Growing their Separate Ways: the Ontogeny of Sexual Segregation in Antarctic Fur Seals

Submitted by Kayleigh Ann Jones to the University of Exeter
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I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

Signature:

Abstract

Sexual segregation occurs in a diverse array of taxa in the animal kingdom and has important ecological implications. Several hypotheses have been proposed to explain sexual segregation in adults, including size dimorphism, social behaviour and predation risk, but its initial development remains poorly understood. We aimed to quantify the ontogeny of sexual segregation in Antarctic fur seals, *Arctocephalus gazella* (a highly polygynous and sexually dimorphic species) to investigate the underlying drivers and ecological consequences of this phenomenon. All fieldwork was conducted at Bird Island, South Georgia. Three-hundred pups were sexed within beach and tussock grass habitats annually from 1989 – 2018. Thirty-five pups (19 males and 16 females) were deployed with GPS tags and tracked between December 2012 and April 2013, and 45 juveniles (26 males and 19 females) were deployed with Global Location Sensors (GLS loggers) and tracked between 2007 and 2014. Whiskers were also collected from 40 adults (20 males and 20 females) and stable isotope values were determined along each whisker. Analysis of pup habitat use revealed that males had a higher association with riskier habitats than females, and travelled further at sea toward the end of lactation. Sexual segregation became more pronounced as seals developed, with male juveniles foraging significantly further south than females. Stable isotopes along adult whiskers also indicated that males spent more time foraging south in maritime Antarctica during each annual cycle and that females had two main foraging strategies, with 30 % of females foraging north of the Polar Front and the remainder to the south of it. This sexual segregation likely developed from intense reproductive selection pressures, whereby reproductive success is more varied in males than females, so males prioritise growth (at the expense of increased risk) whereas females prioritise survival. The resulting niche partitioning relaxes competition which elevates population carrying capacity, but also exposes the sexes to different area-specific stressors. Studying the ontogeny of sexual segregation enhances knowledge about selective forces influencing animal behaviour with key implications for ecology, evolution and conservation.

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Author’s Declaration

This thesis was written by Kayleigh A. Jones under the supervision of Dr Iain J. Staniland, Dr Stephen C. Votier and Dr Norman Ratcliffe. A number of collaborations also contributed to this thesis. Fieldwork for chapters 2 – 4 was conducted by British Antarctic Survey scientists and zoological field assistants at Bird Island, South Georgia. Fieldwork for chapter 5 was conducted by Kayleigh A. Jones, Dr Alastair M. M. Baylis and Dr Rachael Orben at Bird Island, Falkland Islands. Dr Simeon Lisovski contributed to GLS logger data processing in Chapter 3. All whisker samples for chapters 4 and 5 were prepared in the British Antarctic Survey laboratory by Kayleigh A. Jones and analysed in the isotope ratio mass spectrometer at the Scottish Universities Environmental Research Centre by Kayleigh A. Jones and Dr Jason Newton.

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Definitions

Central place foraging – returning to the same place (e.g. to provision offspring)

Conspecific – member of the same species

Individual specialisation – individuals using only a subset of resources available to them

Inter-specific competition – competition between species

Intra-specific competition – competition within species

Isotopic niche – an area with stable isotope values as coordinates, broadly indicating the ecological niche

