.31$, at incubation/early chick-rearing and late chick-rearing, respectively). Blood $\delta^{13}$C values of paired birds were not more similar or dissimilar than expected by chance (permutational $p = 0.86$ and $p = 0.74$, at incubation/early chick-rearing and late chick-rearing, respectively). However, blood $\delta^{15}$N values of paired birds were closer than expected by
chance (permutational p = 0.04 and p = 0.01, at incubation/early chick-rearing and late chick-rearing, respectively). Indeed, in contrast to blood δ^{13}C values, male blood δ^{15}N values were positively linearly correlated to female δ^{15}N values (Figure 3.3). As with blood, there were large inter-individual differences in feathers in both δ^{13}C and δ^{15}N values of the sampled Kerguelen shags (difference: 6.7 and 3.9 ‰, respectively), with δ^{13}C values ranging from −20.06 to −13.32 and δ^{15}N values ranging from 13.47 to 17.41. Partners did not have more similar feather isotopic values, whether taking into account both δ^{13}C and δ^{15}N values, δ^{13}C values only, or δ^{15}N values only (permutational p = 0.59, 0.68, and p = 0.10, respectively).
Figure 3.2 Consecutive GPS tracks for all pairs of Kerguelen shags *Phalacrocorax verrucosus* equipped at the Pointe Suzanne colony, Kerguelen Islands
Figure 3.3 Correlations in blood $\delta^{13}$C and $\delta^{15}$N values of partners of Kerguelen shags *Phalacrocorax verrucosus* (partners are indicated by shared colours, $n = 11$ pairs) sampled at the Pointe Suzanne colony, Kerguelen Islands; $\delta^{15}N_{\delta} = 0.89 \delta^{15}N_{\gamma} + 1.42$. 
Discussion and conclusions

In the present study, I investigated the similarity or dissimilarity in the foraging strategies of Kerguelen shag *Phalacrocorax verrucosus* partners using the complementary approaches of bio-logging and stable isotope analysis. The salient results can be summarized as follows: (1) mates did not show assortative or disassortative mating by either morphometrics, or behavioural consistency; (2) they were, however, more similar than expected by chance in foraging behaviour, followed more similar bearings, and overlapped more in foraging areas, and (3) they had more similar diets/similar trophic levels than expected by chance.

Our results confirm previous findings that Kerguelen shags are dimorphic in body size and mass (Cook et al. 2013). Within breeding pairs, males were always heavier and generally structurally larger than their female partners. Such strong sexual dimorphism suggests a differential niche utilization for males and females in the population (Selander 1966, Cook et al. 2013) with the potential to affect pair similarity or dissimilarity in foraging behaviour. Indeed, it is expected that dimorphic mates exhibit a higher dissimilarity compared to monomorphic species, as dimorphic birds can display divergent foraging behaviours based on their morphology (Weimerskirch et al. 2006, Elliott et al. 2010). While Kerguelen shags are dimorphic and exhibit temporal segregation with females foraging mostly in the morning and males mostly in the afternoon, differences in their foraging behaviour and its consistency during the time of this study were showed to be limited (Camprasse et al., 2017a). If sexual dimorphism led males and females to display different foraging strategies, then pair dissimilarity in foraging behaviour would be expected. However, in the present study, differences in foraging behaviour between males and females were limited so if any pair dissimilarity in foraging behaviour were found, it would be due to different factors.
In the present study, I found no evidence of size-assortative or -disassortative mating. Although seabirds are known to mate assortatively by size (Wagner 1999, Forero et al. 2001, Helfenstein et al. 2004), structural size is not necessarily enough to explain mate choice (Bried & Jouventin 2002, Berzins et al. 2009). Indeed, in some cases, assortative mating is based on ornamental traits such as plumage or foot/beak colour, rather than structural size (Berzins et al. 2009, Nolan et al. 2010). For example, in other Phalacrocorax species, assortative mating with respect to crest size has been shown to occur, with crest size being an indicator of individual condition (Daunt et al. 2003). Alternatively, lack of size-assortative mating has been shown in birds and might happen when a specific trait is sexually selected in one sex only (Murphy 2008), which seems less likely in my study species as it has not been shown in shags. Instead of preferring mates that are similar to themselves, all individuals could also show the same preferences for a trait, especially when it is an honest signal indicative of individual quality (Jones et al. 2008, Schuett et al. 2010).

Despite the sexual dimorphism and the lack of size-assortative mating that was expected to reduce the degree of behavioural similarity in dimorphic mates, my findings suggest that partners are still more similar than non-mated birds in foraging behaviour. Indeed, mates exhibited smaller differences in dive depths and total distances travelled compared to non-paired birds. This pairing in terms of foraging behaviour might result from an active choice if individuals are able to evaluate potential mates and their quality, as individual quality and foraging parameters have been shown to be linked (Lewis et al. 2006, Lescroël et al. 2010). For example, in Common murres Uria aalge, females of higher quality had increased chick feeding rates and lower trip durations (Lewis et al. 2006). Similar patterns were found in Adélie penguins Pygoscelis adeliae, especially at the end of the breeding season, with poorer breeders diving deeper and making longer trips (Lescroël et al. 2010).
2010). Alternatively, this pair similarity could be a consequence of developing similar behaviours after pairing, as a result of communication between mates. Studies investigating the similarity or dissimilarity in behaviour in partners are lacking. Contrasting with our results, Imperial shag *Phalacrocorax atriceps* pairs were shown to be constituted of either both benthic members, both pelagic members, or a mixture of both (Harris et al. 2016). Positive assortment by behaviour has been shown in a few studies in groups such as birds (Both et al. 2005, Schuett et al. 2011), fishes (Budaev et al. 1999), and cephalopods (Sinn et al. 2006). In other contexts, better reproductive outcomes might be associated with the fact that more similar individuals exhibit improved cooperation and coordination, leading, for example, to better provisioning of offspring (Spoon et al. 2006, Schuett et al. 2010). This might explain the fact that mates were more similar to each other at incubation/early chick-rearing compared to late chick-rearing, as increased cooperation and coordination is more crucial when mates are incubating or guarding small chicks, as this is the period where parents are most at risk of losing their eggs or chicks through accidental dislodgement, predation, and/or hypothermy (Tveraa et al. 1998, Kober & Gaston 2003, Catry et al. 2006).

There is some evidence that certain combinations of levels of consistency within pairs can influence their reproductive success, and behavioural consistency might be important for mate choice (Schuett et al. 2010, 2011). An individual might benefit from choosing a partner exhibiting consistent behaviour; for example, it might profit from having a mate showing a consistent level of parental care or territory defence by avoiding having to constantly re-assess its mate’s quality and accordingly adjust its own behaviour (Schuett et al. 2010). Assortative mating by behavioural consistency might be expected when consistency is an indicator of quality and/or predictability in provisioning behaviour and parental care; consistent individuals would then be expected to mate preferentially with consistent
individuals, resulting in inconsistent individuals having to mate with each other (Schuett et al. 2010). Furthermore, it might be beneficial to choose a mate with high consistency, associated with the benefits mentioned above, but dissimilar behaviour, linked with the acquisition of more diversified prey items, for example (Watanuki 1992). Risk partitioning can increase fitness in paired individuals, with one partner adopting a risk-averse strategy to provide enough food for chicks to be able to fledge and the other exhibiting a risk-prone strategy to provide the extra bulk for enhanced post-fledgling survival (Elliott et al. 2010). As risk-prone individuals can be more inclined to explore new environments and, therefore be less consistent in their foraging behaviour (Dingemanse et al. 2003, Bremner-Harrison et al. 2004), disassortative mating by behavioural consistency has the potential to be beneficial in pairs, resulting in improved fitness. Despite these apparent advantages of assortative or disassortative mating by behavioural consistency, no such pattern was emphasized in Kerguelen shags at my study site. Hence, individuals in the present study might predict their mates’ provisioning behaviour based on their similarity in foraging behaviour rather than whether they are similarly consistent or not.

I propose that breeding success is related more to foraging behaviour than consistency in foraging behaviour. For example, poorer breeders might have longer trip durations, associated with longer distances travelled and better breeders might dive deeper (Lewis et al. 2006, Lescroël et al. 2010). The breeding success of pairs (number of fledglings, fledgling mass) in our study could not be determined, however, and we could not determine whether more similar or dissimilar partners in terms of behaviour or behavioural consistency had a higher breeding success. Future studies should aim at incorporating such parameters, as well as investigate the influence of differences in environmental conditions and thus prey availability, on pair similarity. In order to better understand the interplay between pair
similarity and environmental conditions, it would be necessary to quantify pair similarity and breeding success in moderate environmental conditions, when among-pair variation is likely to be greatest.

In the present study, partners were found to follow more similar bearings, especially at incubation/early chick-rearing, as well as to overlap significantly more in foraging areas compared to non-mated birds. To the best of my knowledge, such a pattern differs from the only study reporting on mate overlap in spatial use in central-place foragers: Imperial shag partners in Argentina did not seem to overlap, although whether partners overlapped more or less than non-paired birds was not tested (Harris et al. 2016). The results shown in my study suggest that such pattern could result from mate choice and/or could allow birds to reduce time spent searching for food if individuals use information gained regarding their partners’ foraging strategies to adopt more efficient tactics (e.g. local enhancement). Indeed, seabirds, including cormorants, are known to be able to use visual, tactile and olfactory cues from their congeners for more efficient foraging (Ward & Zahavi 1973, Silverman et al. 2004, Weimerskirch et al. 2010) as are other groups of animals (Galef & Wigmore 1983, Drapier et al. 2002, White et al. 2008). Furthermore, seabirds are able to use information transfer and depart the colony following the direction from which conspecifics are returning to the colony (Tremblay et al. 2014). A transfer of information between paired birds would be facilitated by the temporal segregation in foraging between males and females, with males cueing on their partners’ flight directions as they return from morning foraging trips and follow more similar bearings to their partners compared to other conspecifics (Tremblay et al. 2014). Such similarity not only in bearings but also in foraging areas might also explain why mates tended to dive at more similar depths, as Kerguelen shags are benthic divers.
The spatial overlap in foraging range shown here could explain why partners tended to consume prey at similar trophic levels. This pattern did not occur outside of the breeding season, when birds are not constrained to come back to the nest and therefore are less likely to gather information from their partners, as judged by the δ¹⁵N values of feathers. Assortative mating by diet has been shown to occur in fishes and may reflect either the ability of individuals to evaluate potential mates or a consequence of another preference (e.g. habitat choice, morphology) (Snowberg & Bolnick 2008, Martin 2013). Therefore, assortative mating by diet could either reflect a preference for partners that have similar diets or be a consequence of other factors after pairing based on other criteria has occurred. As it is unclear how individuals are able to assess prospective mates’ diet, it seems more likely that individuals choose mates based on their individual quality, for example via the selection of mates with similar crest sizes (Daunt et al. 2003), and then feed at similar trophic levels as a consequence of exhibiting similar foraging behaviour and prospecting for food in similar areas. In contrast, no correlation was observed within breeding pairs in the plasma δ¹⁵N values of Imperial shags and all potential combinations of foraging behaviour were found within pairs (both partners were benthic feeders, or pelagic feeders, or the pairs were mixed, Harris et al. 2016). Similarity in food preferences within breeding pairs has also been reported in Great skuas Stercorarius skua and Slaty-backed gulls Larus schistisagus, in which partners frequently hunt together (Watanuki 1992, Votier et al. 2004). In Slaty-backed gulls, the increase in diet overlap between mates corresponded with a decrease in chick growth rates and number of fledglings produced (Watanuki 1992). Therefore, the benefits for partners of foraging on similar prey remain unclear, unless it derives from mates communicating on where to find food for reduced searching time and improved chick provisioning as suggested above.
Other factors could lead to mates being more similar foragers than expected by chance which also affect their ability to rear offspring (Bradley et al. 1995, Jouventin et al. 1999, Ludwig & Becker 2008); some species exhibit age-specific dietary and spatial segregation, primarily determined by a “cohort effect” that would lead individuals sharing a common life history to forage preferentially together or to share similar foraging limitations (Pelletier et al. 2014). Lastly, subcolony variation, known to occur even in small colonies, could indirectly influence the overlap in foraging areas and the similarity in diet within pairs (Masello et al. 2010, Bogdanova et al. 2014). In these studies, individuals at similar locations within the colony tended to forage in the same direction. In our study, however, birds were equipped within a few meters of each other yet still foraged repeatedly in different directions (Camprasse et al. 2017a).

In conclusion, Kerguelen shags were paired with partners that displayed more similar foraging behaviour, foraging bearings, and overlap in foraging areas and diet/trophic level than expected by chance. I suggest that shags may pair with individual of similar quality (e.g. via selection for individual of similar crest size or other traits signalling quality), resulting in mates having similar foraging abilities. They thus have the potential to forage in areas of similar characteristics. Further exchange of information between mates at change-overs could then lead mates to follow similar bearings and overlap more in foraging areas compared to non-paired birds; in turn, this may lead mates to feed at more similar trophic levels. Investigating the ways in which birds assess mate quality (e.g. in terms of foraging efficiency, ornamentation, condition or experience) is crucial to build on the conclusions of the present study. Collecting data over during years of different environmental conditions will also help understand if the patterns highlighted in my study are maintained in years of better food availability. Lastly, more studies are necessary to understand the reproductive
consequences of mate similarity, and should incorporate, for example, long-term measures of reproductive success (Fraser et al. 2002). Such a step is crucial to understand the repercussions of mate choice in seabirds.
Supporting documentation

Table S3.1 Summary of diving metrics for Kerguelen shags (n = 12) instrumented at the Pointe Suzanne colony, Kerguelen Islands (means ± standard deviations, and coefficients of variation).

<table>
<thead>
<tr>
<th>Bird/pair number</th>
<th>Sex</th>
<th>Modal depth (m)</th>
<th>Vertical distance travelled (m)</th>
<th>Dive duration (s)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mean ± SD</td>
<td>CV</td>
<td>Mean ± SD</td>
</tr>
<tr>
<td>1/8 (n = 8 trips)</td>
<td>male</td>
<td>63.6 ± 22.5</td>
<td>0.11</td>
<td>1053.0 ± 372.3</td>
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<tr>
<td></td>
<td></td>
<td>191.1 ± 68.8</td>
<td>0.14</td>
<td></td>
</tr>
<tr>
<td>2/9 (n = 5 trips)</td>
<td>female</td>
<td>27.1 ± 12.1</td>
<td>0.04</td>
<td>1371.4 ± 613.3</td>
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<tr>
<td></td>
<td></td>
<td>126.7 ± 56.5</td>
<td>0.04</td>
<td></td>
</tr>
<tr>
<td>3/9 (n = 9 trips)</td>
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<td>24.0 ± 8.0</td>
<td>0.04</td>
<td>1508.9 ± 503.0</td>
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<tr>
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<td></td>
<td>100.9 ± 34.2</td>
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<td></td>
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<tr>
<td>4/8 (n = 4 trips)</td>
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<td>24.7 ± 12.3</td>
<td>0.15</td>
<td>1566.8 ± 783.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>128.3 ± 63.0</td>
<td>0.10</td>
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</tr>
<tr>
<td>5/10 (n = 5 trips)</td>
<td>female</td>
<td>21.5 ± 9.6</td>
<td>0.16</td>
<td>1183.7 ± 529.4</td>
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<tr>
<td></td>
<td></td>
<td>119.3 ± 55.6</td>
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<tr>
<td>6/11 (n = 5 trips)</td>
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<td>13.8 ± 6.2</td>
<td>0.07</td>
<td>1515.8 ± 677.9</td>
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<tr>
<td></td>
<td></td>
<td>86.1 ± 39.4</td>
<td>0.07</td>
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</tr>
<tr>
<td>7/12 (n = 5 trips)</td>
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<td>56.3 ± 25.2</td>
<td>0.24</td>
<td>1326.6 ± 593.3</td>
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<td></td>
<td></td>
<td>190.5 ± 85.7</td>
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</tr>
<tr>
<td>8/12 (n = 3 trips)</td>
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<td>70.3 ± 40.6</td>
<td>0.25</td>
<td>1697.4 ± 980.0</td>
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<td></td>
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<td>229.1 ± 126.9</td>
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<tr>
<td>9/10 (n = 9 trips)</td>
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<td>55.8 ± 18.6</td>
<td>0.20</td>
<td>949.1 ± 316.4</td>
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<td>179.6 ± 59.3</td>
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<tr>
<td>10/11 (n = 7 trips)</td>
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<td>38.7 ± 14.6</td>
<td>0.15</td>
<td>1158.4 ± 437.8</td>
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<td>150.2 ± 58.0</td>
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<td>11/13 (n = 10 trips)</td>
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<td>59.6 ± 19.6</td>
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<td>12/13 (n = 6 trips)</td>
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<td>22.0 ± 8.7</td>
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Table S3.2 Spatial summary for Kerguelen shags (n = 13 pairs) equipped at the Pointe Suzanne colony, Kerguelen Islands (INC = incubation/early chick-rearing, CR = late chick-rearing); all values are (n) mean ± SD

<table>
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<th>Pair</th>
<th>Stage</th>
<th>Trip duration (h)</th>
<th>Maximum distance (km)</th>
<th>Total distance (km)</th>
<th>Bearing (°)</th>
<th>Index of spatial use variability</th>
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<td>Male</td>
<td>Female</td>
<td>Male</td>
<td>Female</td>
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<tr>
<td>1</td>
<td>CR</td>
<td>(5) 8.0 ± 0.8</td>
<td>(6) 3.8 ± 2.2</td>
<td>(5) 19.0 ± 1.1</td>
<td>(6) 7.0 ± 2.3</td>
<td>(5) 44.0 ± 3.6</td>
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<tr>
<td>2</td>
<td>INC</td>
<td>(4) 3.8 ± 2.4</td>
<td>(12) 2.1 ± 1.4</td>
<td>(4) 6.0 ± 2.5</td>
<td>(12) 0.8 ± 0.3</td>
<td>(4) 14.6 ± 6.6</td>
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<tr>
<td>3</td>
<td>CR</td>
<td>(8) 5.5 ± 2.3</td>
<td>(7) 4.7 ± 3.4</td>
<td>(8) 8.7 ± 0.2</td>
<td>(7) 15.3 ± 6.5</td>
<td>(8) 23.8 ± 3.6</td>
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<td>(5) 16.0 ± 3.5</td>
<td>(7) 33.0 ± 8.4</td>
<td>(5) 38.4 ± 34.7</td>
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<td>± 8.2</td>
<td>1.9</td>
<td>± 20.0</td>
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<td>8.9 ± 0.6</td>
<td>± 3.8</td>
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<tr>
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<td>(8) 7.5</td>
<td>(18)</td>
<td>5.0 ± 2.3</td>
<td>(18)</td>
<td>3.0 ± 1.5</td>
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<tr>
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<td>CR</td>
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<tr>
<td></td>
<td></td>
<td>± 2.7</td>
<td>4.6 ± 3.0</td>
<td>± 2.6</td>
<td>16.5 ± 5.8</td>
<td>± 7.9</td>
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<td>(5) 5.9</td>
<td>(9)</td>
<td>4.8 ± 1.3</td>
<td>(5)</td>
<td>14.2 ± 3.8</td>
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94
<table>
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<th>(5) 5.3 ± 3.7</th>
<th>(9) 10.4 ± 9.9</th>
<th>(9) 8.9 ± 1.4</th>
<th>(5) 26.4 ± 23.3</th>
<th>(9) 22.4 ± 7.9</th>
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<td>(5) 12.1 ± 5.6</td>
<td>(7) 13.8 ± 7.7</td>
<td>(5) 32.8 ± 15.5</td>
<td>(7) 32.5 ± 17.5</td>
<td>(5) 21.0 ± 0.2</td>
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</tr>
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<td>(5) 17.9 ± 3.6</td>
<td>(3) 12.4 ± 5.4</td>
<td>(5) 38.6 ± 6.9</td>
<td>(3) 31.8 ± 14.7</td>
<td>(5) 48.8 ± 0.1</td>
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</table>
Table S3.3 Isotope values for Kerguelen shags (n = 12) sampled at the Pointe Suzanne colony, Kerguelen Islands, in blood (incubation/early chick-rearing and late chick-rearing) and in feathers.

<table>
<thead>
<tr>
<th>Pair</th>
<th>Sex</th>
<th>Carbon blood incubation/early chick-rearing</th>
<th>Nitrogen blood incubation/early chick-rearing</th>
<th>Carbon blood late chick-rearing</th>
<th>Nitrogen blood late chick-rearing</th>
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Figure S3.1 $\delta^{13}$C and $\delta^{15}$N values for males (triangles) and females (circles) within breeding pairs of Kerguelen shags sampled at the Pointe Suzanne colony, Kerguelen Islands (partners are indicated by shared colours, n = 15 pairs).
CHAPTER 4

Intra- and inter-individual variation in the foraging ecology of a generalist subantarctic seabird, the Gentoo penguin

A version of this chapter has been accepted as:

Elodie C.M. Camprasse, Yves Cherel, Paco Bustamante, John P.Y. Arnould, Charles-André Bost (2017). Intra- and inter-individual variation in the foraging ecology of a generalist subantarctic seabird, the Gentoo penguin. Marine Ecology Progress Series. DOI 10.3354/meps12151
Abstract

Individual specialisations have been suggested to improve foraging efficiency by optimising individual capacity (physiological and behavioural) and reducing intra-specific competition in exploiting prey resources. In this study, I investigated the inter- and intra-individual variation in behaviour in an opportunistic forager, the Gentoo penguin *Pygoscelis papua*, at Kerguelen Islands, southern Indian Ocean. I used complementary bio-logging and stable isotope analyses, coupled with morphometric measurements, to: 1) determine the inter-individual variation in morphology and foraging behaviour; 2) quantify intra-individual variation in foraging behaviour; 3) investigate the links between consistency in foraging, distances travelled and body condition; and 4) determine if dietary specialisations exist and are maintained outside the breeding season. I show that this species exhibits a large inter-individual variation in foraging behaviour, with some individuals conducting very short trips close to the colony while others travelled considerably farther. Heavier individuals tended to forage in more distant locations, dive deeper and perform more benthic dives. Individual specialisation in behaviour was low to moderate at the population level, yet some individuals were very consistent. The rate of travel was not influenced by consistency, and there was a lack of correlation between body condition and foraging consistency. High inter-individual variation in feeding ecology and dietary specialisations outside of a single breeding season were observed, consistent with Gentoo penguins being Type “B” generalists (i.e. generalist populations composed of individuals each consuming a different range of foods).
**Introduction**

According to the optimal foraging theory, individuals implement feeding strategies aimed at maximizing energetic gains while minimizing costs (Stephens & Krebs 1986). Individual specialisations have been suggested to improve feeding efficiency by reducing intra-specific competition or allowing individuals to catch prey they can handle and digest most efficiently (Bolnick et al. 2003, Estes et al. 2003). Food consumption rates and body condition differ among diet specialists, and these differences may reflect differences in an individual’s intrinsic quality (dit Durell et al. 2001, Bolnick et al. 2003, Anderson et al. 2009, Svanbäck & Persson 2009, Cucherousset et al. 2011). Specialisations in foraging, involving the repetition of specific behaviours to acquire food or dietary choices over time, have until recently been poorly investigated (Bolnick et al. 2003, Estes et al. 2003, Cook et al. 2006).

Individual specialists have been defined as “individuals whose niche is substantially narrower than their population’s niche for reasons not attributable to their sex, age or discrete morphological group” (Bolnick et al. 2003, p.3). Even populations usually thought to be generalists can actually be composed of individual specialists, referred to as Type “B” generalists (individuals each specializing on a different but narrow range of food types) as opposed to Type “A” generalists (individuals all taking a wide range of food types) (Araújo et al. 2011, Loxdale et al. 2011, Layman & Allgeier 2012, Fodrie et al. 2015).

Information on individual specialisations is crucial as they may have significant ecological consequences at the individual and population levels, and impact ecological processes and foraging dynamics (Bolnick et al. 2003, Matich et al. 2011, Ceia & Ramos 2015). Thus, it is of importance to identify the mechanisms generating inter-individual variation and study the wider implications of variation in foraging behaviour to understand trophic relationships between the animals and their environment (Bolnick et al. 2003, Baylis...
et al. 2015b, Ceia & Ramos 2015, Kernaléguen et al. 2015a). The study of individual specialisations requires longitudinal sampling, in which the same individuals are sampled over time (Bolnick et al. 2003, Araújo et al. 2011). Ideally, the use of complementary techniques that represent different timescales and resolutions should be implemented to accurately describe individual specialisations and their persistence (Kernaléguen et al. 2015b). Seabirds are suitable models to study individual specialisations, as most species nest in large colonies that allow for easy access to individuals that use the same environment, are strongly constrained during breeding as central place foragers and may compete for the same resources (Ratcliffe et al. 2013).

Gentoo penguins *Pygoscelis papua* are among the most widespread penguin species, distributed from the northern subantarctic islands (Crozet; 46°S) to the Antarctic Peninsula (62 to 69°S; Williams 1995). These birds are considered inshore opportunistic foragers, consuming both benthic and pelagic species, and exhibiting high plasticity in their diet, marine habitat use and dive behaviour (Bost & Jouventin 1990, Woehler 1995, Lescroël & Bost 2005, Miller et al. 2009). They consume patchy prey encompassing a large size range, from small crustaceans to large fish species (Hindell 1989, Robinson & Hindell 1996). Accordingly, their diets vary substantially among breeding locations, within colonies, and also within individuals of the same colony (Croxall et al. 1988, Bost & Jouventin 1990, Robinson & Hindell 1996, Lescroël et al. 2004, Polito et al. 2015).

As Gentoo penguins are long-lived and sedentary (Williams & Rodwell 1992), individuals are expected to learn to apply efficient foraging tactics throughout their lifetime and, thus, increase their individual efficiency when foraging under situations of competition or food limitation (Estes et al. 2003). Indeed, recent studies suggest that individuals exhibit some degree of prey selection and specialisation, as judged by stomach content analysis and
stable isotope values (Polito et al. 2015). However, there is little information on individual consistency in foraging behaviour and on whether such specialisations are linked to diet in this species.

In the present study, I investigated inter- and intra-individual variation in the foraging ecology of Gentoo penguins. I used complementary bio-logging and stable isotope analysis, coupled with morphometric measurements to: 1) describe their inter-individual variation in morphology, spatial use and dive behaviour; 2) quantify their intra-individual variation in foraging behaviour; 3) investigate the links between consistency in foraging behaviour, distances travelled and body condition; and 4) describe their inter-individual variation in feeding ecology, and determine if dietary specialisations exist and are maintained outside of the breeding season. I predicted that: 1) individuals would differ greatly in foraging metrics as Gentoo penguin diet and behaviour are known to vary among colonies and between individuals of the same colonies, and that such variation would be attributed to differences in body mass, which influences dive depth (Lescroël et al. 2004, Lescroël & Bost 2005, Cook et al. 2013, Polito et al. 2015, Campras et al. 2017a); 2) dietary and behavioural consistency would be detected, as populations usually considered generalists are increasingly shown to be composed of individual specialists (Woo et al. 2008, Araújo et al. 2011, Loxdale et al. 2011, Layman & Allgeier 2012, Fodrie et al. 2015); and 3) individuals displaying higher consistency in foraging behaviour would travel shorter distances and have higher body condition, as such consistency is thought to allow individuals to forage more efficiently (Bolnick et al. 2003, Estes et al. 2003).
Materials and methods

Study site and instrumentation

The study was performed at Kerguelen Islands in the southern Indian Ocean, one of the major breeding grounds for Gentoo penguins (thereafter referred to as Gentoos) with 40,000 pairs (Lescroël et al. 2004, Lynch 2013). Gentoos breed along most of the Kerguelen coastline in many small to medium-sized colonies ranging from 15 to >400 pairs). As the diet and foraging behaviour of this species are known to vary substantially among colonies and within breeding locations, especially on Kerguelen Islands (Lescroël et al. 2004, Lescroël & Bost 2005), 2 colonies were selected to make sure that the patterns observed were not solely dependent upon colony location. Accordingly, field work was conducted at the Pointe Suzanne and Estacade colonies (ca. 20 km apart, 49°26’S, 70°26’E and 49°15’S, 70°33’E, respectively, with ca. 50 and 25 chicks, respectively; Figure 4.1). Both colonies face the open ocean. The Pointe Suzanne colony, however, faces a wider range of foraging habitats due to its proximity to a more sheltered bay (Baie Norvégienne). The Estacade colony is localized westward of the Polar Front, a productive frontal zone, on the eastward side of the Kerguelen shelf. Gentoos were in the late chick-rearing (i.e. crèche) stage at both study sites. Logistical constraints prevented sampling other colonies, as well as greater sample sizes, and so my results on site effects must be interpreted with caution.
Figure 4.1 One track per Gentoo penguin *Pygoscelis papua* instrumented at Pointe Suzanne (left panel) and Estacade (right panel) during the crèche period in December 2014 to January 2015.
I deployed data loggers on breeding Gentoos during the late chick-rearing period (crèche stage: chicks > 4-5 weeks-old), in the 2014/15 breeding season (Table 4.1). To determine the at-sea movements and diving behaviour of the penguins, I used Fastloc GPS loggers (F2G 134A; FastLoc ®; Sirtrack; 69 x 28 x 21 mm, 39 g in air), alone or in combination with time-depth recorders (TDR, LAT1800S, Lotek Wireless; 36.0 x 11.0 x 7.2 mm, 4.8 g in air). GPS loggers were programmed to sample position every 5 min. The TDR units were set to record depth and temperature at 1 s intervals. All attached devices, alone or in combination, weighed < 1% body mass.

At Pointe Suzanne, sampling occurred between 24 November and 9 December 2014. In total, 24 birds were instrumented for 4 to 16 d according to the possibilities of recapture. I used either 2 kinds of instruments (GPS+TDR: n = 18), or only 1 instrument (GPS: n = 4, TDR: n = 2). At Estacade, 9 birds were instrumented between 20 December 2014 and 4 January 2015 with GPS+TDR for 4 to 15 d.

All instrumented birds were confirmed breeders, with only birds that were observed feeding chicks being sampled. Individuals were weighed in a cloth bag using a suspension scale (±25 g, Pesola) before data loggers were attached to the dorsal feathers using waterproof tape (Tesa 4651) and cyanoacrylate glue (Loctite 401 Instant Adhesive). Individuals were then released and resumed normal behaviours. With the exception of 3 individuals from Estacade that were recaptured on the beach a few kilometres north or south of the colony, all birds were recaptured at the colony after several foraging trips. The data loggers were removed and individuals were weighed again. Measurements of bill length and depth were taken with Vernier calipers (±0.05 mm) and flipper length with a metal ruler (±1 mm). In addition, a blood sample (0.5 to 1.5 ml) was obtained by venipuncture of a tarsal vein for stable isotope analysis and molecular sex determination. Feathers (n = 3 to 6) were
plucked from the thorax region for stable isotope analysis. Handling times ranged from 15 to 20 min, during which the bird’s head was covered with a hood to reduce stress. Of the 33 birds instrumented at the 2 study sites, 28 birds were recaptured, of which 4 did not go to sea to forage and 2 individuals had TDRs that malfunctioned. Overall, 22 individuals provided data which were analysed (Pointe Suzanne: \( n = 17 \), Estacade: \( n = 5 \)). All 22 individuals conducted more than 1 trip, with 19 providing both TDR and GPS data.

**Isotopic analyses**

The \( \delta^{13}C \) values of seabirds reflect their foraging habitats (Cherel & Hobson 2007, Jaeger et al. 2010), while their \( \delta^{15}N \) values increase with trophic level (Cherel et al. 2010). Isotopic values were measured on whole blood and feathers. The rationale is that the 2 complementary tissues integrate different periods of information, due to the fact that the keratin in feathers is inert after synthesis (details in Cherel et al. 2008). Blood is a metabolic active tissue that integrates a period of weeks before sampling, whereas feathers reflect the diet at the time they were grown as feathers are metabolically inert after they are grown (Cherel et al. 2000). In the present study, blood isotopic values integrated a few weeks before sampling, thus corresponding to the breeding period (Bearhop et al. 2006). In contrast, Gentoos moult once a year, at the end of the breeding period, after a period of 10 d at sea dedicated to replenishment of body reserves (Croxall & Davis 1999, Polito et al. 2011).
Table 4.1 Summary of bio-logging deployments for Gentoo penguins *Pygoscelis papua*

instrumented and retrieved at Pointe Suzanne and Estacade (Kerguelen Islands, Indian Ocean) during the crèche period in December 2014 to January 2015.

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<th>Bird</th>
<th>Sex</th>
<th>Body condition index</th>
<th>Initial mass (kg)</th>
<th>Bill depth (mm)</th>
<th>Bill length (mm)</th>
<th>Flipper length (mm)</th>
<th>Tracking time (d)</th>
<th>Trip #</th>
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They then fast ashore for about 3 wk, using their body reserves to cover the energetic and nutrient needs for moultng and fasting (Croxall & Davis 1999). Hence, the isotopic values of feathers document the foraging ecology of penguins during the pre-moult period of hyperphagia at sea during which they build up energy reserves (Cherel et al. 2008), here almost 1 yr before sampling the instrumented Gentoo.

In the laboratory, blood samples were freeze-dried and powdered. Lipid extraction was unnecessary as the C:N mass ratio was < 3.5 for all blood samples (Cherel et al. 2005b); C:N mass ratios were indeed 3.29 ± 0.06 (whole blood, n = 25) and 3.17 ± 0.05 (feathers, n = 27). A pool of 3 feathers bird⁻¹ was cleaned of surface lipids and contaminants using a 2:1 chloroform:methanol bath, air-dried and cut into small pieces. For each feather, the rachis and the top 5 mm of the feather synthetised at sea were discarded before analysis so that the remaining feather sections were homogeneous and corresponded to the fasting period (Cherel et al. 2005a).

Nitrogen and carbon isotopic ratios were measured on aliquots of 0.2 to 0.4 mg with a continuous-flow isotope-ratio mass spectrometer (Thermo Scientific Delta V Advantage) coupled to an elemental analyser (Thermo Scientific Flash EA 1112). Results are presented in the usual δ notation relative to Vienna PeeDee Belemnite (VPDB) for carbon and atmospheric N₂ (AIR) for nitrogen. Replicate measurements of internal laboratory standards (acetanilide and peptone) indicated measurement errors < 0.15 ‰ for both δ¹³C and δ¹⁵N. Blood and/or feather sampling was not possible on all individuals instrumented, resulting in the collection of either no samples, only feathers, only blood, or both samples for each individual. Stable isotope values were obtained from 25 individuals for blood (11 females, 14 males), and 27 individuals for feathers (11 females, 13 males, 3 unknown). Both tissues were sampled in 24 individuals (11 females, 13 males). Of these 24 individuals, 16 also had both
GPS and TDR data, 1 had TDR data only, 3 had GPS data only, and 4 did not have any bio-logging data.

Data processing

All data analyses were conducted in the R Statistical Environment in version 3.3 (R Team, 2015). The GPS records for each bird were visually inspected to identify individual foraging trips. As some birds hauled out in some locations distant from the colony for a few hours to a couple of days, foraging trips were defined as the time between an individual left a land-based position until it came back ashore. The *diveMove* package (Luque 2007) was used to apply a speed filter to the GPS data to remove erroneous locations (with a speed threshold of 1.5 m·s\(^{-1}\) based on the 95\(^{th}\) percentile of swim speeds for all individuals). The GPS records were interpolated to 1 s intervals in the *adehabitatLT* package (Calenge 2015) to provide spatial information for the dive records. Furthermore, the packages *trip* (Sumner 2013) and *sp* (Pebesma & Bivand 2015) were used to obtain summaries of at-sea movements and investigate the consistency in habitat use. Individual tracks were overlaid with a grid comprised of 2 x 2 km cells, where the number of grid cells used were calculated for each trip. Means and coefficients of variation for each individual were calculated for trip duration, maximum range, and horizontal distance travelled per trip and per hour. Bearing for each trip was calculated as the angle between the colony and the most distal point of the tracks, and standard deviation in bearing was calculated for each individual using the *circular* package (Agostinelli & Lund 2011).

The *diveMove* package was used to obtain summaries of diving metrics from TDR records (only dives deeper than 2 m were considered to be foraging dives following Lescroël
The *lubridate* package (Grolemund & Wickham 2011) was used to identify night and day dives based on sunset and sunrise times at the relevant sites. Benthic and pelagic dives were determined based on the proportion of dive time that was spent in the bottom phase for each dive (phase detected by the “diveStats” function after descent and before ascent), and the depth achieved on consecutive dives. If the dive depth stayed within 5% of the maximum depth for this dive for more than 15 s, and if the dive was within 5% of the maximum depth achieved during the last 15 min of diving, the dive was labelled as “flat-benthic”. If the dive was within 5% of the maximum depth achieved for “flat-benthic” dives during the last 15 min of diving, but the other criterion was not met, the dive was labelled as “V-benthic”. If the dive met neither of these criteria, the dive was labelled as “pelagic”. The proportion of pelagic dives was then determined. Means and standard deviations per trip were calculated for bottom time and mean bottom depth of each dive, the total vertical distance travelled per trip and per hour, and the proportion of pelagic and night diving. Horizontal and vertical distances travelled were summed to provide an index of foraging energy expenditure per trip and per hour (Wilson et al. 1986).

An index of consistency in habitat use was calculated for each animal. For each trip, the number of grid cells used by the individuals was identified. The number of shared grid cells between each pair of trips (e.g. trip 1 and trip 2, trip 2 and trip 3, trip 1 and trip 3 etc.) was determined and the average of these calculated. This number was then divided by the average number of grid cells used per trip. Different grid cell sizes were tested to calculate the index of consistency in habitat use (from 1 x 1 km to 10 x 10 km) to check the influence of grid cell size on my estimate of spatial consistency. Indices obtained, regardless of cell grid sizes, were highly correlated, and data from the 2 x 2 km grid cell size are presented.
**Statistical analyses**

Body mass and morphometric measurements were correlated (linear regressions: beak depth: $F_{1,18} = 14.62, R^2 = 0.42, P = 0.001$; flipper length: $F_{1,18} = 14.15, R^2 = 0.65, P = 0.001$) and therefore, only relationships with body mass were further investigated in models. A principal component analysis was run on flipper and bill length and bill depth with the \textit{FactoMineR} package (Lê et al. 2008). Residuals from a linear regression of the first principal component against body mass were then used as an index of body condition (Cuervo et al. 2009). The first principal component of the morphometric measurements explained 72.2% of the total variation and was therefore used as an estimate of structural size. There was no significant difference between the sexes in the slopes or elevations of the linear regressions of body mass on this estimate of structural size. Therefore, data were pooled to estimate individual body condition.

The following spatial metrics were highly correlated: trip duration and maximum range (linear mixed effects models: $F_{1,17} = 61.17, R^2 = 0.78, P < 0.001$); and maximum range and total distance travelled (linear mixed effects models: $F_{1,17} = 285.70, R^2 = 0.94, P < 0.001$). Consequently, only maximum range was used in linear mixed effects models. Similarly, the following diving metrics were highly correlated: bottom depth and total vertical distance travelled (linear mixed effects models: $F_{1,17} = 41.41, R^2 = 0.69, P < 0.001$); and dive time and bottom depth (linear mixed effects models: $F_{1,17} = 91.04, R^2 = 0.83, P < 0.001$). Thus, only bottom depth was included in further analyses.

Following a preliminary analysis to remove outliers, we used linear regressions, and linear mixed effects models in the package \textit{lme4} (Bates et al. 2011) where individuals had repeated samples, to investigate relationships between morphometric measurements,
consistency in foraging strategies and stable isotope values. For all models, backward-stepwise model selection was used to select the most parsimonious model (Ratcliffe et al. 2013). First, the most appropriate random effects structure was identified with the restricted maximum likelihood (REML), then the best fixed effects structure was determined using maximum likelihood (ML) after models were compared with the “anova” function, and the most parsimonious models were found based on their Akaike’s Information Criteria. For models in which 1 observation per trip was used (i.e. for spatial use metrics), individuals were included in the random effects. For models in which multiple observations per trip were used (i.e. for diving behaviour metrics), trip nested within individuals was included in the random effects. The selected models were refitted with REML to estimate the model parameters (Zuur et al. 2009). The residuals of the models were inspected and, whenever there was evidence of heterogeneity in the residuals, a sex- and/or site-specific variance structure was applied (Zuur et al. 2009).

More specifically, in order to describe the inter-individual variation in morphology and foraging behaviour, I investigated the effects of sex and stage on morphometric measurements, and the effects of sex, site and body mass on foraging metrics (interactions between fixed effects could not be investigated due to small sample sizes). A $k$-means clustering analysis was performed to determine whether individuals clustered according to their foraging behaviour. In order to quantify the intra-individual variation in diving behaviour and spatial use, I used the R package *ape* (Paradis et al. 2004) to perform a variance component analysis. This method calculates the variance, standard deviation and proportion of total variance occurring at the levels of individual, and trip within individual when multiple observations per trip were obtained, as well as the residual variation (Ratcliffe et al. 2013, Harris et al. 2014). An estimate of individual specialisation is given by the
proportion of variance explained by the individual variance component (Bolnick et al. 2003, Dingemanse & Dochterman 2013, Ratcliffe et al. 2013). When models including sex, site or body mass were better than the equivalent models without fixed effects (i.e. null models), the variance component analysis was run on both null and optimal models to quantify the reduction in variance explained by the individual, or the trip effects after the inclusion of the fixed effects (Ratcliffe et al. 2013). In order to investigate the links between consistency in foraging behaviour, vertical and horizontal distances travelled, and body condition, linear regressions were used. In order to quantify the inter-individual variation in trophic niche and foraging behaviour, and determine if dietary specialisations were maintained outside of a single breeding season, relationships between carbon and nitrogen values in blood and feathers, respectively, were investigated. Results presented are means ± SD, unless stated otherwise.