Monomorphic – the sexes have the same size or appearance

Niche hypervolume – niche composed of multiple dimensions

Ontogeny – development as animals grow and age

Ontogenetic niche shifts – shifts in resource use as animals develop

Otariid – member of the eared seal family

Resource partitioning – division of resources

Sexual segregation – differential resource use between the sexes

Stable isotopes – non-radioactive forms of elements with different atomic masses

Sexual size dimorphism – one sex is larger than the other

Polygyny – breeding system whereby males mate with multiple females

Chapter 1. Introduction

1.1. The Importance of Sexual Segregation

Sexual segregation is a widespread phenomenon in the animal kingdom, in which males and females can segregate in space, time, diet and behaviour. Male and female ecological niches may therefore differ so greatly that they better resemble those of separate species (Clutton-Brock et al. 1982; Ruckstuhl & Clutton-Brock 2005). This can have profound implications for ecology. Indeed, sex differences in resource use enables resource partitioning, which can reduce intra-specific competition (Schoener 1986) and consequently elevate population carrying capacity (Tschumy 1982; Johst et al. 2008; Zhao et al. 2014). Sexual segregation can also reduce inter-specific competition, as a subset of a species will be less likely to compete with a subset of another species, allowing conspecifics to co-exist. However, sexual segregation can also expose the sexes to different area-specific stressors (e.g. hunting, fishing, and habitat degradation), which could lead to biased sex ratios and local extinctions (Ruckstuhl & Clutton-Brock 2005). Understanding the causes and consequences of sexual segregation therefore enhances knowledge about selective forces influencing animal behaviour and population dynamics, which is vital to develop effective management plans to conserve species (Ruckstuhl & Clutton-Brock 2005; Rubin & Bleich 2005; Wearmouth & Sims 2008).

1.2. Sex Differences in Reproductive Priorities

Males and females invest differently in reproduction, which forms the basis of sexual selection and life history theories (Hayward & Gillooly 2011). Sexual selection is usually more pronounced in males than females, acting on males to mate with as many females as possible to pass on their genes to the next generation (Darwin 1871; Andersson & Iwasa 1996). Males may produce sperm at a rate that enhances sperm competition (Ginsberg 1989; Moller 1991; Hosken & Ward 2001), whereas females within a range of taxa (invertebrates, reptiles, amphibians, fishes, birds, and mammals) invest 2 – 4 orders of magnitude more energy in producing eggs (Hayward & Gillooly 2011) of an optimal size and at a rate that could enhance lifetime reproductive success (Trivers 1972; Smith & Fretwell 1974). In polygynous species, there is a steeper relationship between mating success and offspring production in males than females, known as the

Bateman gradient (Bateman 1948; Arnold 1994; Andersson & Iwasa 1996; Fig. 1.1.). Gradients are reversed in polyandrous species where sexual selection pressures are stronger in females than males, and gradients will be close to zero in monogamous species that have weak sexual selection pressures (Andersson & Iwasa 1996). The sexes consequently have different reproductive priorities. For example, in most polygynous species and in 95 % of mammals, males prioritise producing many offspring, whereas females prioritise offspring survival and are the sole providers of parental care (Gonzalez-Voyer & Kolm 2010; Trivers 1972). These different reproductive priorities may play important roles in driving sexual segregation.

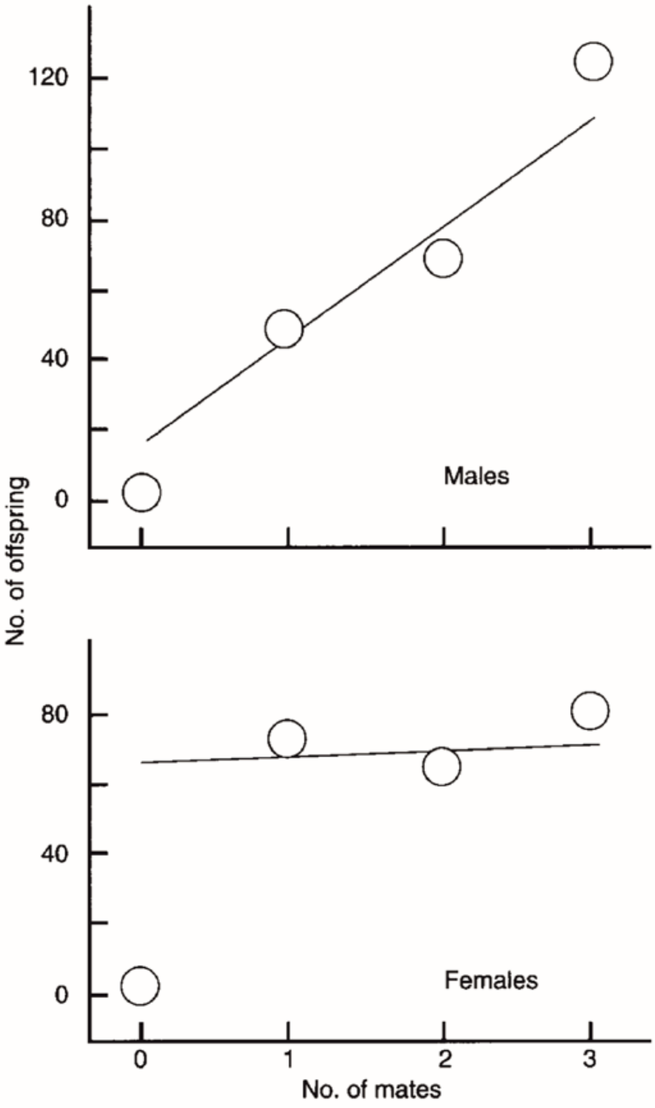

Figure. 1.1. The Bateman gradient (Bateman 1948) for polygynous species: male fecundity increases with the number of females he mates with, whereas female fecundity does not increase if she mates with more than one male. Males hence experience stronger competition for mates (Figure: Andersson & Iwasa 1996).

1.3. Hypotheses for Sexual Segregation

1.3.1. Sexual Size Dimorphism

Several non-mutually exclusive hypotheses have been proposed to explain sexual segregation, which have mostly derived from studies on polygynous species in the adult life stages, particularly ungulates (Ruckstuhl & Neuhaus 2000; Main 2008). Much attention has been devoted to the sexual size dimorphism hypothesis, which states that sexes use different resources as one sex is larger than the other (Main et al. 1996). In mammals, polygyny is the predominant mating strategy (Heyning 2003) and sexual selection favours larger males (Trivers 1972; Isaac 2005), as a large body size (as well as weapons e.g. antlers or large canines) can improve fighting ability to compete for mates and enhance reproductive success (Arak 1988). With a larger body size, males have a larger bite size (Illius & Gordon, 1987) and higher absolute energetic requirements, so may be less selective in their food choices (Beier & McCullough 1990; Staines & Crisp 1978). In contrast, females may require higher quality (i.e. more nutritious) food as a result of their reproductive demands and smaller body size (Stokke & Toit 2000; Conradt 2005). For example, male African elephants, *Loxodonta africana,* consume a greater diversity of plant parts to maximise energy intake by reducing time browsing, whereas females select the most nutritious parts of the plant (Stokke & Toit 2000). However, sexual segregation is apparent in many monomorphic polygynous animals, such as zebras, *Equus burchelli*, South African oryxes, *Oryx gazella* (Ruckstahl & Neuhaus 2001, 2002), and many bat species (Altringham & Senior 2005), as well as some monomorphic monogamous animals such as northern gannets, *Morus bassanus* (Lewis et al. 2002). Assuming that sexual segregation primarily arises from sexual size dimorphism may therefore be over-simplistic (Blundell et al*.* 2002; Mooring et al. 2003) and other hypotheses must be explored.

1.3.2. Predation Risk

The predation risk hypothesis states that the sexes use different habitats owing to costs and benefits associated with predation risk (Ruckstuhl & Neuhaus 2002; Croft et al. 2006). This predation risk hypothesis could also link to the sexual size dimorphism hypothesis as smaller animals are more vulnerable to predation. For example, small females and females with young may be more vulnerable to predation and prefer habitats with lower predation risk, whereas larger males may prefer habitats with greater food availability at the cost of higher predation risk (Ruckstuhl & Neuhaus 2000, 2002). Indeed, female Alaskan moose, *Alces alces gigas*, and their calves use forested regions in summer to reduce predation risk from bears, wolves, and coyotes, *Canis latrans*, whereas males use habitats with greater forage biomass (Miquelle et al. 1992; Oehlers et al. 2011). The opposite occurs in Trinidadian guppies, *Poecilia reticulata*, as females are less vulnerable to predation than males (as males are more colourful and conspicuous; Olendorf et al. 2006) so have a stronger preference for higher risk habitats, which also reduces sexual harassment from males (Croft et al. 2006). The predation-risk hypothesis could therefore apply to a range of different costs and benefits.