Results

Inter-individual variation in morphometry and at-sea behaviour

Gentoo penguins varied considerably in their body condition, mass and morphometric measurements (Tables 4.1 & 4.2). Body condition indices were lower at Pointe Suzanne (linear regression: $F_{1,18}=14.42$, $R^2=0.40$, $P=0.001$) compared to Estacade but similar between sexes (linear regression: $F_{1,18}=0.37$, $R^2=-0.03$, $P=0.5$). Lastly, females had smaller bill lengths than males (linear regression: $F_{1,18}=32.68$, $R^2=0.63$, $P<0.001$), as well as flipper lengths (linear regression: $F_{1,18}=4.96$, $R^2=0.20$, $P=0.04$).
Table 4.2 Summary of morphometric measurements for Gentoo penguins *Pygoscelis papua* instrumented and retrieved at Pointe Suzanne and Estacade (Kerguelen Islands, Indian Ocean) during the crèche period in December 2014 to January 2015.

<table>
<thead>
<tr>
<th></th>
<th>Mean ± SD</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Body condition index</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pointe Suzanne</td>
<td>-0.1 ± 0.5</td>
<td>-1.7</td>
<td>0.4</td>
</tr>
<tr>
<td>Estacade</td>
<td>1.3 ± 0.2</td>
<td>1.1</td>
<td>1.4</td>
</tr>
<tr>
<td>Females</td>
<td>-0.1 ± 0.4</td>
<td>-0.4</td>
<td>0.4</td>
</tr>
<tr>
<td>Males</td>
<td>0.1 ± 0.8</td>
<td>-1.7</td>
<td>1.4</td>
</tr>
<tr>
<td><strong>Body mass (kg)</strong></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Pointe Suzanne</td>
<td>5.2 ± 0.8</td>
<td>3.7</td>
<td>6.8</td>
</tr>
<tr>
<td>Estacade</td>
<td>7.1 ± 1.0</td>
<td>6.4</td>
<td>7.8</td>
</tr>
<tr>
<td>Females</td>
<td>4.8 ± 0.6</td>
<td>3.7</td>
<td>5.8</td>
</tr>
<tr>
<td>Males</td>
<td>5.9 ± 0.9</td>
<td>4.3</td>
<td>7.8</td>
</tr>
<tr>
<td><strong>Bill depth (mm)</strong></td>
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<tr>
<td>Pointe Suzanne</td>
<td>16.1 ± 1.5</td>
<td>13.3</td>
<td>18.4</td>
</tr>
<tr>
<td>Estacade</td>
<td>18.0 ± 2.2</td>
<td>16.4</td>
<td>19.5</td>
</tr>
<tr>
<td>Females</td>
<td>14.9 ± 1.0</td>
<td>13.3</td>
<td>16.0</td>
</tr>
<tr>
<td>Males</td>
<td>17.5 ± 1.0</td>
<td>16.4</td>
<td>19.5</td>
</tr>
<tr>
<td><strong>Bill length (mm)</strong></td>
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<tr>
<td>Pointe Suzanne</td>
<td>85.5 ± 6.3</td>
<td>75.0</td>
<td>95.0</td>
</tr>
<tr>
<td>Estacade</td>
<td>88.5 ± 4.9</td>
<td>85.0</td>
<td>92.0</td>
</tr>
<tr>
<td>Females</td>
<td>82.3 ± 6.1</td>
<td>75.0</td>
<td>95.0</td>
</tr>
<tr>
<td>Males</td>
<td>88.7 ± 4.7</td>
<td>79.4</td>
<td>95.0</td>
</tr>
<tr>
<td><strong>Flipper length (mm)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pointe Suzanne</td>
<td>228.4 ± 9.2</td>
<td>210.0</td>
<td>245.0</td>
</tr>
<tr>
<td>Estacade</td>
<td>229.0 ± 7.8</td>
<td>224.0</td>
<td>235.0</td>
</tr>
<tr>
<td>Females</td>
<td>224.1 ± 10.1</td>
<td>210.0</td>
<td>244.0</td>
</tr>
<tr>
<td>Males</td>
<td>232.2 ± 5.9</td>
<td>224.0</td>
<td>245.0</td>
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</tbody>
</table>
Overall, a total of 113 foraging trips were obtained (16 from Estacade, 97 from Pointe Suzanne) with 2 to 15 trips recorded per individual (mean = 5) lasting 4.0 to 15.4 d each (mean = 7.3; Table 4.1). Individuals varied considerably in their spatial use of the marine environment (Table 4.3), even within the same colony, with some individuals foraging close to the shore, while others travelled towards the continental shelf. Individual maximum distances from the colony averaged 21.6 ± 18.7 (3.3–78.3) km, trip durations averaged 26.6 ± 22.8 (5.1–77.6) h, total horizontal distances covered averaged 65.0 ± 56.7 (9.9–217.4) km, and horizontal distances per hour averaged 2.7 ± 0.5 (1.8–3.7) km. Furthermore, individual birds exploited different areas around the colony (Figure 4.1). 6 birds hauled out in locations away from the colony for periods of 10 to 57 h. Birds did not go on 2 consecutive long trips, but rather tended to alternate long and short trips. A k-means clustering analysis revealed 3 different foraging strategies: birds that travelled farther, dived deeper and were less pelagic (n = 5, means ± SE: 49.3 ± 19.3 km, 40.2 ± 15.8 m, 70.9 ± 11.4%, respectively); birds that stayed close to colony had the shallowest dives and displayed the highest percentage of pelagic diving (n = 8, means ± SE: 8.1 ± 4.6 km, 13.6 ± 7.1 m, 89.7 ± 6.9%, respectively); and birds with intermediate foraging metrics (n = 6, means ± SE: 22.0 ± 5.0 km, 30.7 ± 5.4 m, 73.7 ± 10.2%, respectively). Both sexes and sites were represented in each cluster. Lastly, sex and site did not influence spatial metrics (Table 4.4).

There was also considerable inter-individual variation in the diving behaviour of the instrumented birds, irrespective of colony. Some individuals performed very short and shallow dives and travelled short vertical distances, while others dived for much longer and deeper, and travelled much greater vertical distances (Table 4.5).
Table 4.3 Summary of spatial use metrics for Gentoo penguins *Pygoscelis papua* instrumented and retrieved at Pointe Suzanne and Estacade (Kerguelen Islands, Indian Ocean) during the crèche period in December 2014 to January 2015 (values are means ± SD).

<table>
<thead>
<tr>
<th>Bird</th>
<th>Sex</th>
<th>Mean bearing (°)</th>
<th>Trip duration (h)</th>
<th>Maximum range (km)</th>
<th>Total horizontal distance (km)</th>
<th>Horizontal distance h⁻¹(km)</th>
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<tr>
<td>2</td>
<td>male</td>
<td>66.3 ± 0.5</td>
<td>8.5 ± 5.7</td>
<td>7.7 ± 4.6</td>
<td>22.4 ± 15.1</td>
<td>2.9 ± 0.6</td>
</tr>
<tr>
<td>3</td>
<td>male</td>
<td>56.3 ± 0.8</td>
<td>77.6 ± 43.7</td>
<td>78.3 ± 62.8</td>
<td>217.4 ± 187.3</td>
<td>2.5 ± 1.0</td>
</tr>
<tr>
<td>5</td>
<td>male</td>
<td>125.2 ± 0.1</td>
<td>20.2 ± 16.5</td>
<td>25.4 ± 10.8</td>
<td>67.1 ± 41.3</td>
<td>3.7 ± 0.7</td>
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<td>11</td>
<td>male</td>
<td>56.4 ± 0.5</td>
<td>56.0 ± 75.2</td>
<td>59.4 ± 70.2</td>
<td>164.4 ± 211.0</td>
<td>3.2 ± 0.4</td>
</tr>
<tr>
<td>12</td>
<td>male</td>
<td>107.0 ± 0.1</td>
<td>70.0 ± 38.6</td>
<td>32.3 ± 3.8</td>
<td>140.5 ± 60.9</td>
<td>2.1 ± 0.3</td>
</tr>
<tr>
<td>14</td>
<td>male</td>
<td>91.2 ± 0.1</td>
<td>18.8 ± 10.7</td>
<td>21.9 ± 10.2</td>
<td>53.2 ± 28.2</td>
<td>2.9 ± 0.3</td>
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<td>17</td>
<td>male</td>
<td>114.4 ± 0.1</td>
<td>19.8 ± 17.1</td>
<td>17.6 ± 12.2</td>
<td>49.5 ± 38.8</td>
<td>2.5 ± 0.4</td>
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<tr>
<td>Estacade</td>
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<tr>
<td>27</td>
<td>female</td>
<td>127.9 ± 0.2</td>
<td>11.1 ± 12.8</td>
<td>9.5 ± 6.3</td>
<td>23.3 ± 16.8</td>
<td>3.1 ± 1.4</td>
</tr>
<tr>
<td>25</td>
<td>male</td>
<td>79.7 ± 0.2</td>
<td>44.8 ± 5.3</td>
<td>28.7 ± 2.4</td>
<td>89.4 ± 2.4</td>
<td>2.0 ± 0.3</td>
</tr>
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<td>30</td>
<td>male</td>
<td>77.3 ± 0.3</td>
<td>17.9 ± 1.0</td>
<td>16.9 ± 2.1</td>
<td>48.9 ± 3.4</td>
<td>2.7 ± 0.2</td>
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<tr>
<td>26</td>
<td>-</td>
<td>137.2 ± 0.1</td>
<td>12.9 ± 7.7</td>
<td>15.4 ± 12.3</td>
<td>35.1 ± 29.0</td>
<td>2.5 ± 0.8</td>
</tr>
<tr>
<td>28</td>
<td>-</td>
<td>86.3 ± 0.8</td>
<td>42.9 ± 61.0</td>
<td>36.9 ± 42.9</td>
<td>120.7 ± 164.5</td>
<td>3.5 ± 1.0</td>
</tr>
</tbody>
</table>
Table 4.4 Model ANOVA testing the effect of Gentoo penguin *Pygoscelis papua* sex and site on maximum range, bottom depth and repeatability, including bird as a random factor or trip nested within bird (likelihood ratio [LR] for linear mixed effects models and *F* values for simple linear regressions). The last row reports on the linear mixed effects model testing the effect of dive depth on the proportion of pelagic dives. Values in **bold** are significant.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Type of model</th>
<th>Parameters</th>
<th>LR/F test</th>
<th>df</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum range</td>
<td>Linear mixed effects</td>
<td><strong>Random effect: bird</strong></td>
<td>33.21</td>
<td>6</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fixed effects</td>
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<td></td>
<td></td>
<td>Sex</td>
<td>3.21</td>
<td>8</td>
<td>0.07</td>
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<tr>
<td></td>
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<td>Site</td>
<td>0.00</td>
<td>8</td>
<td>0.98</td>
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<tr>
<td></td>
<td></td>
<td><strong>Body mass</strong></td>
<td>3.15</td>
<td>8</td>
<td>0.08</td>
</tr>
<tr>
<td>Bottom depth</td>
<td>Linear mixed effects</td>
<td><strong>Random effect: bird/trip</strong></td>
<td>1236.29</td>
<td>9</td>
<td>&lt;0.0001</td>
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<tr>
<td></td>
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<td>Fixed effects</td>
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<tr>
<td></td>
<td></td>
<td>Sex</td>
<td>3.20</td>
<td>8</td>
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<td><strong>Body mass</strong></td>
<td>7.29</td>
<td>8</td>
<td><strong>0.01</strong></td>
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<tr>
<td>Repeatability indices</td>
<td>Linear model</td>
<td>Sex</td>
<td>Site</td>
<td>Fixed effects</td>
<td>Dive depth</td>
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<td>Linear model</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Linear mixed effects</td>
<td>Fixed effects</td>
<td>Dive depth</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Proportion of pelagic dives</td>
<td>Linear mixed effects</td>
<td>Fixed effects</td>
<td>Dive depth</td>
<td>84.83</td>
<td>4</td>
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</tbody>
</table>
Table 4.5 Summary of dive metrics and distances travelled for Gentoo penguins *Pygoscelis papua* instrumented and retrieved at Pointe Suzanne and Estacade (Kerguelen Islands, Indian Ocean) during the crèche period in December 2014 to January 2015 (values are means ± SD).

<table>
<thead>
<tr>
<th>Bird</th>
<th>Sex</th>
<th>Bottom time (s)</th>
<th>Bottom depth (m)</th>
<th>Total vertical distance (km)</th>
<th>Hourly vertical distance (km)</th>
<th>Total (horizontal+vertical) distance travelled per trip (km)</th>
<th>Total (horizontal+vertical) distance travelled per hour (km)</th>
<th>Pelagic diving (% of all dives)</th>
<th>Night diving (% of all dives)</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>female</td>
<td>29.5 ± 15.1</td>
<td>5.1 ± 2.0</td>
<td>3.4 ± 2.1</td>
<td>0.5 ± 0.2</td>
<td>13.3 ± 7.5</td>
<td>2.3 ± 0.8</td>
<td>93.8 ± 3.8</td>
<td>43.8 ± 27.3</td>
</tr>
<tr>
<td>7</td>
<td>female</td>
<td>71.8 ± 30.3</td>
<td>32.6 ± 26.1</td>
<td>33.3 ± 35.8</td>
<td>0.9 ± 0.5</td>
<td>87.6 ± 78.5</td>
<td>3.8 ± 0.7</td>
<td>75.4 ± 20.3</td>
<td>22.5 ± 19.2</td>
</tr>
<tr>
<td>9</td>
<td>female</td>
<td>33.9 ± 14.7</td>
<td>5.2 ± 1.8</td>
<td>3.4 ± 3.5</td>
<td>0.6 ± 0.3</td>
<td>14.4 ± 9.5</td>
<td>2.8 ± 0.8</td>
<td>89.3 ± 9.9</td>
<td>40.9 ± 34.3</td>
</tr>
<tr>
<td>10</td>
<td>female</td>
<td>51.6 ± 20.5</td>
<td>11.1 ± 5.4</td>
<td>7.6 ± 5.3</td>
<td>0.9 ± 0.3</td>
<td>25.0 ± 13.9</td>
<td>3.3 ± 0.4</td>
<td>92.0 ± 5.6</td>
<td>39.7 ± 33.8</td>
</tr>
<tr>
<td>13</td>
<td>female</td>
<td>86.4 ± 10.7</td>
<td>40.1 ± 8.9</td>
<td>72.3 ± 66.2</td>
<td>1.1 ± 0.1</td>
<td>206.1 ± 164.8</td>
<td>3.6 ± 0.7</td>
<td>77.9 ± 7.2</td>
<td>15.6 ± 9.4</td>
</tr>
<tr>
<td>15</td>
<td>female</td>
<td>88.2 ± 31.6</td>
<td>17.5 ± 11.9</td>
<td>9.9 ± 10.1</td>
<td>0.7 ± 0.3</td>
<td>44.9 ± 26.8</td>
<td>4.0 ± 0.2</td>
<td>96.1 ± 5.1</td>
<td>24.4 ± 18.3</td>
</tr>
<tr>
<td>20</td>
<td>female</td>
<td>68.3 ± 32.2</td>
<td>18.6 ± 15.1</td>
<td>8.8 ± 11.7</td>
<td>0.8 ± 0.5</td>
<td>33.7 ± 36.9</td>
<td>3.8 ± 0.5</td>
<td>87.6 ± 11.7</td>
<td>52.4 ± 42.9</td>
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<td>22</td>
<td>female</td>
<td>79.5 ± 28.3</td>
<td>26.6 ± 13.9</td>
<td>31.0 ± 30.3</td>
<td>0.8 ± 0.4</td>
<td>103.5 ± 99.3</td>
<td>3.1 ± 0.6</td>
<td>80.4 ± 14.7</td>
<td>14.5 ± 5.8</td>
</tr>
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<td>---</td>
<td>---</td>
<td>---</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>male</td>
<td>54.8 ± 17.0</td>
<td>9.7 ± 5.5</td>
<td>2.1 ± 1.9</td>
<td>0.4 ± 0.3</td>
<td>13.0 ± 8.1</td>
<td>3.1 ± 1.2</td>
<td>95.7 ± 5.3</td>
<td>36.5 ± 25.9</td>
</tr>
<tr>
<td>2</td>
<td>male</td>
<td>89.6 ± 13.8</td>
<td>15.7 ± 8.2</td>
<td>7.2 ± 7.3</td>
<td>0.8 ± 0.2</td>
<td>29.6 ± 22.3</td>
<td>3.6 ± 0.7</td>
<td>88.2 ± 9.5</td>
<td>54.8 ± 17.9</td>
</tr>
<tr>
<td>3</td>
<td>male</td>
<td>101.6 ± 3.2</td>
<td>61.6 ± 8.8</td>
<td>62.2 ± 51.4</td>
<td>0.7 ± 0.3</td>
<td>279.6 ± 238.7</td>
<td>3.3 ± 1.2</td>
<td>52.7 ± 6.9</td>
<td>15.4 ± 5.7</td>
</tr>
<tr>
<td>5</td>
<td>male</td>
<td>69.5 ± 5.3</td>
<td>26.2 ± 6.6</td>
<td>23.2 ± 20.2</td>
<td>1.1 ± 0.3</td>
<td>90.4 ± 61.5</td>
<td>4.8 ± 0.8</td>
<td>86.5 ± 5.1</td>
<td>6.3 ± 5.5</td>
</tr>
<tr>
<td>11</td>
<td>male</td>
<td>53.8 ± 11.3</td>
<td>22.5 ± 6.9</td>
<td>48.3 ± 67.3</td>
<td>0.8 ± 0.1</td>
<td>212.7 ± 278.3</td>
<td>4.1 ± 0.4</td>
<td>80.6 ± 6.6</td>
<td>24.1 ± 5.2</td>
</tr>
<tr>
<td>12</td>
<td>male</td>
<td>106.8 ± 8.9</td>
<td>48.8 ± 3.6</td>
<td>74.5 ± 45.1</td>
<td>1.0 ± 0.1</td>
<td>215.0 ± 106.0</td>
<td>3.1 ± 0.2</td>
<td>66.8 ± 4.8</td>
<td>15.2 ± 4.8</td>
</tr>
<tr>
<td>14</td>
<td>male</td>
<td>57.6 ± 12.0</td>
<td>25.3 ± 8.7</td>
<td>17.7 ± 14.0</td>
<td>0.8 ± 0.3</td>
<td>70.9 ± 42.2</td>
<td>3.7 ± 0.3</td>
<td>74.6 ± 3.9</td>
<td>12.9 ± 6.9</td>
</tr>
<tr>
<td>25</td>
<td>male</td>
<td>72.7 ± 5.3</td>
<td>36.9 ± 9.5</td>
<td>37.1 ± 12.0</td>
<td>0.9 ± 0.4</td>
<td>126.5 ± 14.4</td>
<td>2.9 ± 0.7</td>
<td>68.1 ± 7.3</td>
<td>6.0 ± 2.7</td>
</tr>
<tr>
<td>30</td>
<td>male</td>
<td>88.0 ± 11.6</td>
<td>36.5 ± 10.0</td>
<td>18.6 ± 6.9</td>
<td>1.0 ± 0.3</td>
<td>67.4 ± 6.7</td>
<td>3.8 ± 0.2</td>
<td>57.0 ± 12.4</td>
<td>15.5 ± 3.6</td>
</tr>
<tr>
<td>26</td>
<td>-</td>
<td>65.1 ± 15.5</td>
<td>25.6 ± 19.8</td>
<td>12.9 ± 15.2</td>
<td>0.8 ± 0.7</td>
<td>48.0 ± 44.2</td>
<td>3.3 ± 1.5</td>
<td>74.7 ± 13.0</td>
<td>5.7 ± 8.1</td>
</tr>
<tr>
<td>28</td>
<td>-</td>
<td>78.0 ± 52.1</td>
<td>28.0 ± 24.4</td>
<td>32.5 ± 43.5</td>
<td>0.7 ± 0.5</td>
<td>153.2 ± 208.0</td>
<td>4.2 ± 0.7</td>
<td>76.6 ± 26.8</td>
<td>17.0 ± 16.1</td>
</tr>
</tbody>
</table>
On average, individuals spent 70.9 ± 20.1 (29.5–106.8) s at the bottom of dives, dived to bottom depths of 26.0 ± 14.7 (5.1–61.6) m, and travelled total vertical distances of 26.6 ± 23.2 (2.1–74.5) km, and hourly vertical distances of 0.8 ± 0.2 (0.4–1.1) km. Accordingly, the distance travelled (both horizontal and vertical) varied between individuals (mean distance per trip: 96.6 ± 81.0 [13.3–279.6] km; mean distance per hour of foraging: 3.5 ± 0.6 [2.3–4.8] km).