1.3.3. Social Behaviour

Sexual segregation can also arise from sex differences in social behaviour, defined as the social roles hypothesis, which relates back to male and female reproductive roles (Pellegrini 2004). Sex-specific behaviours are not limited to the mating season and can occur year-round and influence future reproductive success (Main & Toit 2005). Males tend to be more physically active to evaluate rivals, develop fighting skills, and gain dominance to compete for mates (McCullough, 1989; Beier & McCullough 1990), whereas females tend to be more sedentary as their social roles relate better to protecting and provisioning offspring (Pellegrini et al. 2005). As a result of these different behavioural styles, males and females may prefer to interact in same-sex groups (Maccoby 1998; Bon & Campan 1989), which also benefits their social learning (Appleby 1982, 1983; Villaret & Bon 1995). Females may avoid dangerous behaviour by males (Pellegrini 2004) or segregate from males due to heightened aggression in mixed-sex groups (Ruckstuhl & Clutton-Brock 2005). For example, female Roosevelt elk, *Cervus elaphus roosevelti*, are more aggressive with each other when males are present than when they are absent (Weckerly et al. 2001). Since the sexes have different behaviours and foraging rhythms, they may segregate to synchronise activities (Conradt 1998). For example, red deer, *Cervus elaphus*, live in single-sex groups outside of the mating season, which reduces energetic costs by enabling better spatial coherence of activities, such as foraging and resting (Conradt 1998). Sex differences in social behaviour could therefore be an important driver of sexual segregation.

1.3.4. Disentangling Hypotheses

Hypotheses for sexual segregation are interlinked and are therefore difficult to disentangle. However, attempting to disentangle these hypotheses is important to determine their respective roles (Kernaléguen et al. 2016). Several predictions can be made to test hypotheses separately. If sexual segregation is driven by sexual size dimorphism then the degree of sexual segregation (in space, time, diet and/or behaviour) is predicted to increase as sex differences in body size diverge. If sexual segregation is driven by predation risk then the sex that is more vulnerable to predation is predicted to use safer habitats, while the sex that is less vulnerable to predation will use riskier habitats that offer particular benefits (e.g. greater food availability) (Conradt 2005). If social roles influence sexual segregation, it is predicted that the sexes will differ in their activities (e.g. play-fighting may be more apparent in males) to prepare for their future reproductive roles (Pellegrini 2004). Studying the ontogeny of sexual segregation, i.e. the development of sexual segregation as animals grow and age, provides an excellent opportunity to better understand the underlying mechanisms of sexual segregation (Stewart 1997; Breed et al. 2011; Kernaléguen et al. 2016).

1.4. Ontogeny of Sexual Segregation

Although various hypotheses have been developed to explain sexual segregation in adults, few studies have examined the ontogeny of sexual segregation (Kernaléguen et al. 2016). As animals develop, their energetic requirements and physiological abilities change, which alters functions such as prey handling, digestion capacity and metabolic rate (Claessen & Dieckmann 2002). Animals may adapt to these changes by shifting patterns in their resource use (i.e. selection of food and habitat) in the form of ontogenetic niche shifts (Werner & Gilliam 1984). Ontogenetic niche shifts may differ between the sexes because of their different life history constraints, such as growth rate, age of sexual maturity and breeding mechanisms. For example, males often grow faster than females and become reproductively active later in life (Payne 1979; Clutton-Brock et al. 1985; Georgiadis 1985). The hypotheses for sexual segregation in adults could apply differently to developing animals, as sexual size dimorphism might be minimal and the sexes have no immediate reproductive constraints (i.e. females have no parental responsibilities and males have no territory holding duties).