Sex and site did not significantly influence dive depth (Table 4.4). Some individuals performed almost entirely pelagic dives while, for others, benthic dives represented up to 48% of all dives (Table 4.5). Furthermore, individuals varied in their diving schedule, with some individuals diving half of their time at night, and other individuals diving mostly during the day (Table 4.5, Figure 4.2). Daylight dives were on average 30.3 ± 37.5 m deep and 68.5 ± 53.2 s long (n = 24,336, 75% of dives recorded) while night dives were on average 9.2 ± 10.2 m deep and 52.3 ± 39.9 s long (n = 8,298, 25% of dives recorded). Several individuals dived at night during multiple-day trips while other birds performed short trips (ca. 10 km from the colony) and dived predominantly at night. The frequency of night diving increased with the proportion of pelagic diving, which averaged 76.8% during the day and 92.9% at night (Figure 4.2).

**Intra-individual variation and consistency in foraging behaviour**

The large differences in standard deviations between individuals indicate a substantial degree of intra-individual variation both in spatial use and dive metrics (Tables 4.3, 4.4, and 4.5, respectively). At the population level, the variance component analysis showed low to moderate individual specialisations both in dive behaviour and spatial use (Table 4.6).
Figure 4.2 (A) Frequency of night diving, (B) distribution of dive depths across time of day and (C) relationship between night and pelagic diving in Gentoo penguins *Pygoscelis papua* (panels A and B show individuals representative of the most benthic and the most pelagic individuals) instrumented at Pointe Suzanne during the crèche period in December 2014 to January 2015.
Table 4.6 Variance component analysis of dive depths, total distances travelled and bearings to most distal point for Gentoo penguins *Pygoscelis papua* instrumented at Pointe Suzanne and Estacade (Kerguelen Islands, Indian Ocean) during the crèche period in December 2014 to January 2015. $\sigma^2\%$ is an estimate of individual specialisation (see “Materials and methods” for details).

<table>
<thead>
<tr>
<th>Variance component</th>
<th>$\sigma^2$</th>
<th>$\Sigma$</th>
<th>$\sigma^2%$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Maximum range</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Individual</td>
<td>127.6</td>
<td>11.3</td>
<td>13.7</td>
</tr>
<tr>
<td>Residual</td>
<td>802.6</td>
<td>28.3</td>
<td>86.3</td>
</tr>
<tr>
<td><strong>Bearings to most distal point</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Individual</td>
<td>1572.7</td>
<td>39.7</td>
<td>52.9</td>
</tr>
<tr>
<td>Residual</td>
<td>1397.6</td>
<td>37.4</td>
<td>47.1</td>
</tr>
<tr>
<td><strong>Mean bottom depth (null model)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Individual</td>
<td>244.2</td>
<td>15.6</td>
<td>6.2</td>
</tr>
<tr>
<td>Trip</td>
<td>62.6</td>
<td>7.9</td>
<td>1.6</td>
</tr>
<tr>
<td>Residual</td>
<td>3612.8</td>
<td>60.1</td>
<td>92.2</td>
</tr>
<tr>
<td><strong>Mean bottom depth (model with mass)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Individual</td>
<td>150.9</td>
<td>12.3</td>
<td>4.0</td>
</tr>
<tr>
<td>Trip</td>
<td>62.6</td>
<td>7.9</td>
<td>1.6</td>
</tr>
<tr>
<td>Residual</td>
<td>3612.4</td>
<td>60.1</td>
<td>94.4</td>
</tr>
<tr>
<td><strong>Proportion of pelagic diving (null model)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Individual</td>
<td>166.4</td>
<td>12.9</td>
<td>67.5</td>
</tr>
<tr>
<td>Residual</td>
<td>80.1</td>
<td>9.0</td>
<td>32.5</td>
</tr>
<tr>
<td><strong>Proportion of pelagic diving (model with mass)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Individual</td>
<td>33.5</td>
<td>5.8</td>
<td>51.3</td>
</tr>
<tr>
<td>Residual</td>
<td>31.9</td>
<td>5.6</td>
<td>48.7</td>
</tr>
</tbody>
</table>
The indices of consistency in habitat use were not influenced by sex or site (Table 4.4, mean 0.37 ± 0.2, range: 0.05-0.73, Figure 4.3). Some penguins were very consistent in the proportion of pelagic or benthic dives they performed (e.g. individual 14 stayed within 10% of its own values) while others varied greatly (e.g. individual 28 ranged from 47-98% of pelagic dives between trips) (Figure 4.4). The total (horizontal + vertical) distance travelled per hour was not correlated with repeatability indices (linear regression: $F_{1,17} = 0.97$, $R^2 = -0.002$, $P = 0.34$). Lastly, body condition did not vary with consistency in habitat use (linear regression: $F_{1,12} = 0.16$, $R^2 = -0.07$, $P = 0.70$).

**Stable isotope values and link with foraging metrics**

Tissue isotope values varied widely among individuals, with $\delta^{13}C$ and $\delta^{15}N$ ranges of 4.0 and 5.8‰ in blood and 4.2 and 4.4‰ in feathers, respectively (Table 4.7). Values for $\delta^{13}C$ and $\delta^{15}N$ co-varied positively in both tissues (linear regression: $F_{1,23} = 31.94$, $R^2 = -0.56$, $P < 0.001$ and $F_{1,22} = 38.72$, $R^2 = -0.62$, $P < 0.001$ in blood and feathers, respectively) (Figure 4.5). There was no significant difference between the sexes in their $\delta^{13}C$ values, but males had higher $\delta^{15}N$ values in blood and feathers (linear mixed effects models: $t_{23} = 3.4$, $P = 0.002$ and $t_{23} = 0.9$, $P = 0.4$, for nitrogen and carbon, respectively). Site did not influence $\delta^{15}N$ and $\delta^{13}C$ values ($t_{23} = -0.6$, $P = 0.5$, and $t_{23} = -0.5$, $P = 0.6$, respectively). Isotopic values in blood and feathers were positively and linearly correlated. Excluding an outlier (that was depicted by a preliminary statistical analysis) increased the strength of the relationships that explained 67 and 70% of the inter-individual $\delta^{13}C$ and $\delta^{15}N$ variations, respectively (Figure 4.6).
Figure 4.3 Representative examples for 3 individual Gentoo penguins *Pygoscelis papua* of spatial use and repeatability index (RI) for a highly repeatable individual (grey), a moderately repeatable one (orange) and an individual with limited repeatability (black) among instrumented birds at Pointe Suzanne and Estacade during the crèche period in December 2014 to January 2015.
Figure 4.4 Boxplots for the proportion of pelagic diving performed in subsequent trips by individual Gentoo penguins *Pygoscelis papua* instrumented at Pointe Suzanne and Estacade during the crèche period in December 2014 to January 2015. Bold horizontal line: median of the distribution; box: interquartile range, IQR (first quartile Q1 to third quartile Q3); whiskers: (Q1 + 1.5 x IQR) to (Q3 + 1.5 x IQR); points: outliers.
Table 4.7 Summary of stable isotope values for Gentoo penguins *Pygoscelis papua* sampled at Pointe Suzanne and Estacade (Kerguelen Islands, Indian Ocean) in December 2014 to January 2015. NA: missing data.

<table>
<thead>
<tr>
<th>Bird</th>
<th>Sex</th>
<th>Blood δC&lt;sup&gt;13&lt;/sup&gt;</th>
<th>Blood δN&lt;sup&gt;15&lt;/sup&gt;</th>
<th>Feather δC&lt;sup&gt;13&lt;/sup&gt;</th>
<th>Feather δN&lt;sup&gt;15&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
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<td>-18.76</td>
<td>11.49</td>
<td>-18.03</td>
<td>11.99</td>
</tr>
<tr>
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<td>10.93</td>
<td>-18.7</td>
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</tr>
<tr>
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<td>12.55</td>
<td>-15.52</td>
<td>13.42</td>
</tr>
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<td>female</td>
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<td>11.38</td>
<td>-18.37</td>
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</tr>
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<td>11.64</td>
</tr>
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<td>9.95</td>
<td>-19.06</td>
<td>12.33</td>
</tr>
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<td>-19.28</td>
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</tr>
<tr>
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<td>10.86</td>
<td>-16.75</td>
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</tr>
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<tr>
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<td>male</td>
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<td>12.50</td>
<td>-17.18</td>
<td>14.12</td>
</tr>
<tr>
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<td>11.90</td>
<td>-17.97</td>
<td>12.66</td>
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<td>11.26</td>
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<td>-17.55</td>
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</tr>
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<td>Gender</td>
<td>Weight</td>
<td>Height</td>
<td>Body Mass Index</td>
<td>Body Fat Percentage</td>
</tr>
<tr>
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<td>--------</td>
<td>--------</td>
<td>--------</td>
<td>-----------------</td>
<td>--------------------</td>
</tr>
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<td>NA</td>
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</tr>
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<td>8.43</td>
<td>-18.94</td>
<td>12.40</td>
</tr>
<tr>
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<td>7.95</td>
<td>-18.59</td>
<td>11.86</td>
</tr>
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<td>11.62</td>
<td>-17.88</td>
<td>12.79</td>
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<td>-15.69</td>
<td>15.47</td>
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<td>-18.71</td>
<td>12.78</td>
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<td>NA</td>
<td>-18.82</td>
<td>12.32</td>
</tr>
<tr>
<td>28</td>
<td>-</td>
<td>NA</td>
<td>NA</td>
<td>-18.03</td>
<td>13.39</td>
</tr>
</tbody>
</table>
**Figure 4.5** Relationship between stable isotopes values in carbon and nitrogen in blood and in feathers of Gentoo penguins *Pygoscelis papua* sampled at Pointe Suzanne and Estacade during the crèche period in December 2014 to January 2015 (light blue squares = males from Pointe Suzanne, pink circles = females from Pointe Suzanne, dark blue squares = males from Estacade, purple circles = females from Estacade, grey diamond = 1 unsexed bird from Pointe Suzanne, black diamonds = 2 unsexed birds from Estacade).
Figure 4.6 Correlations between stable isotope values in blood and feather for carbon and nitrogen in Gentoo penguins *Pygoscelis papua* sampled at Pointe Suzanne and Estacade during the crèche period in December 2014 to January 2015 (light blue squares = males from Pointe Suzanne, pink circles = females from Pointe Suzanne, dark blue squares = males from Estacade, purple circles = females from Estacade).
There was no relationship between maximum distances reached and blood $\delta^{15}$N or $\delta^{13}$C values (linear mixed effects model: $t_{18} = 0.1$, $P = 0.9$, and $t_{18} = -1.1$, $P = 0.3$). This was also the case for stable isotopes values and bearings to the most distal point (linear mixed effects model: $t_{18} = -0.2$, $P = 0.9$, and $t_{18} = 0.1$, $P = 0.9$, respectively). Lastly, $\delta^{15}$N or $\delta^{13}$C values were not influenced by repeatability in spatial use (linear mixed effects model: $t_{10} = 1.0$, $P = 0.3$, and $t_{10} = 1.0$, $P = 0.3$, respectively) or body condition (linear mixed effects model: $t_{11} = 1.9$, $P = 0.1$, and $t_{11} = 1.8$, $P = 0.1$, respectively).

**Discussion**

The salient findings of this study concerning an opportunistic coastal forager, the Gentoo penguin, can be summarized as follows. (1) Individuals exhibited very large inter- and intra-individual variation in spatial use and diving behaviour. Heavy individuals tended to dive deeper, perform more benthic dives, and travel further. (2) Despite the large intra-individual variation in foraging, some consistency in bearing, proportion of pelagic and night diving, maximum ranges and dive depths was observed in approximately a third of individuals. Foraging behaviour and behavioural consistency were not influenced by sex and site. (3) There were large inter-individual variations in stable isotopes values and dietary specialisations were present and maintained outside of the single breeding season sampled.

As inshore foragers, Gentooos are known to strongly differ in their foraging behaviour according to the local environment (Lescroël & Bost 2005). My first prediction was that instrumented individuals would differ greatly in foraging metrics among colonies and among individuals of the same colony. In the present study, site did not seem to influence foraging metrics. However, within a single colony, birds exhibited a large inter-individual variation in
foraging behaviour with some birds conducting very short trips within 5 to 10 km of the colony while others travelled to areas 120 to 140 km away. The more pelagic individuals performed up to half of their dives at night during short trips, while more benthic foragers dived predominantly during the day and reached greater depths, regardless of colony. This is consistent with other studies reporting that this species has high behavioural flexibility over its wide range (Wilson et al. 1991, Robinson & Hindell 1996, Miller et al. 2009, Kokubun et al. 2010). Such flexible foraging habits likely provide a buffer against changes in prey availability and distribution in a limited, coastal environment (Lescroël & Bost 2005, Miller et al. 2009), as shown in other inshore foragers (Hoskins et al. 2008, Saraux et al. 2011, Camprasse et al. 2017a).

In the present study, some of the individuals performed trips longer (up to 5.6 d) than previously reported during the crèche period in Gentooos on Kerguelen Islands (on average 1.3 d in Estacade, Lescroël et al. 2009). It is possible that some of these birds abandoned breeding during the study as continued provisioning status could not be determined upon recapture for all birds. However, a third of birds known to still be provisioning chicks at the end of the study conducted such long trips. The large inter-individual variation in foraging behaviour observed in instrumented birds could be related to inter-individual variation in morphology (Bost & Jouventin 1990, this study). Indeed, individuals with higher body mass tended to travel farther, dive deeper and perform more benthic dives, contributing to the observed inter-individual differences in foraging. Differences in dive patterns, associated with larger oxygen stores in heavier birds, have been reported in other diving birds (Mori 1998, Cook et al. 2013).

I predicted that behavioural consistency would be detected in instrumented individuals, as numerous populations considered generalists have actually been shown to be
comprised of individual specialists (Woo et al. 2008, Araújo et al. 2011, Loxdale et al. 2011, Layman & Allgeier 2012, Fodrie et al. 2015). In the present study, at the population level, individual specialisations in foraging metrics were low to moderate, with bearings to most distal locations and the proportion of pelagic diving exhibiting the highest repeatability. This suggests that Gentooos stay consistent in some aspects of their foraging behaviour, which may help to reduce intra-specific competition and/or allow individuals to catch prey they can easily handle and digest (Bolnick et al. 2003, Estes et al. 2003). This seems particularly relevant in inshore foragers, as they are restricted in their foraging range (Cook et al. 2006, Ratcliffe et al. 2013, Harris et al. 2014).

However, a significant degree of behavioural consistency at the population level does not mean that all individuals are consistent (Woo et al. 2008, Ceia et al. 2012). Indeed, I observed large variation in the degree of individual consistency in spatial use and dive behaviour between instrumented individuals. While some birds exhibited similar foraging strategies over the course of multiple consecutive trips, others did not. For example, some individuals displayed consistency in the proportion of pelagic diving from one trip to the next while others were able to switch from being mostly benthic on one trip to being entirely pelagic. This highlights the need to sample multiple trips to obtain a more accurate description of a bird’s foraging behaviour, particularly in inshore foragers which may exhibit behavioural plasticity (Saraux et al. 2011, Carpenter-Kling et al. 2017). The large inter- and intra-individual variation in foraging behaviour discussed here might contribute to Gentooos having stable or expanding populations in parts of their range (e.g. Antarctic Peninsula), where sympatrically breeding penguin species, more dependent on specific resources such as Antarctic krill, experience strong population declines (Miller et al. 2009, Polito et al. 2015).

My third prediction was that individuals displaying higher consistency in foraging
behaviour would have reduced horizontal and vertical distances travelled, and higher body conditions as individual specialisations are thought to improve foraging efficiency (Watanuki 1992, Voslamber et al. 1995, Annett & Pierotti 1999, Golet et al. 2000, Votier et al. 2004).

Contrary to this prediction, no difference in distance travelled (per hour) or body condition was found between consistent and non-consistent individuals in the present study. Thus, it seems that instrumented individuals adopted different strategies based on intrinsic factors (i.e. morphology, prey preferences, etc.), ultimately resulting in different repeatability indices. Indeed the heavier, more benthic individuals performed more distant and longer trips, and were, thus, less repeatable within the timeframe of the study.

Generally, it is unclear whether specialists perform better than generalists, as contradictory results have been reported in the literature (Golet et al. 2000, Votier et al. 2004, Ceia et al. 2012, Dehnhard et al. 2016). My findings are in agreement with results on a long-distance forager, the Wandering albatross *Diomedea exulans*, demonstrating that specialist and generalist individuals had similar levels of body condition (Ceia et al. 2012). No effect of specialisation on reproductive outcomes has been also detected in other bird species (Votier et al. 2004, Katzner et al. 2005, Dehnhard et al. 2016). Indeed, even though generalists may deliver somewhat less energy per day, specialisation may not have an impact on measures of evolutionary fitness (Woo et al. 2008). In contrast, other studies on gulls, cormorants, guillemots and skuas have shown specialists to have higher reproductive success, food delivery rates, chick condition or adult survival (Watanuki 1992, Voslamber et al. 1995, Annett & Pierotti 1999, Golet et al. 2000, Votier et al. 2004). In Gentoos, individual specialisations in foraging behaviour may be linked with intrinsic factors, and may be more or less advantageous depending on prey availability, with generalists performing better when food availability is low.
Lastly, in agreement with my second prediction, long-term dietary consistency was detected in the birds sampled. Stable isotope values in blood and feathers in breeding Gentoo s were positively correlated, indicating that dietary specialisations are maintained outside of the breeding season. This is consistent with recent stomach contents and stable isotope analysis studies on the diet of Gentoo s, indicating that they may not be as opportunistic as previously thought (Clausen et al. 2005, Polito et al. 2015). Within generalist populations, 2 types can be found: type “A” generalists, when individuals all take a wide range of food type; and type “B” generalists, when individuals each specialise on a different range of food types (Bearhop et al. 2004). The results from my study, documenting a large inter-individual variation in diet, matching the high inter-individual variation in foraging behaviour, and documenting the fact that instrumented birds tend to display a similar feeding ecology in the breeding and inter-breeding seasons, seem to indicate that Gentoo s at the studied site are type “B” generalists.

The results of the present study should be interpreted with caution for two main reasons: the large difference in sample sizes between colonies where deployments were performed, and the potentially poor environmental conditions the instrumented birds experienced, seemingly leading to low prey availability as judged by the low number of chicks raised by Gentoo s and sympatrically breeding shags (E.C.M. Camprasse pers. obs.). More data are needed from Estacade to confirm the lack of a site effect on the Gentoo s’ foraging behaviour and feeding ecology. Factors including a high incidence of night diving and long trip durations could reflect poor environmental conditions in the 2014/2015 breeding season, forcing penguins to forage in suboptimal conditions. This is consistent with poor breeding success on Kerguelen Islands during deployments compared with normal years, with brooders losing chicks at the crèche stage (E. C. M. Camprasse, pers. obs.).
present study, shallow nighttime dives were observed in the more pelagic individuals, probably to allow them to take advantage of pelagic prey distributed near the surface at night during their diurnal vertical migration. Night/twilight diving has been recorded in pygoscelid penguins including Gentooos (Croxall et al. 1988, Williams et al. 1992, Robinson & Hindell, 1996) and other penguin species (Schiavini & Rey 2004, Rey et al. 2012), but was thought to be uncommon in such visual predators (Williams 1995, Bost et al. 2002). Lastly, low prey availability, linked with the seemingly poor environmental conditions experienced by the birds instrumented in the present study, could increase the degree of individual specialisation, as individuals are forced to add different alternative prey not consumed by conspecifics to their diet (Svanbäck & Bolnick 2007, Tinker et al. 2008).

In summary, I showed that Gentoo penguins on Kerguelen Islands exhibited large inter- and intra-individual variations in foraging behaviour. These may provide Gentooos greater resilience to buffer against changes in prey availability and fast changing environmental conditions, especially as their foraging range is usually limited (Lescroël & Bost 2005, Polito et al. 2015). However, within this context, Gentooos still exhibit individual specialisation, helping them reduce intra-specific competition and/or increasing their foraging efficiency (dit Durell 2000, Masello et al. 2013). Dietary specialisations outside of a single breeding season were also highlighted, suggesting Gentoo penguins are type “B” generalists. The next step to understand the consequences of individual specialisations would be to look at the link between behavioural consistency and reproductive output, which could not be done in this study due to logistical constraints. In order to fully understand the effects of individual consistency of parents on their offspring, researchers should also aim at obtaining information on both partners of breeding pairs (Polito et al. 2015). In the future, repetitive sampling of the same individuals across stages of the same breeding season and across years
will help to characterize the persistence of dietary specialisations at different temporal scales in seabirds.
CHAPTER 5

Changing with the times: Little penguins exhibit flexibility in foraging behaviour and low behavioural consistency

A version of this chapter has been published as:
Abstract

Individual foraging consistency is commonly seen in wild populations, even in species considered generalists and allows individuals to forage more efficiently. It may, therefore, have important consequences on ecological processes, for individuals and populations. Within seabirds, data on timescales over which consistency is maintained is lacking, despite its potential to determine how adaptable individuals and populations are to face environmental changes. Little penguins *Eudyptula minor* were tracked at two colonies in south-eastern Australia during 5 years, using GPS data loggers and dive recorders. This study investigated the presence of consistency, its persistence through time and the influence of extrinsic and intrinsic factors on behaviour and consistency. Individual consistency was compared between colonies, among consecutive foraging trips, among different breeding stages/clutches and years. Individuals showed high plasticity, with foraging metrics influenced by site, year, stage/clutch. Low to moderate short-term consistency in foraging metrics was highlighted, except for bearing. Over larger timescales, no consistency in these metrics was detected. Mass and morphology are known to influence foraging behaviour and consistency, but seemed not to affect consistency, which varied with year and site instead. This further highlights the plasticity animals foraging on prey highly spatially and temporally variable in their distribution. I emphasize the importance of taking timescale into account when assessing behavioural consistency. Finally, mechanisms other than behavioural consistency seem to allow Little penguins to find mobile food in the water column (e.g. group foraging, and switching from short to long trips at specific times of the breeding season).
Introduction

Individual consistency in foraging, leading to specialisations, is widespread in wild populations, and is thought to help foragers avoid competition with conspecifics and maximize their foraging efficiency (Bolnick et al. 2003, Araújo et al. 2011, Ceia & Ramos 2015). Recent research has brought to light the fact that even populations that are usually considered generalists can in fact be composed of individual specialists (Araújo et al. 2011, Loxdale et al. 2011, Matich et al. 2011, Layman & Allgeier 2012, Fodrie et al. 2015). As top predators, at the top or near the top of foodwebs, have the potential to affect prey populations and induce trophic cascades, it is important to understand their pattern of specialisations (Matich et al. 2011). Quantitative approaches to document their magnitude in populations in different contexts are necessary to understand how ecological interactions may influence the amount of among-individual variation, and how the amount of variations affects ecological dynamics (Araújo et al. 2011).

While this knowledge gap is increasingly being filled, few studies have focused on quantifying timescales over which individual specialisations are maintained. Failure to account for timescale in studies of individual specialisations likely results in inconsistent predictions regarding the effects of intraspecific variation on predator–prey interactions (Kernaléguen et al. 2015b, Novak & Tinker 2015). Studying timescales over which behavioural or dietary specialisations are maintained can help predict how adaptable individuals can be when faced with environmental changes (Hamer et al. 2007, Harris et al. 2014). Also, if maintained over long timescales, it is suggested that these specialisations can be subject to natural selection and lead to species diversification (Bolnick et al. 2003, Knudsen et al. 2010, Harris et al. 2014). Such specialisations have been shown, in a few studies in marine animals, to be maintained over timescales ranging from days to years, but
with decreasing consistency over long time spans (Woo et al. 2008, Harris et al. 2014).

Seabirds are top predators that face the challenge of finding food in complex and dynamic environments (Grémillet & Charmantier 2010, Cook et al. 2013). In their review, Ceia and Ramos (2015) suggested that the incidence of individual specializations is potentially widespread, but may fluctuate spatio-temporally among/within species and populations due to the frequency of specialists, predictability of resources or environmental conditions. Within this group, some studies report on strong individual specialisations in foraging behaviour and in diet, which can sometimes be maintained over several weeks and years within the same individuals (Wanless & Harris 1993, Cook et al. 2006, Elliott et al. 2009, Ratcliffe et al. 2013, Harris et al. 2014).

Seabirds are ideal to study consistency in behaviour as they generally nest in colonies. They are central-place foragers during the breeding season and often display a high level of nest fidelity, which allows the repetitive access necessary for longitudinal studies (Camprasse et al. 2017a). In addition, collecting data from multiple members of the same colony allows the level of variation in behaviour between individuals that arises from specialisation to be determined since animals have access to the same resources and are exposed to the same environmental conditions (Ratcliffe et al. 2013, Ceia & Ramos 2015, Camprasse et al. 2017b).

I chose to study Little penguins *Eudyptula minor* as they are considered generalists but have been suggested to exhibit fidelity to specific dive depths (Ropert-Coudert et al. 2003; Kowakczyk et al. 2014). This inshore forager relies mostly on small pelagic schooling prey such as Clupeiformes (Reilly 1974, Stahel et al. 1987, Hobday 1991, Cullen et al. 1992, Chiaradia et al. 2007b, Hoskins et al. 2008, Saraux et al. 2011). Little penguins, being limited in their range and restricted to hunting during daylight hours (Reilly 1974, Dann & Norman...
2006, Chiaradia et al. 2007a, Ropert-Couët et al. 2009a, Kowalczyk et al. 2015), have to find ways to maximize their foraging effort, which warrant further investigation. Therefore, the aims of the present study were to: 1) determine the factors influencing foraging behaviour; 2) quantify the magnitude of behavioural consistency and assess timescales over which it is maintained; and 3) investigate the influence of various intrinsic and extrinsic factors on behavioural consistency.

Materials and methods

Data collection

Data loggers, which allow the characterisation of foraging behaviour, including GPS trackers and dive recorders, were deployed on Little penguins at 2 colonies in south-eastern Australia, sometimes over multiple consecutive trips, in 5 breeding seasons (2011/2012-2015/2016; all breeding seasons are referred to as the year they started in), including different breeding stages and/or clutches. Field work was conducted at 2 sites in south-eastern Australia, London Bridge (LB, 38°62’S, 142°93’E), a small mainland colony (ca. 70 - 80 nests) (Berlincourt & Arnould 2014) and Gabo Island (GI, 37°56’S, 149°91’E), a large insular colony (ca. 35 000 nests) (Fullagar et al. 1995) during multiple breeding seasons (2011/2012 – 2015/2016), either at early chick-rearing (guard stage), late chick-rearing (post-guard stage), or both, in clutch 1 or clutch 2, or both. Depending on the year in which instrumentation occurred, either 1 or multiple consecutive trips were obtained (see Table 5.1 for sample sizes). GPS data loggers (I-gotU GT120, Mobile Action, Taiwan; 44.5 x 28.5 x 13.0 mm, 22 g in air corresponding to ca. 1% of mean body mass) were deployed in combination with time-depth recorders (TDR, LAT1800S, Lotek Wireless Inc.; 36.0 x 11.0 x
7.2 mm, 4.8 g in air corresponding to ca. 0.2% of mean body mass). GPS loggers were programmed to sample positions every 1 min or every 2 min depending on sampling years and stages. The TDR units were set to record depth and temperature at 1 s or 2 s intervals depending on sampling years and stages.

Individuals were captured at the colony in their burrows, weighed in a cloth bag using a suspension scale (± 10 g, Salter, Bristol, UK), and microchipped for identification. The GPS loggers - removed from their housings and encased in heat shrink plastic for waterproofing - and the dive recorders were attached to the back feathers using waterproof tape (Tesa 4651, Germany) and cyanoacrylate glue (Loctite 401, Prism, Instant Adhesive, UK). Individuals were recaptured after 1 or multiple consecutive trips depending on sampling year, using the method previously described. The data loggers were removed and individuals were weighed again and morphometric measurements (bill length, bill width, bill depth, head length, flipper length) were taken with a Vernier caliper and metal ruler (± 0.05 and 1 mm, respectively). Handling times ranged 5 to 10 min at deployment and 15 to 20 min at retrieval, during most of which the bird’s head was covered with a hood to reduce stress.
<table>
<thead>
<tr>
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<th>Total</th>
<th>Breeding season</th>
<th>Site</th>
<th>Sex</th>
<th>Breeding stage and clutch</th>
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<td>12</td>
<td>50</td>
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**Table 5.1** Sample sizes associated with the different datasets used (i.e. “full”, “day-to-day”, “stage-to-stage”, “clutch-to-clutch”, and “year-to-year” datasets), for Little penguins instrumented at London Bridge and Gabo Island, Victoria, Australia, in 5 consecutive years between 2011 and 2016. GI = Gabo Island, LB = London Bridge, G1 = guard stage of clutch 1, G2 = guard stage of clutch 2, PG1 = post-guard stage of clutch 1, PG2 = post-guard stage of clutch 2.
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<tbody>
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<td>Dataset</td>
<td>Clutch-to-clutch</td>
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<tr>
<td>Trips (n)</td>
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<tr>
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<tr>
<td>Dataset</td>
<td>Year-to-year</td>
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<tr>
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</table>
Data processing and analysis

All data analyses were conducted in the R Statistical Environment version 3.2.0 (R Core Team 2015). Summaries of dive parameters were obtained thanks to the diveMove package (Luque 2007). A depth threshold of 1 m was used to identify dive events. The diveMove package was also used to apply a speed filter to the GPS data to remove erroneous locations with a threshold of 1.5 m·s⁻¹. The GPS data was separated into individual trips thanks to a custom-made algorithm. GPS records were linearly interpolated to the 1 s intervals in the adehabitatLT package (Calenge 2006) to provide spatial information for the dive records.

From the GPS and TDR data obtained, 4 foraging metrics were calculated and used, in turn, as response variables in my models: bearings (bearings from the colony to the most distal points of tracks, one measure per trip, comprised between 0° and 360°) using the circular package (Agostinelli & Lund 2011), maximum distances from the colony (distances between the colony and the most distal points of tracks, one measure per trip) using the trip package (Sumner 2009), mean bottom depths using the diveMove package (one measure per dive within trips, hereafter dive depth), and total distances travelled per hour (cumulative vertical and horizontal distances travelled divided by the duration of foraging trips, one measure per trip). When multiple trips were obtained for the same deployment, the standard deviations for bearing (circular measure), and the coefficients of variation for the other 3 metrics, were calculated. Linear and linear mixed effects models were run in the nlme package (Pinheiro et al. 2014) and, whenever applicable, full models were dredged using the MuMIn package (Barton 2013) to determine the best fixed effects, based on the models’ AIC. Linear models were run when a single observation was available per individual, while linear mixed effects models were used when repeated data for each individual were available.
To investigate the factors influencing the foraging behaviour of instrumented individuals, I used the “full” dataset (i.e. data obtained from all individuals in both sites and from the 5 years of sampling, including all individuals for which GPS and TDR data covered at least 1 complete trip). I ran 2 different sets of models, 1 taking into account year, site, breeding stage and clutch, sex, and 1 taking into account mass, bill length and flipper length. Indeed, these explanatory variables could not all be used in a single model as sex and morphometric measurements were collinear, as were mass, stages/clutches and years.

Following Zuur et al. (2009), I started with models fitted with “REML”, which included all the explanatory variables considered, I compared models with and without the random effect associated with individual, and chose the models with the lowest AICs. Once I established whether a random effects structure was necessary, I inspected residuals for heterogeneity, and, when necessary included a stage, clutch and year-specific variance structure. The best nesting structure, if any, was selected based on the comparisons of models with the full nested structure (individual nested within stage/clutch nested within year), all the way to models with individual only has a random effect, and all the combinations in-between. These models were compared with the “anova” function. Models were then refitted with “ML” to select the best appropriate fixed effects, comparing models with the “anova” function. Finally, models were refitted with “REML” to estimate model parameters.

To investigate whether Little penguins exhibit consistency in foraging behaviour and if so, over which timescales, 4 different datasets were used: “day-to-day” (i.e. data obtained on subsequent trips on the same individuals), “stage-to-stage” (i.e. data obtained in guard stage and then in post-guard stage of the same clutch, within the same year for the same individuals), “clutch-to-clutch” (i.e. data obtained either in guard or post-guard of the same in clutch 1 and then in clutch 2 of the same year for the same individuals), and “year-to-year”
(i.e. data obtained in the same stage and clutch in different years from the same individuals). Model selection was performed as described above. Once the optimal models were found, a variance component analysis was run following Ratcliffe et al. (2013) and Harris et al. (2014). An estimate of individual specialisation is given by the proportion of variance explained by the individual variance component (Bolnick et al. 2003, Dingemanse & Dochtermann 2013, Ratcliffe et al. 2013). In cases for which the inclusion of the random effect “individual” did not improve the initial model, variance component analyses were not run as otherwise calculations are unreliable (Ratcliffe et al. 2013). For short-term, data analysis were run on dataset with the full “day-to-day” dataset individuals [i.e. individuals for which at least 2 trips were obtained (n =88 individuals and 288 trips)]. As described above, 2 sets of models (1 for year, site, stage/clutch and sex, and for mass and morphometrics) were run to investigate what factors influence the consistency in foraging behaviour of the instrumented individuals.

Results

Factors influencing foraging behaviour

A total of 264 different individuals were sampled, as indicated in Table 5.1. The “full” dataset was comprised 549 foraging trips (mean of 2.1 ± 1.7 trips per individual [1-13]). Little penguins stayed relatively close to the colonies and exploited shallow depths (Table 5.2).
Table 5.2 Summary of the data collected on Little penguins instrumented at London Bridge and Gabo Island, Victoria, Australia, in 5 consecutive years between 2011 and 2016 (“full” dataset), by year, site, sex and breeding stage and clutch; values are mean ± SD. GI = Gabo Island, LB = London Bridge, G1 = guard stage of clutch 1, G2 = guard stage of clutch 2, PG1 = post-guard stage of clutch 1, PG2 = post-guard stage of clutch.

<table>
<thead>
<tr>
<th></th>
<th>Maximum distances from the colony (km)</th>
<th>Total distances travelled per hour (km·h⁻¹)</th>
<th>Mean bottom dive depth (m)</th>
</tr>
</thead>
<tbody>
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<td><strong>Year</strong></td>
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</tr>
<tr>
<td>2011</td>
<td>18.2 ± 18.5</td>
<td>4.1 ± 1.5</td>
<td>10.8 ± 2.9</td>
</tr>
<tr>
<td>2012</td>
<td>18.2 ± 9.1</td>
<td>3.6 ± 1.0</td>
<td>8.6 ± 3.0</td>
</tr>
<tr>
<td>2013</td>
<td>16.9 ± 9.2</td>
<td>3.0 ± 1.0</td>
<td>10.9 ± 4.0</td>
</tr>
<tr>
<td>2014</td>
<td>20.0 ± 15.3</td>
<td>3.5 ± 1.0</td>
<td>8.4 ± 3.9</td>
</tr>
<tr>
<td>2015</td>
<td>21.0 ± 6.1</td>
<td>4.1 ± 1.1</td>
<td>13.1 ± 2.0</td>
</tr>
<tr>
<td><strong>Site</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LB</td>
<td>16.4 ± 7.6</td>
<td>3.5 ± 1.2</td>
<td>11.4 ± 3.5</td>
</tr>
<tr>
<td>GI</td>
<td>20.3 ± 15.8</td>
<td>3.3 ± 1.0</td>
<td>7.8 ± 3.2</td>
</tr>
<tr>
<td><strong>Sex</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>19.0 ± 12.7</td>
<td>3.5 ± 1.0</td>
<td>10.1 ± 4.0</td>
</tr>
<tr>
<td>Female</td>
<td>17.8 ± 12.3</td>
<td>3.3 ± 1.1</td>
<td>9.0 ± 3.6</td>
</tr>
<tr>
<td><strong>Breeding stage and clutch</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G1</td>
<td>16.8 ± 6.9</td>
<td>3.6 ± 1.1</td>
<td>9.5 ± 3.7</td>
</tr>
<tr>
<td>PG1</td>
<td>19.3 ± 17.2</td>
<td>3.3 ± 1.5</td>
<td>9.7 ± 4.3</td>
</tr>
<tr>
<td>G2</td>
<td>19.4 ± 6.2</td>
<td>3.5 ± 1.2</td>
<td>10.6 ± 2.7</td>
</tr>
<tr>
<td>PG2</td>
<td>19.8 ± 13.1</td>
<td>3.0 ± 0.9</td>
<td>7.8 ± 2.9</td>
</tr>
</tbody>
</table>
Bearings to maximum distance were influenced by site, by year and by stage/clutch (linear model: $F_{1,539} = 7.6, P = 0.006, F_{4,539} = 3.0, P = 0.02, F_{3,539} = 5.1, P = 0.001$, respectively). Likewise, maximum distances from the colony were influenced by site, by year and by stage/clutch (linear mixed effects model: $df = 1, F = 7.3, P = 0.007, df = 4, F = 7.2, P < 0.0001, df = 3, F = 5.1, P = 0.002$, respectively). Total distances per hour varied according to site, year, stage/clutch, and sex (linear model: $df = 1, F = 7.5, P = 0.006, df = 4, F = 14.8, P < 0.0001, df = 3, F = 3.2, P = 0.02, df = 1, F = 5.4, P = 0.02$, respectively). In the same way, dive depths varied according to site, year, stage/clutch, and sex (linear mixed effects model: $df = 1, F = 127.6, P < 0.0001, df = 4, F = 9.2, P < 0.0001, df = 3, F = 17.9, P < 0.0001, df = 1, F = 10.9, P = 0.001$, respectively). Bearings and maximum distances travelled were not influenced by mass and morphometric measurements.

**Degree of individual consistency in behaviour and relevant timescales**

Short-term consistency in foraging behaviour over subsequent trips (“day-to-day” dataset) was investigated initially (Figure 5.1). Variance component analysis were performed to determine the proportion of variance associated with the random effects, including the individual components, after model selection was performed to find the best model for each of the 4 foraging metrics (Table 5.3). Overall, the proportion of variance associated with the individual components was low to moderate (from 3.0% for dive depths to 29.8% for bearings). When investigating stage-to-stage consistency, the models including “individual” in the random effects did not differ from the linear models for each of the 4 response variables of interest (all $P > 0.2$). The same pattern was present in the clutch-to-clutch dataset (all $P > 1.0$), as well as in the year-to-year dataset (all $P > 1.0$).
Figure 5.1 Representative examples of short-term foraging area consistency in Little penguins. A single individual is shown from each study site (Gabo Island, top 2 panels, and London Bridge, bottom 2 panels) depicting moderate consistency in distances travelled over subsequent trips (indicated by different colours) and how there was little consistency between breeding stages/years; PG1 = post-guard of the first clutch, PG2 = post-guard of the second clutch.
Table 5.3 Information on the best models selected to run the variance component analysis [significance of the inclusion on an “individual” random effect compared to initial linear model (Likelihood Ratio (LR) test), significance of the best fixed effects, best random effect structure and inclusion of other parameters], and proportion of variance associated with the different random effects obtained after running the variance component analysis.

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<th>Response variable</th>
<th>Inclusion of random effects</th>
<th>Best fixed effects</th>
<th>Best random effects</th>
<th>Other parameters</th>
<th>Proportion of variance associated with random effects</th>
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</thead>
<tbody>
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<td>Bearings</td>
<td>df = 11, LR = 0.4, P = 0.8</td>
<td>NA (inclusion of random effects did not improve the initial model)</td>
<td>NA</td>
<td>NA</td>
<td>Year: 0.0% Stage/clutch: 30.4% Individual: 29.8%</td>
</tr>
<tr>
<td>Maximum distances</td>
<td>df = 5, LR = 11.9, P = 0.0006</td>
<td>site (df = 1, F = 10.6, P = 0.002)</td>
<td>year/stage-clutch/individual</td>
<td>year and stage/clutch variance-specific structure</td>
<td>Year: 0.0% Stage/clutch: 40.1% Individual: 24.7%</td>
</tr>
<tr>
<td>Total distances</td>
<td>df = 11, LR = no fixed effects</td>
<td>no fixed effects</td>
<td>year/stage-</td>
<td>NA</td>
<td>Year: 0.0%</td>
</tr>
<tr>
<td></td>
<td>travelled per hour</td>
<td>9.4, P = 0.002</td>
<td>clutch/individual</td>
<td>Stage/clutch: 17.3%</td>
<td></td>
</tr>
<tr>
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<td></td>
</tr>
<tr>
<td></td>
<td>Dive depths</td>
<td>df = 11, LR = 13436.0, P &lt; 0.0001</td>
<td>site (df = 1, F = 73.8, P &lt; 0.0001) / year (df = 3, F = 3.6, P = 0.02)</td>
<td>Individual: 18.9%</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>stage-clutch/individual/trip</td>
<td>autocorrelation structure (subsequent dives correlated)</td>
<td>Stage/clutch: 24.8%</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Individual: 3.0%</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Trip: 12.1%</td>
<td></td>
</tr>
</tbody>
</table>
Factors influencing individual consistency

I investigated the effects of site, year, stage/clutch and sex on the measures of consistency for the 4 variables of interest (Table S5.1 & S5.2). The standard deviation in bearings averaged 0.3 [0.0 – 3.0], and was lower in 2014 compared to 2013 (-0.2 ± 0.08, t = -2.7, P=0.03). The coefficients of variation for maximum distances from the colony were, on average, 0.3 [0.0 – 1.2], and were lower in London Bridge compared to Gabo Island (-0.09 ± 0.04, t = -2.0, P = 0.04), and in 2014 compared to 2011 (0.02 ± 0.09, t = -2.7, P = 0.04). The coefficients of variation in the total distances travelled per hour averaged 0.2 [0.0-1.0], and did not differ with site, year, stage/clutch, nor sex. The coefficients of variation for dive depths were on average 0.6 [0.3-1.2], and were higher in 2014 compared to 2013 (0.1 ± 0.03, t = 3.0, P = 0.01). Second, I looked at the effects of mass and 2 morphometric measurements (bill and flipper lengths) on the coefficients of variation of the variables previously mentioned (Table S5.3). The best models, as judged by AIC, for bearings, maximum distances from the colony, total distances travelled per hour, and bottom dive depths were the null models including a year and stage/clutch specific variance structure.