The ontogeny of sexual segregation and its underlying drivers have been investigated in several species. For example, in squirrel monkeys, *Saimiri sciureus,* sexual segregation is absent in subadults but present in adults, as adult females are socially attracted to each other due to sex differences in social roles (Coe & Rosenblum 1974). In wandering albatrosses, *Diomedea exulans*, fledglings and adult females have lower wing loading than adult males so are better adapted to exploit lighter winds in subtropical and tropical regions, whereas adult males are better adapted to exploit stronger winds of sub-Antarctic and Antarctic regions (Shaffer et al. 2001). In recently weaned grey seal pups, *Halichoerus grypus*, females show greater persistence in foraging activity than males as they develop, potentially adopting a risk-averse strategy by targeting reliable but lower yield foraging areas, whereas males adopt a risk-prone strategy by spending more time seeking the most productive foraging areas to maximise body growth (Carter et al. 2020). This sex difference in grey seal behaviour occurred in Wales but not Scotland, indicating that environmental factors also influence sexual segregation (Carter et al. 2020). Studying the ontogeny of sexual segregation, using methods such as biologging and stable isotope analysis, over an animal's entire life span is valuable to gain further insights into this phenomenon.

1.5. **Methods to Study the Ontogeny of Sexual Segregation**

1.5.1. Biologging

Biologging involves attaching miniaturised tags to animals to record their movements, behaviour, physiology and/or environment (Rutz & Hays 2009). Main tag types for assessing an animal's location include Global Location Sensors (GLS loggers), Platform Terminal Transmitters (PTTs), and Global Positioning System tags (GPS tags). GLS loggers are archival tags that record the sun's light intensity, so latitude can be derived from day length and longitude derived from time of local midday (Wilson et al. 1992, Hill 1994). GLS loggers are advantageous in that they can record data over long time periods (many months or years), however location estimates have high errors (~185 – 200 km on average; Philips et al. 2004; Shaffer et al. 2005). PTTs work by sending radio signals to satellites, so locations can be calculated using the Doppler shift in transmission frequency as PTTs move relative to satellites (Philips et al. 2004). PTTs can transmit data for up to one year (depending on battery life) and error in location estimates range from 2 – 10 km (Boyd & Brightsmith 2013). Since PTT data is relayed from satellites to data receiving stations, animals do not need recapturing to retrieve tag data. Archival GPS tags receive radio signals from GPS satellites orbiting Earth, so locations can be determined by triangulating positions of satellites (Tomkiewicz et al. 2010). Archival GPS tags are often deployed in conjunction with Very High Frequency (VHF) transmitters, enabling the location of the animal to be determined using a VHF receiver so tags can be recovered. GPS battery life typically lasts only 3 weeks – 6 months (Carter et al. 2016), but GPS tags are advantageous in that errors are minimised (usually to less than or equal to 30 m; Tomkiewicz et al. 2010). Additional tags include GPS-GSM tags that transmit GPS data via mobile phone signal (these are ineffective in regions with poor mobile signal) and GPS relay tags that transmit data via the satellite system (but these often have low battery lives, i.e. 3 – 6 months) (Carter et al. 2016). Tag choice is therefore a major consideration in study design involving trade-offs between required accuracy, deployment duration, the likelihood of tag recovery, ethics (potential effects on the study animals) and cost.

To study the ontogeny of sexual segregation tags can be deployed on males and females at progressive life stages (e.g. offspring, juveniles and adults). For example, Zeppelin et al. (2019) compared tracking data from PTTs deployed on northern fur seal, *Callorhinus ursinu*s, pups, juveniles and adults. They found sex differences in juvenile dispersal and habitat use, similar to adults, despite minimal sexual size dimorphism and lack of immediate reproductive costs (Zeppelin et al. 2019). The authors suggested that other drivers may operate, such as sex-specific energetic demands and sex differences in preparations for future reproductive roles, which require further investigation (Zeppelin et al. 2019). Since tags are usually expensive and only provide data over a snap-shot in time (limited by battery life), biologging can be complemented by additional methods, including stable isotope analysis, to reveal a more complete picture on the ontogeny of sexual segregation.

1.5.2. Stable Isotope Analysis

Stable isotope values can be measured from a range of tissues (e.g. blood, bone, feathers, bone, baleen, whiskers) to indicate an animal's resource use. Stable isotope values in part reflect the animal's diet, plus an added trophic discrimination factor (TDF) signifying the offset in stable isotope values between the animal’s tissues and diet due to processes involved in assimilating resources (DeNiro & Epstein 1981; Ben-David & Flaherty 2012). Nitrogen isotope ratios ($^{15}N/^{14}N$ expressed as $\delta^{15}N$) are used as proxies for trophic position, increasing stepwise with each trophic level (DeNiro & Epstein 1981; Kelly 2000; Fig. 1.2.), whereas carbon isotope ratios ($\delta^{13}C$) reflect geographical source of prey. In marine systems, $\delta^{13}C$ values in particulate organic carbon generally decline with increasing latitude (Goericke & Fry 1994; Cherel & Hobson 2007) and tend to be lower in pelagic and offshore regions than benthic and inshore regions (Hobson et al. 1995; Kaehler et al. 2000). Stable isotope ratios can also indicate the niche of an animal, as isotope values can be represented as the ‘isotopic niche’ (Newsome et al. 2007). However, additional processes can alter stable isotope values, such as temporal and spatial changes in baselines (isotope values at the base of the food chain) and physiological processes (such as during fasting and pregnancy). Additional knowledge on the species diet and movements is therefore valuable to reliably interpret stable isotope data.

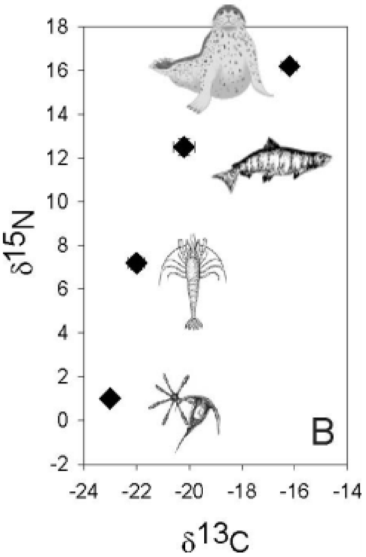

Figure. 1.2. Example of enrichment of stable isotope values with increasing trophic level (Ben-David & Flaherty 2012).

To study the ontogeny of sexual segregation in continuous time, stable isotope values can be analysed along progressively growing tissues to compare male and female life histories (Kernaléguen et al. 2016). Whale baleen and otariid (eared seal) whiskers are ideal tissues to reconstruct life histories as they are composed of keratin (which is metabolically inert so isotope values are fixed at formation) and continuously grow throughout life (Schell et al. 1989; Cherel et al. 2009). By analysing stable isotope values along Antarctic fur seal, *Arctocephalus gazella,* whiskers from Kerguelen, Kernaléguen et al. (2016) found that developing females had a similar isotopic niche to breeding females by age two, whereas male isotopic change changed progressively throughout development. The authors stated that these findings indicate that sexual segregation is not directly driven by sexual size dimorphism or breeding constraints (Kernaléguen et al. 2016). However, further studies are required to determine whether these patterns occur in additional pinniped colonies and to thoroughly investigate the drivers of sexual segregation.