Discussion

This study investigated the factors influencing the foraging behaviour and behavioural consistency of Little penguins, and the timescales over which foraging consistency is maintained, over 5 consecutive years and at 2 sites of different oceanographic regimes in northern Bass Strait, Australia. I confirmed that Little penguins were shallow-divers and inshore foragers at my study sites (Gales et al. 1990, Ropert-Coudert et al. 2003, Kato et al. 2008, Kowalczyk et al. 2015). I looked at the factors influencing foraging behaviour and
found that underlying differences in certain parameters among years, breeding stages, clutches and sites were influential drivers. I investigated the timescales over which foraging consistency is maintained and found low to moderate short-term consistency (subsequent trips), but no consistency for greater timescales. Consistency in foraging behaviour was not related to intrinsic factors, but instead varied between sites, years and stages and clutches.

Factors influencing foraging behaviour

My results suggest that the factors influencing foraging behaviour in Little penguins include extrinsic factors, such as year, breeding stage and clutch, and site, and to a lesser extent sex and body mass. This is consistent with other studies reporting high flexibility in many aspects of the species’ foraging behaviour, and in some years, of their diet (Chiaradia & Nisbet 2006, Hoskins et al. 2008, Chiaradia et al. 2010, Saraux et al. 2011, Berlincourt & Arnould 2015, Kowalczyk et al. 2015). While no data on prey availability, distribution or environmental conditions is available to explain these differences, this flexibility seems to be in response to variations in prey conditions associated with different environmental conditions (Chiaradia & Nisbet 2006, Hoskins et al. 2008, Berlincourt & Arnould 2015). For example, in years of reduced food availability, Little penguins have been found to increase their foraging trip duration, a proxy for maximum distances from the colony (Saraux et al. 2011), instead of decreasing the mass of meals delivered to their chicks (Chiaradia & Nisbet 2006).

The diet of Little penguins is comprised mostly of Clupeiformes, including anchovy, pilchard, and sprat, and exhibits relatively little variation in prey type (Hobday 1991, Cullen et al. 1992, Chiaradia et al. 2010, Deagle et al. 2010, Sutton et al. 2015). Therefore, from my
results, it seems likely that the differences in foraging behaviour across space and time arise from differences in the local distribution and abundance of Clupeiformes, thought to be associated with different environmental conditions, rather than from differences in prey types (Hoskins et al. 2008). As in the present study, the importance of foraging plasticity in coastal marine predators has been highlighted in other seabird species (Ishikawa & Watanuki 2002, Lescroël & Bost 2005, Deagle et al. 2008, Castillo-Guerrero et al. 2016).

**Degree of individual consistency in behaviour and relevant timescales**

Ropert-Coudert et al. (2003) suggested individual Little penguins maintain consistent dive depths; indeed, in their study 12 individuals were observed to be either very shallow divers consistently over 2 to 3 consecutive trips (1.9 ± 1.7 m) or consistently shallow divers (8.1 ± 4.7 m). In the present study, in contrast, I found low short-term consistency in dive depths. Similarly, there was a lack of short-term consistency in bearings to maximum distance indicating that over subsequent days, Little penguins foraged in different locations within their home range. These findings confirm that Little penguins are highly plastic (Cullen et al. 1992, Chiaradia et al. 2010, Deagle et al. 2010, Sutton et al. 2015). In contrast, 20-25% of the variance in maximum distances from the colony and total distances travelled per hour was explained by the individual. This indicates that, despite capturing prey at different depths and different locations each day, over the short-term Little penguins remain moderately consistent in their foraging effort. This is consistent with previous studies which have shown foraging trip duration, which correlates with distances travelled, is correlated with body condition (Numata et al. 2000, Kato et al. 2008, Saraux et al. 2011).
Few previous studies have reported on the variance explained by the individual in foraging metrics of seabirds over the short-term. Interestingly, these values tend to be higher in benthic species than in species exhibiting mixed benthic and pelagic diving, and no other study reports on this in pelagic foragers. For benthic blue-eyed shags *Phalacrocorax georgianus*, *P. verrucosus*, and *P. atriceps*, the proportion of variance in dive depths ranged from 41.5 to 85.1% (Ratcliffe et al. 2013, Harris et al. 2014, Camprasse et al. 2017a). For species exhibiting mixed benthic and pelagic behaviour, like Thick-billed murres *Uria lomvia* and King cormorants *P. albidventer*, these values dropped to 44 and 25%, respectively (Kato et al. 2000, Woo et al. 2008). While the proportion of variance in foraging metrics was not reported, 2 other species with mixed benthic and pelagic behaviour, Japanese cormorants *P. filamentosus* and Pelagic cormorants *P. pelagicus*, have been shown to display individually consistent patterns for depth usage and exhibit foraging site fidelity. These findings suggest short-term individual consistency in foraging behaviour may be linked to the availability and distribution of prey; they are thought to be more predictable for benthic divers (Watanuki et al. 2004, Cook et al. 2006), which have an increased potential to rely on memory of seafloor features for navigation to re-visit specific areas (Davoren et al. 2003, Cook et al. 2006, Woo et al. 2008, Harris et al. 2014) compared to pelagic Little penguins.

Only a few studies have followed the same individuals throughout the breeding season and between years to assess whether individual consistency throughout longer timescales is maintained (Woo et al. 2008, Elliott et al. 2009, Harris et al. 2014). All of these studies show that behavioural consistency decreased through time [see also Bell et al. (2009)]. In the present study, individual consistency in foraging metrics was only present over subsequent foraging trips, with no consistency detected for longer timescales. This suggests that Little penguins feed on prey that is temporally unpredictable on timescales
longer than multiple consecutive days. The fact that Little penguins do not seem to exhibit long-term consistency in foraging behaviour might be beneficial in the face of rapidly changing climate, like the one experienced in the southern parts of Australia (Lima & Wethey 2012). Long-term fidelity in foraging areas and diving behaviour seem indeed to prevent individuals from adapting to rapid environmental change and from avoiding areas that have become unsuitable for foraging (Vander Zanden et al. 2016, McIntyre et al. 2017).

My study highlights the importance of repeated sampling across various timescales, as short-term results have previously been shown to over-estimate individual consistency (Kernaléguen et al. 2015b). More trips could be obtained to confirm the degree of behavioural consistency exhibited in short time frames. For example, increasing the number of consecutive trips obtained could lead to an increased estimate of individual consistency if individuals take longer than a few days to re-visit areas where they had been successful before. Bigger sample sizes for timescales other than day-to-day also should be obtained to confirm the lack of consistency on longer timescales, as it would increase confidence in the estimates of the degree of consistency.

**Factors influencing individual consistency**

No effects of body mass or morphometric measurements were found on foraging behaviour consistency. In contrast, the consistency of these metrics was affected by the year of sampling and site. This suggests that Little penguins are very plastic and respond to variations in prey availability and distribution determined by local environmental conditions instead of relying on set strategies based on individual morphology or body mass. Obtaining data on environmental conditions and prey abundance and distribution at a fine enough scale
would be invaluable to be able to understand the interplay between environmental and prey conditions, time of sampling, and behavioural consistency.

Strong behavioural and/or dietary consistency in seabirds is reported in species exhibiting important variations in foraging habitat and associated prey, as shown by large variations between individuals in both behaviour and diet (Cook et al. 2006, Ratcliffe et al. 2013, Harris et al. 2014). Therefore, the low consistency in foraging behaviour observed in Little penguins could reflect low ecological opportunity (Hobday 1991, Cullen et al. 1992, Hoskins et al. 2008, Chiaradia et al. 2010, Sutton et al. 2015). Indeed, Little penguins are less likely to have access to a wide array of prey or foraging habitats on which to specialise.

Individual consistency, leading to foraging specialisations have been suggested to help increase foraging efficiency by reducing competition with conspecifics and/or by focusing on prey individuals can easily find, handle or digest (Estes et al. 2003, Cook et al. 2006, Ceia et al. 2012, Harris et al. 2014, Kernaléguen et al. 2015a). This would seem particularly relevant for inshore and resident species, such as Little penguins, with a limited foraging range (Cook et al. 2006, Ratcliffe et al. 2013, Harris et al. 2014), which could, for example, benefit from re-visiting areas where profitable prey have been encountered more easily than offshore foragers. As short-term consistency is low or moderate, Little penguins, appear to have other ways of increasing their foraging effort in this limited environment, such as, group foraging and alternating long and short trips at specific times of the breeding season (Ropert-Coudert et al. 2004, Sutton et al. 2015).

In summary, low to moderate consistency in foraging behaviour was observed over the short-term but not over longer timescales. Both foraging behaviour and its consistency varied extensively across sites, years, breeding stages and clutches, showing that Little
penguins are highly plastic, which might be necessary for such small, pelagic predators with limited ranges to forage successfully. Such strategy seems to have the potential to help little penguins cope with their rapidly changing environment, as behavioural adaptations could limit their ability to do so, although this warrants further investigation. One caveat of this study, however, is the relatively low sample sizes for timescales other than short-term consistency, and limited number of trips obtained, which could have affected the estimate of individual specialisations. This study should be replicated on more pelagic divers and species generally considered generalists to see if the patterns highlighted in the present study are widespread within this group.
Supporting documentation

Table S5.1 Model selection for models including the standard deviations in bearings, the coefficients of variation in maximum distances reached, in total distances travelled per hour and in dive depths as response variables, and including site, year, stage/clutch and sex as explanatory variable; output for the dredged models.

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Coefficients of variance in total distances travelled per hour

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Table S5.2. Significance of fixed effects for the models including the standard deviations in bearings, the coefficients of variation in maximum distances reached, in total distances travelled per hour and in dive depths as response variables, and including site, year, stage/clutch and sex as fixed effects; results of best selected models

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**Table S5.3** Model selection for models including the standard deviations in bearings, the coefficients of variation in maximum distances reached, in total distances travelled per hour and in dive depths as response variables, and including mass, flipper and bill lengths as explanatory variable; output for the dredged models.

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**Standard deviations in bearings**

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CHAPTER 6
General discussion: drivers of individual specialisations and timescales involved
Introduction

Individual specialisations have been shown to be widespread in wild populations of broad taxonomic groups, including vertebrates, invertebrates and even plants (Bolnick et al. 2003, Araújo et al. 2011, Dall et al. 2012, Toscano et al. 2016). They have been reported in a wide range of contexts, including: mate choice (Godin & Dugatkin 1995, Forstmeier & Birkhead 2004, Schuett et al. 2011), nesting and egg-laying behaviour (Tabashnik et al. 1981, Janzen & Morjan 2001), migratory and wintering strategies (McFarlane Tranquilla et al. 2014), foraging strategies (Werner & Sherry 1987, Hoelzel et al. 1989, Kohda 1994), space use (Svanbäck & Eklöv 2002, Estes et al. 2003), diet (Howard 1993, Beaudoin et al. 1999, Matich et al. 2011), responses to environmental conditions (Patrick et al. 2014), and boldness levels (Verbeek et al. 1994, Coleman & Wilson 1998, Dingemans et al. 2002, Toscano et al. 2016). Bolnick et al. (2003) defined an individual specialist as “an individual whose niche is substantially narrower than its population’s niche for reasons not attributable to its sex, age, or discrete (a priori) morphological group”. The phrase “individual specialisation” designates either the overall predominance of individual specialists in a population or the degree to which an individual’s diet is restricted compared to that of their population (Bolnick et al. 2003). Individual specialisations in foraging have been shown to help individuals increase their foraging efficiency (including prey finding, handling and digesting) (Partridge 1976, Ehlinger 1990, dit Durell 2000, Estes et al. 2003, Dickman & Newsome 2015), avoid competition with conspecifics (Bolnick et al. 2003), reduce pathogen exposure (Johnson et al. 2009), improve decision-making (Bernays & Funk 1999), and increase body condition, fitness and reproductive output (Basset & Rossi 1987, Holbrook & Schmitt 1992, Annett & Pierotti 1999, Golet et al. 2000, Patrick & Weimerskirch 2014a).

Individual specialisations may, therefore, have significant ecological consequences at
the individual and population levels, and impact ecological processes and foraging dynamics (Trowbridge 1991, Sherratt & Macdougall 1995, Bolnick et al. 2003, Knudsen et al. 2010, Bolnick et al. 2011, Matich et al. 2011, Dall et al. 2012, Ceia & Ramos 2015, Dickman & Newsome 2015). Although recent studies on individual specialisations have moved away from merely reporting the presence of individual specialisations by quantifying its magnitude in the past couple of decades (Bolnick et al. 2003, Araújo et al. 2011), some limitations remain. For example, the failure to take into account timescales over which such specialisations are maintained can lead to biased estimates of individual specialisations (Kernaléguen et al. 2015b). The use of different indices to describe the degree of specialisations exhibited by populations also hinders meaningful comparisons between studies (Bolnick et al. 2003).

Specialisations in foraging, which is the focus of the present thesis, involve the repetition of specific behaviours to acquire food or dietary choices over times (Bolnick et al. 2003). Even populations thought to be dietary generalists are increasingly shown to be composed of individual specialists (Amundsen 1995, Woo et al. 2008, Araújo et al. 2011, Loxdale et al. 2011, Layman & Allgeier 2012, Fodrie et al. 2015). Understanding the degree to which individuals differ in their habitat use and the timescales over which individual specialisations are maintained will help gaining insight into their susceptibility to anthropogenic threats and environmental changes (Bearhop et al. 2006, Ceia et al. 2012, McIntyre et al. 2017). While individual specialisations allow individuals to be more efficient foragers in some contexts, behavioural flexibility might remain important in ensuring individuals are able to cope with changes in prey availability and diversity over longer timescales (Montevecchi et al. 2009) and the balance between both needs to be understood better to predict how changes in the environment might affect populations. Furthermore,
obtaining a better understanding of the individuals is crucial as management plans that aim to protect a species’ resource base by targeting some “average” resource for the population may harm individual specialists; this might be the case when these specialists represent demographically important subsets of the populations that use specific habitat or forage on specific prey (Bolnick et al. 2003). Seabirds, which are particularly sensitive to rapid environmental change (Grémillet & Boulinier 2009, Croxall et al. 2012), are suitable models to study individual specialisations in foraging behaviour because most species nest in large colonies, which allow for easy access to individuals that use the same environment, that are strongly constrained during breeding as central place foragers and that may compete for the same resources (Ratcliffe et al. 2013).

In the present thesis, the use of complimentary bio-logging and stable isotope analyses allowed me to quantify the degree of foraging specialisations in three resident seabird species living in different environments and exhibiting different foraging modes. Kerguelen shags *Phalacrocorax verrucosus* breed in small colonies on Kerguelen Islands, and belong to the blue-eyed shag complex (Siegel-Causey 1988), a group of seabirds, which is predominantly constituted of benthic foragers and is known to exhibit a high intra- and inter- individual variation in diving behaviour and prey choice, as well as inter- individual and inter-sexual differences (Bearhop et al. 2006, Cook et al. 2006, 2007, Harris et al. 2014, Harris et al. 2016). Gentoo penguins *Pygoscelis papua* are one of the most widespread penguin species, and breed on subantarctic islands, including Kerguelen Islands, and in the Antarctic Peninsula (Williams 1995). They are considered an inshore opportunistic forager, consuming both benthic and pelagic species, and are known to exhibit high plasticity in their diet, marine habitat use and dive behaviour (Bost & Jouventin 1990, Woehler 1995, Lescroël & Bost 2005, Miller et al. 2009). Lastly, Little penguins *Eudyptula minor* breed in New

Deployments of data loggers on all three model species allowed me to obtain diving behaviour and spatial use metrics for each trip or dive carried out by individuals, including dive depths, dive durations, total vertical distances, maximum distances reached, total distances travelled, trip durations and bearings to most distal locations. Linear mixed effects models are the most powerful and flexible approach to quantify individual repeatability (Nakagawa & Schielzeth 2010, Dingemanse & Dochtermann 2013, Ratcliffe et al. 2013); they were used in the present work to perform variance component analyses to understand which proportion of the variance in the parameters mentioned above were associated with the individual component. At the individual level, obtaining the coefficients of variation for different metrics allowed me to investigate the links between individual consistency, and intrinsic (morphometrics, body mass, sex, prey preferences, foraging mode) and extrinsic drivers (site, breeding stage, year of sampling, location). In addition, stable isotope analyses from blood and feather tissues were used to get information on dietary specialisations at the time of deployments and on longer timescales (Barrett et al. 2007). My aims were to quantify the degree of individual specialisations in the populations studied and understand the drivers of such specialisations (chapters 2, 4, and 5), to look at within-pair strategies in terms of individual specialisations (chapter 3), and to determine timescales over which specialisations are maintained (chapter 5), which unfortunately could not be done on other species due to logistical constraints.
Prevalence of individual specialisations

Specialisations at the population level

The number of studies reporting on individual specialisations in seabirds has increased over the past decade and it is now clear that a substantial number of seabird populations exhibit at least short-term individual specialisations in foraging behaviour and in diet during the breeding season (Ceia & Ramos 2015), but also display consistent migratory routes and over-wintering strategies (Phillips et al. 2006, Helberg et al. 2009, Dias et al. 2011, 2013, Grist et al. 2014, Müller et al. 2014) (Figure 6.1). Consistent with the view that individual specialisations are widespread in various animal taxa (Bolnick et al. 2003, Bell et al. 2009, Araújo et al. 2011), and in seabirds in particular, I showed evidence of behavioural consistency and individual specialisations in all three study species (Table S6.1). Repeatability in both diving behaviour and space use metrics were detected on a scale of multiple consecutive trips (Chapters 2, 4, 5) and between breeding stages (Chapter 2). Correlations between carbon and nitrogen stable isotope values were observed in the same tissue between breeding stages (Chapter 2) and across tissues (Chapters 2 and 4), indicating medium- to long-term dietary specialisations, respectively.

While it is important to investigate the presence or absence of individual specialisations, early studies on the topic tended to ignore substantial variation in the degree of individual specialisations, which can vary widely among species and populations (Bolnick et al. 2003). In the present work, differences in the degree of individual specialisation exhibited by the three populations studied were highlighted. Indeed, Kerguelen shags displayed the highest consistency with the proportion of variance explained by the individual component in foraging metrics reaching 85% for dive depths in females (short-term), and
correlations between blood and feather stable isotope values reaching up to 0.92 for $\delta^{13}$C values (long-term) (Chapter 2). In comparison, Gentoo penguin foraging metrics showed lower behavioural specialisations, with the proportion of variance explained by the individual component reaching 53% for bearings to most distal locations (short-term) and lower correlations between blood and feather stable isotope values (up to 0.7 for $\delta^{15}$N values, long-term) compared to Kerguelen shags (Chapter 4). Little penguins showed an even lower consistency in foraging metrics, with the highest proportion of variance explained by the individual component reaching 25% for maximum distances travelled, and no repeatability being detected over longer timeframes.

A review of the literature found 34 studies that went beyond simply testing the presence of individual specialisations and quantified the degree of specialisations in foraging behaviour and/or diet exhibited in seabird populations (Table S6.1). Most of them focused on the breeding season as this is the time when access to individuals is facilitated by their central-place foraging. The 22 species for which information on the degree of individual specialisation is available include shags, cormorants, gannets and boobies (Suliformes), prions, albatrosses, and shearwaters (Procellariformes), guillemots, gulls and skuas (Charadriiformes), and penguins (Sphenisciformes). Out of the 34 studies, 19 were conducted in polar and sub-polar locations, while 14 were in temperate locations and only one in the tropics. This imbalance reflects the one highlighted for all studies reporting on individual specialisations in seabirds by Ceia and Ramos (2015) (Figure 6.2).
Figure 6.1 Number of seabird species in which any type of individual specialisation in foraging and/or feeding strategies was positively and negatively documented, and total number of species for the five seabird orders (a), and for the 12 extant seabird families (b). The fraction (%) between the number of studied species and the total number of species for each order is shown in the bars. From Ceia and Ramos (2015).
Figure 6.2 Ocean regions showing the number of studies (black bars) and seabird species (grey bars) in which any type of individual specialisation in the foraging and/or feeding strategies of seabirds was documented (both positive and negative results). From Ceia and Ramos (2015).
The studies listed in Table S6.1 highlight the importance of using common and carefully selected foraging metrics of consistency for comparisons. Variables reported in the literature to illustrate this topic include the proportion of variance explained by the individual, repeatability calculations, the proportion of individuals exhibiting a specific behaviour or diet, spatial overlap at different times, and correlations between metrics at different times, between stable isotope values or Hg concentrations in different tissues (Table S6.1). The use of these different parameters hinders comparisons of the degree of specialisations exhibited by different populations, a problem identified in reviews on this topic (Bolnick et al. 2002, 2003, Sargeant 2007).