1.6. Sexual Segregation in Pinnipeds

The suborder Pinnipedia (meaning ‘fin-footed’) consists of three families: Phocidae (earless seals), Odobenidae (walruses) and Otariidae (eared seals, i.e. fur seals and sea lions). Almost all species are annual breeders, with females giving birth to one pup per year (Boyd 2000). However, sexual size dimorphism, mating system, reproductive strategy, and lactation length vary substantially among species. Despite this variability, species from all three families have demonstrated sexual segregation in habitat, diving behaviour and/or diet composition (Staniland 2005).

1.6.1. Phocidae

The family Phocidae consists of 18 species, which have a diverse array of mating systems. These mating systems include monogamy (present in most ice-breeding seals), promiscuity (e.g. in monk seals), and polygyny (e.g. in elephant seals) (Staniland 2005). Sexual size dimorphism is minimal in most species and harem sizes range from 1 to 5 females among species (Lindenfors et al. 2002). However, elephant seals are an exception with males weighing up to 7 times heavier than females and harem size generally exceeding 12 females (Lindenfors et al. 2002). Most female phocids are classed as capital breeders, as mothers fast ashore while relying on stored fat reserves to suckle their pups (Houston et al. 2007). Lactation length differs substantially among species, ranging from 4 days in Hooded seals, *Cystophora cristata*, to 2 months in Baikal seals, *Pusa sibircia* (Schulz & Bowen 2004). Given the variability in breeding mechanisms, Phocidae is a useful family to examine the potential influence of breeding strategies on sexual segregation.

Sexual segregation is more apparent in polygynous phocids than promiscuous and monogamous phocids (e.g. Staniland 2005). For example, in the polygynous and highly sexually dimorphic northern elephant seal, *Mirounga angustirostris,* females range widely over deep water and feed on patchily distributed prey, whereas males forage along the continental shelf and feed on benthic prey (Le Boeuf et al. 2000). Additionally, in the polygynous and sexually dimorphic grey seal, juveniles and adult females in Canada mainly feed on pelagic prey, whereas adult males mainly feed on benthic prey, potentially as a result of their larger body size (Tucker et al. 2007). In the polygynous and usually sexually monomorphic Weddell seal, *Leptonychotes weddellii*, males forage closer inshore in shallower water than females in winter, potentially enabling males to improve chances of securing underwater territories for the breeding season (Langley et al. 2018). Sexual segregation has not been documented in several monogamous species, such as crabeater seals, *Lobodon carcinophaga*, bearded seals, *Erignathus barbatus*, or ribbon seals, *Histriophoca fasciata* (Staniland 2005), hinting that polygynous mating systems may play an important role in sexual segregation.

1.6.2. Odobenidae

The family Odobenidae consists of two subspecies: the Pacific walrus, *Odobenus rosmarus divergens*, and the Atlantic walrus, *Odobenus rosmarus rosmarus*. Walruses have a polygynous mating system and demonstrate sexual size dimorphism, with males weighing nearly two times heavier than females and harem size ranging from 5 – 9 females (Lindenfors et al. 2002). Female walruses used a mixed strategy of capital breeding and income breeding, using fat sequestered during pregnancy to support their pup during the first month of lactation, in addition to foraging at sea (Noren et al. 2014) during the ~ 24 month lactation period (Schulz & Bowen 2004). Sexual segregation is evident in Atlantic walruses in the Svalbard region, as males are predominantly distributed in north and south-east Svalbard and females in north-east Svalbard and Franz Josef Land (Gjertz & Wiig 1995). Males also consume a greater proportion of seals than females, leading to higher levels of organochlorine levels in their skin (Wiig et al.

2000). Understanding of the causes of this sexual segregation in walrus distribution and diet is lacking.