Furthermore, some metrics seem to have relatively low or no repeatability, such as trip duration (4 out of 5 studies using this metrics reported no repeatability or repeatability only reaching 33% on short timescales) (Soanes et al. 2013, Harris et al. 2014, Patrick et al. 2014, Baylis et al. 2015b). Other metrics, such as headings to most distal location or outbound portion of trip, seem to have generally higher repeatability (5 out of 6 studies using this metric reported values above 53% and reaching 96%) (Patrick et al. 2014, Baylis et al. 2015b, Oppel et al. 2015, Chapters 2 and 4). Lastly, metrics such as dive depth seem to range from very low to very high degrees of repeatability depending on the population studied (out of 9 studies reporting on consistency in dive depth, values of repeatability ranged anywhere from 3% to 92%), which raises the need for careful consideration and choice of study variables. This is also illustrated in Patrick et al. (2014) where Northern gannets *Morus bassanus* appear to be highly specialised when taking into account metrics such as headings to most distal location, most distal longitude/latitude, dive locations, and certain environmental conditions at dive locations, but less specialised when taking into account dive metrics, which could be linked to variation in prey behaviour affecting this species’ foraging.
habits (e.g. plunge-diving).

Out of the 34 studies cited in Table S6.1, 16 investigated the degree of individual specialisation from dietary information only (from stable isotope values mostly, but also more rarely from mercury concentrations, pellet analysis, or direct delivery observations), 15 only used behavioural data, and only 3 used both dietary and behavioural data. In Woo et al. (2008) and in Chapter 2, the degree of individual specialisations determined from dietary analysis and that determined from behavioural data are consistent with a high degree of individual specialisation. In other cases, however, there can be a mismatch between the degree of behavioural and dietary specialisation which could be attributed to the different timescales represented by both (Chapter 4) or to flexible behavioural tactics. Indeed, while foraging metrics show low to moderate short-term repeatability in my study on Gentoo penguins, the correlation in stable isotope values in blood and feather are strong, indicating long-term dietary specialisations. This highlights the importance of working with both kinds of data (diet and behaviour) when documenting the degree of individual specialisations in a population to obtain a more accurate representation of such specialisations.

**Specialisations at the individual level**

At the individual level, there can also be quite large differences in the degree of specialisation within overall specialist or generalist populations (Woo et al. 2008, Ceia et al. 2012). This was emphasized in Chapters 2, 4 and 5, in which the coefficients of variation for most of the foraging metrics presented could vary widely among individuals. Some individuals were very consistent across trips while others were less so, which highlights the need to obtain information from multiple trips to get an accurate description of individual
behaviour. These variations are also important to account for as they can have repercussions on individual fitness and reproductive success, although conclusions in the literature on the consequences of individual specialisations in seabirds remain contradictory. Some studies have linked individual specialisations with higher reproductive success included higher number of fledglings, improved chick growth and condition (e.g. Slaty-backed gulls *Larus schistisagus*, Watanuki (1992), Western gulls *Larus occidentalis*, Annett and Pierotti (1999), Pigeon guillemots *Cepphus columba*, Golet et al. (2000), Great skuas *Stercorarius skua*, Votier et al. (2004)), and adult survival (Annett & Pierotti 1999). Other studies, however, did not detect such link and suggest that being a specialist or being a generalist are different but equally profitable strategies (Votier et al. 2004, Katzner et al. 2005, Ceia et al. 2012, Dehnhard et al. 2016); this could be linked with the need to achieve some balance between stereotyped behaviour and fidelity to foraging site, and behavioural flexibility needed to cope with changes in prey availability and diversity linked with changing environmental conditions (Ceia et al. 2014a, Montevecchi et al. 2009).

Furthermore, studying individual differences in consistency may help understand patterns of mate choice (Sinn et al. 2006, Schuett et al. 2010, Schuett et al. 2011). Indeed, although mates were not found to display similar behavioural consistency in Kerguelen shags (Chapter 3), they had similar dietary preferences, at least in terms of trophic level, and overall similar foraging strategies (e.g. more similar bearings, total distances travelled, and dive depths than expected by chance) despite not exhibiting size-assortative mating. Whether these behavioural and dietary preferences are the basis for mating or they evolve as a result of communication after mating has occurred based on other criteria remains unknown. Nevertheless, it is of importance to study pair similarity in behaviour and diet as it is known to influence reproductive success (Both et al. 2005, Spoon et al. 2006, Elliott et al. 2010,
Schuett et al. 2010).

**Timescales of individual specialisations**

In the present work, both behavioural and dietary specialisations were investigated at different timescales (Chapters 2 and 4). Kerguelen shags were shown to be consistent in the foraging areas they exploited and to display similar trip characteristics, not only on multiple consecutive days, but also at a one-month interval between breeding stages (Chapter 2). Carbon and nitrogen stable isotope values in instrumented shags were also correlated in blood between breeding stages (representing medium-term consistency), and in blood and feathers (representing long-term consistency). Likewise, short-term behavioural consistency was detected in Gentoo penguins (on a trip-to-trip scale), and correlations in stable isotope values in blood and feather were strong. Unfortunately, for these 2 species, obtaining behavioural data over longer timescales was not possible because of logistical constraints preventing us from re-accessing the study sites to extend sampling.

Only a third of the studies listed in Table S6.1 quantified the degree of individual specialisations exhibited in seabird populations at different timescales and in different times in the annual cycle, despite the fact that the temporal persistence of individual specialisation has implications for evolutionary and ecological processes (Bolnick et al. 2003). From these studies, it appears that repeatability in the same metrics at short, medium and long timescales is higher when the interval between observations is short (Quillfeldt et al. 2008b, Woo et al. 2008, Ceia et al. 2012, Ceia et al. 2014b, Harris et al. 2014), a finding which has been proposed as a universal pattern in animal studies (Bell et al. 2009). This was particularly marked in pelagic Little penguins, in which only short-term consistency in foraging metrics
could be detected (Chapter 5). Similarly, in pelagic Thin-billed prions *Pachyptila belcheri*, there were significant correlations in chick isotope values only at 20 and 40 day, and no correlation between blood sampled in spring and in summer or between blood and feathers, representing longer timescales (Quillfeldt et al. 2008b).

Studying the consistency of individual specialisations through time is important when trying to assess the adaptability of populations (Bolnick et al. 2003, Bearhop et al. 2006, Ceia et al. 2012, McIntyre et al. 2017). For example, populations of long-term individual specialists are unable to respond quickly to environmental or habitat changes, and are more subject to frequency-dependent effects (Thiemann et al. 2011, McIntyre et al. 2017). Multi-year studies are essential to engage food web and environmental variability (Montevecchi et al. 2009), as extrinsic drivers can override intrinsic drivers in determining the degree of individual specialisations exhibited by population. Furthermore, frequency-dependent competition, or selection, is unlikely to operate on short-term specialists as they can quickly alter their preferences when their preferred prey becomes rare (Bolnick et al. 2003). Lastly, individual specialisations could have evolutionary consequences, such as trait evolution and speciation depending on the heritability and temporal consistency of such inter-individual variations (Bolnick et al. 2003, Knudsen et al. 2010).

The use of methods such as stomach content or pellet analysis, video cameras recording prey capture, or short-term deployment of loggers, in isolation, can lead to biases in the estimates of the degree of individual specialisations exhibited by individuals (Araújo et al. 2007, Ceia et al. 2012, Kernaléguen et al. 2015b). This highlights the need to use different complementary approaches to quantify individual specialisations because no single timescale may provide a complete and accurate picture of the degree to which they are displayed (Kernaléguen et al. 2015b). Conventional dietary analyses (pellet, regurgitate or stomach
content analysis) provide important information on prey species but only represent a “snapshot” of individual prey preferences at a given times. Analysis of tissue stable isotopes helps determine dietary preferences over longer timescales because of the differences in turnover in different tissues, and the fact that some tissues are inert after synthesis, and helps determine which timescale is representative of an individual’s niche width (Bearhop et al. 2004, Del Rio et al. 2009, Kernaléguen et al. 2015b). Animal movement tracking, on the other hand, has the potential to provide important information on 3-dimensional space use, to identify behavioural consistency on scales ranging from days to weeks (Kernaléguen et al. 2015a).

Another issue to take into consideration is the potentially important differences in the degree of individual specialisations exhibited by some seabird species between breeding stages and/or years. This is illustrated in a study by Ceia et al. (2014b), in which extreme variations in the correlations between plasma and red blood cells were observed in individual Cory’s shearwaters *Calonectris borealis*. These correlations were not significant in some years and stages, but reached values as high as 0.91 for $\delta^{13}$C values and 0.88 for $\delta^{15}$N values in others. This pattern is likely due to the fact that such a pelagic species might need to display important behavioural flexibility to deal with temporal and spatial resource unpredictability (Ceia et al. 2014b). In this study, sampling in a single breeding stage or year would have led to a misrepresentation of the degree of individual specialisations displayed by this population. This is consistent with the results obtained in the present work on Little penguins, in which behavioural consistency varied with years and breeding stages (Chapter 5). Thus, repetitive sampling, ideally in years of different prey availabilities and distributions, seems crucial for such highly plastic species to accurately quantify individual specialisations and further understand the drivers of individual specialisations.
Drivers of individual specialisations

Because the factors promoting ecologically relevant behavioural specialisation within natural populations are likely to have far-reaching ecological and evolutionary consequences (Dall et al. 2012), identifying them should be a priority. In the present thesis, the influence of various intrinsic and extrinsic drivers on individual consistency was investigated. More specifically, in Kerguelen shags, I investigated the relationship between sex, stage and morphology, and the degree of short-term individual consistency in foraging metrics (Chapter 2). In Gentoo penguins, the effect of sex, body condition and site on short-term consistency in habitat use was investigated (Chapter 4). In Little penguins, I determined how short-term measures of behavioural consistency were influenced by the sex of the individuals, their body mass and morphometric measurements, the location of the colonies, the breeding stages and clutches, and the year in which deployments were done (Chapter 5).

Intrinsic drivers

In Kerguelen shags, the only consistency metric that was influenced by sex was the coefficient of variation in dive depth (Chapter 2), which is consistent with results from other studies on populations of blue-eyed shags (Kato et al. 2000, Ratcliffe et al. 2013). In contrast, sex did not influence any other measures of short-term consistency, and clusters identifying foraging strategies associated with differences in consistency were not biased by sex (Chapter 2). Likewise, no sex effect on short-term behavioural consistency was found on Gentoo and Little penguins (Chapters 4 and 5). In all three studies, no relationship between morphometric measurements and measures of individual specialisations were found, which matches the results of other studies (Ropert-Coudert et al. 2003, Woo et al. 2008, Provencher et al. 2013).
These findings agree with the view that individual specialisations occur even after sex and discrete morphological differences have been accounted for (Maret & Collins 1997, Bolnick et al. 2003, Woo et al. 2008).

No clear link was found in the literature between the degree of individual specialisations and the species studied (Table S6.1). For example, Northern gannets were shown to be either highly repeatable in most foraging metrics over the short-term in one study (Patrick et al. 2014), while they were shown to exhibit generally low consistency in spatial overlap in others (Pettex et al. 2012, Soanes et al. 2013). Similarly, the foraging metrics of Brünnich’s guillemot *Uria lomvia* were shown to be highly correlated at different timescales, from days to years, but the correlations in isotopic values between prey found in stomachs and the muscle tissue of birds were weak (Provencher et al. 2013). Lastly, no seabird order or family seemed to stand out and be more or less specialised than others (Table S6.1). These patterns suggest either the potential for intrinsic drivers not measured in the present work, or the importance of extrinsic over intrinsic drivers, in determining the degree of individual specialisations exhibited by populations.

*Extrinsic drivers*

Bird species for which the degree of individual specialisations was studied evolve in very different contexts. Table S6.1 reports on the degree of individual specialisations for species in different environments (polar or sub-polar, temperate and tropical), and with different foraging modes (pelagic, benthic and mixed) and sites (offshore and inshore). Polar and sub-polar species seem to show high repeatability in foraging metrics and dietary specialisations (this is the case for approximately half of the species), while the proportion of
species exhibiting such high levels of specialisations reached less than 20% in temperate locations. Therefore, the degree of individual specialisations seems to be influenced to some extent by the kind of environment the populations studied live in. There is not enough data to infer patterns from tropical locations as only one of the 34 studies in Table S6.1 was carried out in such an environment. Potentially, this could be due to the under-reporting of negative results, which would hinder the establishment of broad conclusions (Bolnick et al. 2003).

Although the number of studies quantifying individual specialisations in foraging behaviour for offshore species is three times lower than the ones for inshore species, offshore species appear to display proportionally lower levels of consistency. Furthermore, the degree of individual specialisations is influenced by the seabirds’ foraging mode. Out of the studies in Table S6.1, 83% of species of benthic foragers were shown to be highly specialised, while 70% of species with mixed foraging strategies showed moderate degrees of specialisations, and 43% and 36% of species of pelagic foragers showed low and moderate repeatability, respectively. This trend fits well with that observed in the present thesis with benthic Kerguelen shags being the most specialised, Gentoo penguins showing intermediate levels of specialisations and Little penguins exhibiting the lowest behavioural consistency of all three species.

These findings support the notion that ecological opportunity could represent an important driver of the degree of consistency exhibited by populations (Simpfendorfer et al. 2001, Estes et al. 2003, Staniland et al. 2004, Woo et al. 2008, Araújo et al. 2011, Provencher et al. 2013, Kernaléguen et al. 2015a). In Newfoundland, Canada, a sub-polar environment, a single species of guillemot (the Brünnich’s guillemot) exhibits many polymorphisms, each specialising on one or several variety of prey items (Woo et al. 2008). This contrasts with the situation in the High Arctic, an area with low ecological opportunity, where the species preys
on a small diversity of prey items and the within-population variation in trait is low (Falk et al. 2000, Benvenuti et al. 2002, Falk et al. 2002, Woo et al. 2008). Specific techniques that are best suited for certain prey items might be required when prey are diverse and plentiful; this would lead to individuals being restricted in the kind of prey they will exploit as an individual can only master a limited range of techniques (Bolnick et al. 2003, Estes et al. 2003, Newsome et al. 2015). Indeed, individuals that specialise on a single food type form more successful search images, which improves the speed of decision-making, which in turn reduces the risk of predation during foraging (Bernays & Funk 1999, Bolnick et al. 2003).

Lastly, the link between specific foraging strategies and prey types has been established in guillemots for example, in which dive characteristics and foraging metrics correlate with prey type (Elliott et al. 2008, Elliott et al. 2009).

Individual prey preferences can be linked with chance encounter first and then learning how to handle specific prey, which is positively reinforced by foraging success (Estes et al. 2003). Ecological opportunity might work in association with intrinsic factors such as learning capabilities and memory of optimal feeding locations (Montevecchi et al. 2009, Regular et al. 2013), and behaviour to reinforce the degree of individual specialisations (Woo et al. 2008). In this context, benthic foragers could use their memory of seafloor characteristics to return to areas previously visited, and where satisfactory prey have been encountered (Cook et al. 2006, Mattern et al. 2007). This might explain the important differences in the degree of individual specialisations in benthic foragers such as Kerguelen shags (Chapter 2) and in pelagic foragers such as Little penguins, faced with the challenge to find mobile food in the water column (Chapter 5). Interestingly, while dietary information for Little penguins was not obtained for this study, previous studies indicate the species has a low diversity diet (Hobday 1991, Cullen et al. 1992, Chiaradia et al. 2010, Deagle et al. 2010,
Sutton et al. 2015). In contrast, Kerguelen shags have a diversified diet (Chapter 2). Lastly, individual specialisation on specific prey is reinforced by the predictability of resources, which makes it profitable to return to areas where foraging success was enhanced (Davoren et al. 2003, 2010, Ceia et al. 2014b). Species such as Northern gannets have been shown to display strategies involving both general fidelity to foraging sites and flexibility in behaviour and diet over longer time scales to maintain stable populations despite changes in environmental conditions affecting prey availability and diversity (Montevecchi et al. 2009).

**Summary and future directions**

In the present study, I determined the degree of individual specialisations exhibited by three coastal seabird species. I showed that Kerguelen shags, which are benthic foragers, displayed the highest degree of short- and medium-term behavioural consistency and medium- and long-term dietary specialisations. Gentoo penguins, which can both forage pelagically and benthically, displayed lower levels of short-term behavioural consistency, but still exhibited long-term dietary specialisations. Lastly, Little penguins, which are pelagic foragers were shown to exhibit relatively low consistency in short-term foraging metrics, and no consistency on longer timescales (stage-to-stage, clutch-to-clutch or year-to-year). Their behavioural consistency varied with years and breeding stages, potentially as a result of changes in prey abundance and distribution. Analysis of the literature, in conjunction with the results of the present study, suggests extrinsic drivers are more important in determining the degree of individual specialisations displayed in seabird populations than intrinsic factors tested in the present work, although these can reinforce the level of individual consistency through differences in cognitive abilities (learning and memory). I also showed that
individual specialisations and mate choice can be linked, with Kerguelen shag mates displaying significant similarity in foraging strategy and in diet.

As studies increasingly focus on quantifying the degree of individual specialisations exhibited by different populations, it is crucial to develop standardised metrics and analytical methods to use in order to be able to make meaningful comparisons between species and between populations of the same species. More species, covering a wider range of individual morphological and physiological variations, should be included in such studies and researchers should aim at obtaining bigger sample sizes. Arguably, obtaining data on the degree of individual specialisations displayed in the same seabird species in populations that experience differences in ecological opportunity, prey preferences and foraging modes depending on location will help understand the drivers of individual specialisations better. As suggested above, more studies in tropical locations should also be conducted to confirm the existence of a latitudinal gradient in the degree of individual specialisations that seem to be depicted in Table S6.1. Potentially, foraging site (offshore versus inshore) could also influence the degree of individual specialisations, but more data on species displaying offshore foraging is needed to confirm whether that could be the case.

Other processes susceptible of influencing the degree of consistency exhibited by individuals should be investigated (Bolnick et al. 2003). Physiology incurs trade-offs in prey selection that may result in individual specialisations (Bolnick et al. 2003, Araújo et al. 2011). For example, at any given time, an individual might be specialised because its digestive enzyme production suits its current diet, as seen in sparrows (Afik & Karasov 1995). However, this kind of interaction could not be studied in the present thesis. Furthermore, as competitive pressure increases, individuals might be able to switch to novel resources, and the selection on suboptimal resources becomes stronger (Bolnick 2001,
Bolnick et al. 2003), but the influence of such mechanism on the degree of individual specialisations could not be determined in the present study.

To better understand the interplay between individual specialisations and species adaptability in the face of global changes, data also need to be collected on longer timescales, and at different times during the annual cycle. To obtain a better representation of the repercussions of individual specialisations on ecological processes, there is an urgent need to investigate their consequences on reproduction through long-term studies and obtain information on both members of breeding pairs. Results reported in the literature on the consequences of individual specialisations on fitness and reproductive success are fairly rare compared to the number of studies testing the presence of or quantifying individual specialisations. In some instances, either being a specialist altogether or specialising on a specific kind of resource seem to be beneficial and results in improved survival, food delivery rates, and better reproductive output (Pierotti & Annett 1991, Watanuki 1992, Voslamber et al. 1995, Annett & Pierotti 1999, Golet et al. 2000). In other studies, being a generalist or being a specialist seemed equally profitable strategies (Votier et al. 2004, Woo et al. 2008, Ceia et al. 2012). This might be linked with a need to display both individual specialisations and behavioural flexibility at different time scales to cope with environmental changes (Montevecchi et al. 2009). Getting more consistent results, however, might be achieved by obtaining data on both members of pairs, which has rarely been done (Schuett et al. 2010, Schuett et al. 2011). As pair similarity can have important consequences on the reproductive success of pairs (Dingemanse et al. 2004, Elliott et al. 2010, Schuett et al. 2010, Rangassamy et al. 2015, Fayet et al. 2017), researchers should aim at integrating the study of individual specialisations with that of similarity between mates. It is currently unknown whether pair similarity in terms of foraging behaviour, behavioural consistency and diet is common
**Table S6.1** Estimate of individual specialisations in foraging behaviour and/or diet (e.g. var\textsubscript{IND} or proportion of variance explained by the individual variance component, see Bolnick et al. (2003), and Dingemanse and Dochtermann (2013), R or R\textsuperscript{2} correlation coefficient, r repeatability or other measure) gathered from the literature for different seabird populations.

<table>
<thead>
<tr>
<th>Species</th>
<th>Metrics used</th>
<th>Measure of the degree of individual specialisations in the population</th>
<th>Timescales studied</th>
<th>Ecological and dietary information</th>
<th>Study site</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kerguelen shags</td>
<td>Maximum dive depths</td>
<td>var\textsubscript{IND} = 41.7% (males), 85.1% (females) (D)</td>
<td>Short-term measures of individual specialisation (day-to-day), medium-term (MT), and long-term (LT) measures of consistency</td>
<td>Coastal benthic diver, feeds on a variety of benthic fish and invertebrates</td>
<td>Kerguelen Islands</td>
<td>Chapter 2</td>
</tr>
<tr>
<td>Phalacrocorax verrucosus</td>
<td>Total distance travelled</td>
<td>var\textsubscript{IND} = 84.5% (D)</td>
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<td></td>
<td>Heading to most distal point</td>
<td>var\textsubscript{IND} = 72.7% (D)</td>
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<td></td>
<td>δ\textsuperscript{13}C values</td>
<td>90 ± 9% (MT: correlations between incubation and chick-rearing blood isotopic values)</td>
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<td></td>
<td>δ\textsuperscript{15}N values</td>
<td>92 ± 1% (LT: correlations between blood and feather isotopic values)</td>
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<td></td>
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<td>93 ± 6% (MT: correlations between blood and feather isotopic values)</td>
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<tr>
<td><strong>δ^{13}C values</strong></td>
<td>incubation and chick-rearing blood isotopic values) 84 ± 1% (LT: correlations between blood and feather isotopic values)</td>
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<td>Kerguelen Islands</td>
<td>Bearhop et al. (2006)</td>
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<tr>
<td><strong>δ^{15}N values</strong></td>
<td>$R^2 = 0.74$ (LT: correlations between blood and feather isotopic values)</td>
<td></td>
<td>$R^2 = 0.58$ (LT: correlations between blood and feather isotopic values)</td>
<td>long-term (LT) measures of consistency</td>
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<tr>
<td>Crozet shags, <em>Phalacrocorax melanogenis</em></td>
<td>Percentage of consistent individuals in dive depth 75% of individuals showed fixed modal depth</td>
<td></td>
<td></td>
<td>Short-term measure of individual specialisations</td>
<td>Coastal benthic diver, feeds on a variety of benthic fish and invertebrates</td>
<td>Crozet Island</td>
</tr>
<tr>
<td>South Georgia</td>
<td>Maximum dive depths</td>
<td>( \text{var}_{\text{IND}} = 41.5% ) (males), 82.0% (females)</td>
<td>Short-term measures of individual specialisation (day-to-day)</td>
<td>Coastal benthic diver, feeds on a variety of benthic fish and invertebrates</td>
<td>South Georgia</td>
<td>Ratcliffe et al. (2013)</td>
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<td>shag</td>
<td>( \delta^{13} \text{C values} )</td>
<td>( R^2 = 0.32 ) (LT: correlations between blood and feather isotopic values)</td>
<td>( R^2 = 0.41 ) (LT: correlations between blood and feather isotopic values)</td>
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<td>( Phalacrocorax )</td>
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<td>( georgianus )</td>
<td>( \delta^{15} \text{N values} )</td>
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<td>Imperial shag</td>
<td>Trip duration</td>
<td>( \text{var}_{\text{IND}} = 33% ) (D), 55% (S), 28% (Y)</td>
<td>Short-term measures of individual</td>
<td>Coastal benthic diver, feeds mainly on Cusk-</td>
<td>Punta León, Argentina</td>
<td>Harris et al. (2014)</td>
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<td>( Phalacrocorax )</td>
<td>Maximum range</td>
<td>( \text{var}_{\text{IND}} = 91% ) (D), 50% (S), 0% (Y)</td>
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<td>( atriceps )</td>
<td>Maximum distance from the</td>
<td>( \text{var}_{\text{IND}} = 99% ) (D), 43% (S), 25% (Y)</td>
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<td>Shore</td>
<td>Time flying</td>
<td>Time diving</td>
<td>Total dives</td>
<td>Depths of area-restricted search</td>
<td>Specialisation (day-to-day D), medium-term (stage-to-stage S), long-term (year-to-year Y)</td>
<td>Japanese cormorants</td>
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<td>var(_{IND}) = 86% (D), 5% (S), 5% (Y)</td>
<td>eels Raneya brasiliensis</td>
<td>Maximum dive depths</td>
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<tr>
<td><strong>King Cormorants</strong></td>
<td><strong>Phalacrocorax</strong></td>
<td><strong>Dive depth</strong></td>
<td><strong>var$_{IND} = 25.1%$</strong></td>
<td><strong>Short-term measure of individual specialisation</strong></td>
<td><strong>Coastal diver, feeds mainly on benthic fishes</strong></td>
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<td><em>Phalacrocorax albiventer</em></td>
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<td>Macquarie Island</td>
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<td><strong>Northern gannets</strong></td>
<td><strong>$\delta^{13}$C values</strong></td>
<td><strong>$\delta^{15}$C values</strong></td>
<td><strong>$R = 0.46$ (correlation between red blood cells and plasma)</strong></td>
<td><strong>Medium-term measures of repeatability</strong></td>
<td><strong>Coastal plunge-diver, feeds on pelagic fishes and fishery discards with large differences between</strong></td>
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<td><em>Morus bassanuss</em></td>
<td>$\delta^{13}$C values</td>
<td>$\delta^{15}$C values</td>
<td>$R = 0.55$ (correlation between red blood cells and plasma)</td>
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<td>Wales, UK (W)</td>
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<td>Terminal latitude</td>
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<td>$r = 0.54 \pm 0.13$ (W), $0.57 \pm 0.15$ (B)</td>
<td><strong>Short-term measures of</strong></td>
<td></td>
<td>Votier et al. (2010)</td>
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<td></td>
<td>Terminal longitude</td>
<td></td>
<td>$r = 0.53 \pm 0.13$ (W), $0.66 \pm 0.13$ (B)</td>
<td><strong>between</strong></td>
<td></td>
<td>Patrick et al. (2014)</td>
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<tr>
<td>Parameter</td>
<td>Measure (W)</td>
<td>Measure (B)</td>
<td>Repeatability</td>
<td>Repeatability</td>
<td>Individuals in the proportion of discards in diet</td>
<td>Location</td>
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<td>Departure angles</td>
<td>$r = 0.71 \pm 0.09$</td>
<td>$r = 0.55 \pm 0.14$</td>
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<tr>
<td>Trip duration</td>
<td>$r = 0.00 \pm 0.13$</td>
<td>$r = 0.00 \pm 0.07$</td>
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<td>Total distance travelled</td>
<td>$r = 0.06 \pm 0.08$</td>
<td>$r = 0.05 \pm 0.09$</td>
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<tr>
<td>Dive locations</td>
<td>$r = 0.86 \pm 0.10$</td>
<td>$r = 0.84 \pm 0.10$</td>
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<tr>
<td>Environmental conditions at dive locations</td>
<td>Sea-Surface Temperature: $r = 0.06 \pm r =$ 0.14 (W)</td>
<td>Chlorophyll-a concentration: $r = 0.77 \pm 0.15$ (W)</td>
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<tr>
<td>Environment conditions at dive locations</td>
<td>Copepod abundance: $r = 0.76 \pm 0.13$ (W)</td>
<td>$r = 0.18 \pm 0.07$</td>
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<tr>
<td>Maximum dive depths</td>
<td>$r = 0.18 \pm 0.07$</td>
<td>$r = 0.18 \pm 0.08$</td>
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<tr>
<td>Dive shape</td>
<td>$r = 0.18 \pm 0.08$</td>
<td>$r = 0.18 \pm 0.08$</td>
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<td>Maximum distance</td>
<td>$r = 0.789$</td>
<td>$r = 0.789$</td>
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<tr>
<td>Core foraging area / area of active use / total distance</td>
<td>No repeatability on subsequent trip</td>
<td>$r = 0.789$</td>
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</table>

Soanes et al. (2013)
<table>
<thead>
<tr>
<th>travelled / trip duration</th>
<th>Percentage area in core foraging area</th>
<th>Percentage area in area of active use</th>
<th>Fidelity in visited areas</th>
<th>Masked booby <em>Sula dactylatra</em></th>
<th>Trip duration</th>
<th>Maximum distance from colony</th>
<th>Total distance travelled</th>
<th>Short-term measure of overlap</th>
<th>Inshore, surface feeding predator, feeds on pelagic fishes</th>
<th>Ascension Island (AI) and St Helena (SH), South</th>
<th>Oppel et al. (2015)</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>16 ± 5% (67% of birds showed some degree of overlap)</td>
<td>25 ± 3% (100% of birds showed some degree of overlap)</td>
<td>mean overlap for all trips: 12-27% depending on location (ranges: 1-55% and 5-56%)</td>
<td>Trip duration</td>
<td>( r = 0.63 ) (0.46-0.80 AI), ( 0.71 ) (0.62-0.80 SH)</td>
<td>( r = 0.44 ) (0.21-0.66 AI), ( 0.48 ) (0.35-0.61 SH)</td>
<td>( r = 0.52 ) (0.31-0.72 AI), no repeatability (SH)</td>
<td>Short-term measure of overlap</td>
<td>Inshore, surface feeding predator, feeds on pelagic fishes</td>
<td>Ascension Island (AI) and St Helena (SH), South</td>
<td>Oppel et al. (2015)</td>
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<tr>
<td>Heading</td>
<td>$r = 0.69$ (0.55-0.84 AI), no repeatability (SH)</td>
<td>Measure of short- (ST), medium- (MT), and long-term (LT) consistency</td>
<td>Atlantic</td>
<td>Falkland Islands</td>
<td>Golet et al. (2000)</td>
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<td>Thin-billed prion <em>Pachyptila belcheri</em></td>
<td>$\delta^{13}C$ values</td>
<td>$R = 0.82$ (ST: correlation between chick isotope values at 20 and 40 day), MT: no correlation between spring and summer blood isotopic values, LT: no correlation between spring blood and feather isotope values</td>
<td>Offshore predators, feeds on pelagic crustaceans and cephalopods</td>
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<td>$\delta^{15}N$ values</td>
<td>$R = 0.83$ (ST: correlation between chick isotope values at 20 and 40 day), MT: no correlation between spring and summer blood isotopic values, LT: no correlation between spring blood and feather isotope values</td>
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<td>Wandering albatross (Diomedea exulans)</td>
<td>δ¹³C values</td>
<td>43% (ST)</td>
<td>29% (LT)</td>
<td>43%</td>
<td>Proportion of individuals that short-term consistency (ST) and long-term consistency (LT)</td>
<td>Offshore predator, feeds on pelagic fishes, cephalopods, crustaceans, and carrion</td>
<td>South Georgia</td>
<td>Ceia et al. (2012)</td>
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<tr>
<td>Shy albatross (Thalassarche cauta)</td>
<td>percentage overlap (areas revisited) by individual birds on successive foraging trips at: fine-scale (0.05° X 0.05° blocks)</td>
<td>Between 9 ± 5.8% and 14 ± 6.4% depending on breeding stage and year</td>
<td>Short-term measures of spatial overlap</td>
<td>Offshore predator, feeds on surface-schooling prey such as jack mackerel and redbait</td>
<td>Bass Strait, Australia</td>
<td>Hedd et al. (2001)</td>
<td>202</td>
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<tr>
<td>Species</td>
<td>Measurement</td>
<td>Value</td>
<td>Description</td>
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<td>Black-browed albatross</td>
<td>$\delta^{13}$C values</td>
<td>$R = 0.07$</td>
<td>Measure of long-term consistency (correlation between blood and feather)</td>
<td>Falkland Islands</td>
<td>Granadeiro et al. (2014)</td>
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<td>Thalassarche melanophris</td>
<td>$\delta^{15}$N values</td>
<td>$R = 0.06$</td>
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<td>Percentage of birds</td>
<td>5%</td>
<td>Short-term measure of repeatability</td>
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<td>Boldness towards novel object</td>
<td>$r = 0.32 \pm 0.22$</td>
<td>Short-term measure of repeatability</td>
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<td>Foraging personality score</td>
<td>$r = 0.49 \pm 0.07$</td>
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<tr>
<td>Cory’s shearwater</td>
<td>$\delta^{13}$C values</td>
<td>From none to $r = 0.91$ (correlation between red blood cells and plasma)</td>
<td>Medium-term consistency</td>
<td>Berlenga Island,</td>
<td>Ceia et al. (2014b)</td>
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<tr>
<td><strong>Calonectris borealis</strong></td>
<td>( \delta^{15}N ) values</td>
<td>From none to ( r = 0.88 ) (correlation between red blood cells and plasma, values vary between years and stage)</td>
<td>epipelagic fishes and squids</td>
<td>Portugal</td>
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<tr>
<td>Brünnich’s guillemot <em>Uria lomvia</em></td>
<td>Average dive depth</td>
<td>( R^2 = 0.92 ) (D), 0.92 (W), 0.83 (Y)</td>
<td>Correlation coefficients between different temporal scales (day D, week W, year Y)</td>
<td>Coastal diver, feeds on wide variety of pelagic and benthic fishes and invertebrates</td>
<td>Nunavut, Canada</td>
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<td>Flight time</td>
<td>( R^2 = 0.88 ) (D), 0.86 (W), 0.69 (Y)</td>
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<td>Woo et al. (2008)</td>
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<td>Dive shape</td>
<td>( R^2 = 0.72 ) (D), 0.79 (W), 0.68 (Y)</td>
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<td></td>
<td>( \delta^{13}C ) values</td>
<td>( R^2 = 0.46 ) (correlation between plasma isotopic values in 2003 and 2006, Y)</td>
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<td>( \delta^{15}N ) values</td>
<td>( R^2 = 0.75 ) (correlation between plasma isotopic values in 2003 and 2006, Y)</td>
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<td>( \delta^{13}C ) values</td>
<td>( R^2 = 0.08 - 0.12 ) depending on colony</td>
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Woo et al. (2008)
<table>
<thead>
<tr>
<th>Species</th>
<th>Percentage of specialist vs generalist pairs in the population</th>
<th>Short-term measures or proportion of specialist pairs</th>
<th>Inshore opportunistic predator, feeds on fish, crustaceans,</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pigeon guillemot <em>Cephus colomba</em></td>
<td>58.9% specialist (from 39.0 to 76.5% depending on year) vs 41.1% generalist (from 28.1 to 61.1% depending on year)</td>
<td>Coastal diver, feeds on benthic and schooling fishes</td>
<td>Naked Island, Alaska</td>
<td>Golet et al. (2000)</td>
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<td>Yellow-legged gull <em>Larus michahellis</em></td>
<td>$r = 0.49$ (2011), $r = 0.64$ (2012) (correlation between red blood cells and plasma – between prey-laying and incubation)</td>
<td>Medium- and long-term consistency</td>
<td>Berlenga Island, Portugal</td>
<td>Ceia et al. (2014a)</td>
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<tr>
<td></td>
<td>( \delta^{15}N ) values</td>
<td>( \delta^{13}C ) values</td>
<td>refuse and terrestrial invertebrates</td>
<td>Arizaga et al. (2013)</td>
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<td>( r = 0.49 ) (2011), ( r = 0.45 ) (2012) (correlation between P1 and S8 – between summer and the wintering seasons)</td>
<td>( r = 0.87 ) (2011), ( r = 0.57 ) (2012) (correlation between red blood cells and plasma – between prey-laying and incubation)</td>
<td>( r = 0.38 ) (correlations between feathers formed during breeding and during Medium-term consistency)</td>
<td>Northern Spain</td>
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<td></td>
<td><strong>δ^{15}N values</strong></td>
<td><strong>δ^{34}S values</strong></td>
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<tr>
<td></td>
<td>winter) r = 0.54 (correlations between feathers formed during breeding and during winter)</td>
<td>winter) r = 0.38 (correlations between feathers formed during breeding and during winter)</td>
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<thead>
<tr>
<th><strong>Herring gull</strong></th>
<th><strong>Larus argentatus</strong></th>
<th><strong>Percentage of specialist vs generalist pairs</strong></th>
<th><strong>Specialisations over the breeding season</strong></th>
<th><strong>Inshore opportunistic predator, feeds on invertebrates, seabirds, and refuse</strong></th>
<th><strong>Eastern Canada</strong>,Pierotti and Annett (1991)</th>
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<tbody>
<tr>
<td></td>
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<td>44.5% (1977) vs 49.9% (1978) of pair were mussel specialists</td>
<td>Specialisations over the breeding season</td>
<td>Inshore opportunistic predator, feeds on invertebrates, seabirds, and refuse</td>
<td>Eastern Canada</td>
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<td>23.3% (1977) vs 17.3% (1978) of pair were garbage specialists</td>
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<td>8.6% (1977) vs 14.0% (1978) of pair were petrel specialists</td>
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<td>Eastern Canada</td>
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<td></td>
<td></td>
<td>23.6% (1977) vs 18.8% (1978) of pair were generalists</td>
<td></td>
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<td>Pierotti and Annett (1991)</td>
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| Great Skuas  
| *Stercorarius skua*  
| Percentage of specialist vs generalist pairs  
| **δ¹⁵N values**  
| **Hg concentrations**  
| More pairs switched from specialising on mussel, petrel and garbage than remained generalists  
| 20% (1998) vs 17% (1999) seabird specialists  
| 68% (1998) vs 71% (1999) fishery discard specialists  
| 12% (1998) vs 12% (1999) generalists  
| 20% (1998) vs 17% (1999) seabird specialists  
| 68% (1998) vs 71% (1999) fishery discard specialists  
| 12% (1998) vs 12% (1999) generalists  
| 20% (1998) vs 17% (1999) seabird specialists  
| 68% (1998) vs 71% (1999) fishery discard specialists  
| 12% (1998) vs 12% (1999) generalists  
| Specialisations over the breeding season  
| Inshore opportunistic predator, feeds on seabirds and/or fishery discards  
| R = 0.35 - 0.40 depending on location  
| (correlation between blood and feather isotopic values)  
| R = 0.66 (correlation between feather and liver values)  
| R = 0.66 (correlation between feather and liver values)  
| Long-term measure of specialisation  
| Medium- and long-term measure of specialisation  
| Shetland, UK  
| Shetland, Western Isles  
| Shetland  
| Bearhop et al. (2000)  
| Votier et al. (2004)  
| Thompson et al. (1991)  

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<table>
<thead>
<tr>
<th>Gentoo penguins</th>
<th>Bottom dive depths</th>
<th>$R = 0.56$ (correlation between feather and kidney values)</th>
<th>specialisation</th>
<th>Coastal mixed benthic-pelagic diver, feeds on a variety of pelagic and benthic fishes and invertebrates</th>
<th>Carraveri et al. (2013)</th>
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<tr>
<td>Pygoscelis papua</td>
<td>Maximum range</td>
<td>$R = 0.31$ (correlation between feather and muscle values)</td>
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<td>Kerguelen Islands</td>
<td>Chapter 4</td>
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<td>Proportion of pelagic diving</td>
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<td>Heading to most distal point</td>
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<td>$\delta^{13}$C values</td>
<td>var$_{IND} = 4%$</td>
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<td>$\delta^{13}$C values</td>
<td>var$_{IND} = 13.7%$</td>
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<td>$\delta^{15}$N values</td>
<td>var$_{IND} = 51.3%$</td>
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<td></td>
<td>$\delta^{15}$N values</td>
<td>var$_{IND} = 52.9%$</td>
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<td>$\delta^{13}$C values and Hg in feathers</td>
<td>$R = 0.61$</td>
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<td>Short-term measures of individual specialisations (day-to-day), and long-term consistency</td>
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<td>Correlation between $\delta^{13}$C values and Hg in feathers</td>
<td>$67%$ (LT: correlations between blood and feather isotopic values)</td>
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<td>$70%$ (LT: correlations between blood and feather isotopic values)</td>
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<td>Little penguins</td>
<td>Bottom dive depths</td>
<td>Correlation between $\delta^{15}$N values and Hg in feathers</td>
<td>$R = 0.74$</td>
<td>Short-term measures of individual specialisations / No consistency detected over longer timescales (stage-to-stage, clutch-to-clutch, year-to-year)</td>
<td>Coastal pelagic diver, feeds mainly on Clupeiformes</td>
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<tr>
<td><em>Eudyptula minor</em></td>
<td>Maximum range</td>
<td>$\text{var}_{\text{IND}} = 3%$</td>
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<td>Total distance travelled per hour</td>
<td>$\text{var}_{\text{IND}} = 24.7%$</td>
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<td>Heading to most distal point</td>
<td>$\text{var}_{\text{IND}} = 18.9%$</td>
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<td></td>
<td>$\text{var}_{\text{IND}} = 0%$</td>
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<tr>
<td>Species</td>
<td>Percentage of individuals exhibiting foraging site fidelity</td>
<td>Short-term measure of site fidelity</td>
<td>Inshore diver, feeds on pelagic fishes and krill</td>
<td>Antarctica</td>
<td>Authors</td>
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<td>Adélie penguin</td>
<td>62.5%</td>
<td>Inshore diver</td>
<td>Antarctica</td>
<td>Watanuki et al. (2003)</td>
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<td>Pygoscelis adeliae</td>
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<td>King penguin</td>
<td>Maximum distance</td>
<td>Short-term measure of repeatability and overlap (consecutive trips)</td>
<td>Offshore diver, feeds on pelagic myctophid fishes</td>
<td>Falkland Islands</td>
<td>Baylis et al. (2015b)</td>
</tr>
<tr>
<td>A. patagonicus</td>
<td>Trip duration</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Bearing on the outbound portion of the trip</td>
<td></td>
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</tr>
<tr>
<td></td>
<td>Bearing to maximum distance</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Overlap in time spent in an area between consecutive trips</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>No repeatability</td>
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<td>No repeatability</td>
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<tr>
<td></td>
<td>$r = 0.96$</td>
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<tr>
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<td>$r = 0.31$</td>
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<tr>
<td></td>
<td>Mean 25 ± 21% (range 2-73%)</td>
<td></td>
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</tbody>
</table>
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