1.6.3. Otariidae

Otariids (for which there are 15 species) are ideal candidates to study the ontogeny of sexual segregation as they are highly polygynous and demonstrate the most extreme sexual size dimorphism within vertebrates (Weckerly 1998; Ralls & Mesnick 2002; Staniland 2005). Intense sexual selection pressures act on males to grow large to compete for mates to ultimately maximise their reproductive success (Staniland 2005). Males therefore grow faster than females and attain a larger body size, which is apparent in all otariid species (Weckerley 1998). Species that demonstrate greater sexual size dimorphism generally have larger harem sizes (Lindenfors et al. 2002), with harem sizes ranging from 4 in New Zealand sea lions, *Neophoca cinerea*, to 29 in Cape fur seals, *Arctocephalus pusillus pusillus* (Lindenfors et al. 2002). Female and male otariids also have contrasting reproductive strategies: female otariids are income breeders since they provision offspring using energy obtained by foraging (Houston et al. 2007), whereas dominant male otariids could be classed as capital breeders as they rely on stored reserves while holding territories to gain access to mates (Staniland 2005). Lactation length varies considerably among species, ranging from ~ 4 months in Antarctic fur seals and northern fur seals, up to 18 months in Galapagos fur seals, *Arctocephalus galapagoensis* and South American sea lions, *Otaria flavescens* (Schulz & Bowen 2004). These intense sexual selection pressures, sex-specific growth trajectories, and sex-specific reproductive strategies in otariids may facilitate sexual segregation.

Sexual segregation in habitat, diving behaviour and/or diet has been identified in a range of otariid species in the adult life stage, including New Zealand fur seals, *Arctocephalus forsteri* (Page et al. 2005), South American sea lions (Campagna et al. 2001) and Antarctic fur seals (Staniland & Robinson 2008). The causes of this sexual segregation have been frequently explained by sexual size dimorphism and the constraints of parental care on females (Staniland 2005; Staniland & Robinson 2008; Page et al. 2006). Larger males have greater physiological capabilities, including greater oxygen reserves and lower rates of oxygen consumption (Kooyman 1989), enabling them to dive deeper and handle larger prey more efficiently than smaller females (Staniland 2005). Additionally, during the breeding season, females are the sole providers of parental care, so are limited in their foraging range while suckling their pups, whereas males have no such parental constraints (Staniland 2005). However, during the mating season males may fast while holding territories (Riedman 1990) so are constrained in their foraging movements at this time. Despite these explanations for sexual segregation in adults, the initial development of sexual segregation in otariids remains poorly explored, which is vital to address to better understand the underlying drivers of sexual segregation. To fill this research gap we principally investigate the ontogeny of sexual segregation in Antarctic fur seals – one of the most well-studied otariid species. We additionally explore foraging ecology and potential sex differences in South American fur seals**,** *Arctocephalus australis* – one of the most poorly-studied otariid species.

1.7. Natural History of Antarctic Fur Seals

1.7.1. Distribution and Habitat

Antarctic fur seals were intensively hunted for their fur from the late 18th century until the early 20th century, when the population was driven to the brink of extinction (Bonner 1968; Jefferson et al. 1993). Following conservation concerns, the species was fully protected in 1972 by the Convention for the Conservation of Antarctic Seals (CCAS). The population size then recovered rapidly in the latter half of the 20th century (Boyd 1993) and now approximates 1 million mature individuals (Hofmeyr 2016). Antarctic fur seals are currently listed as ‘Least Concern’ by the International Union for the Conservation of Nature (IUCN) (Hofmeyr 2016).

Antarctic fur seals are now widely distributed south and some areas north of the Polar Front (where cold Antarctic waters meet warmer sub-Antarctic waters) (Bonner 1968). They tend to haul out on rocky shores, but also like sandy beaches and tussock grass (Jefferson et al. 1993). Antarctic fur seals breed at sub-Antarctic and Antarctic islands in the South Atlantic and Indian sectors of the Southern Ocean, and ~ 95 % of the population breed at South Georgia (Forcada & Staniland 2009; Fig. 1.3.). The South Georgia population has been particularly well-studied, especially regarding male territory behaviour, adult female foraging behaviour during lactation, and pup production.

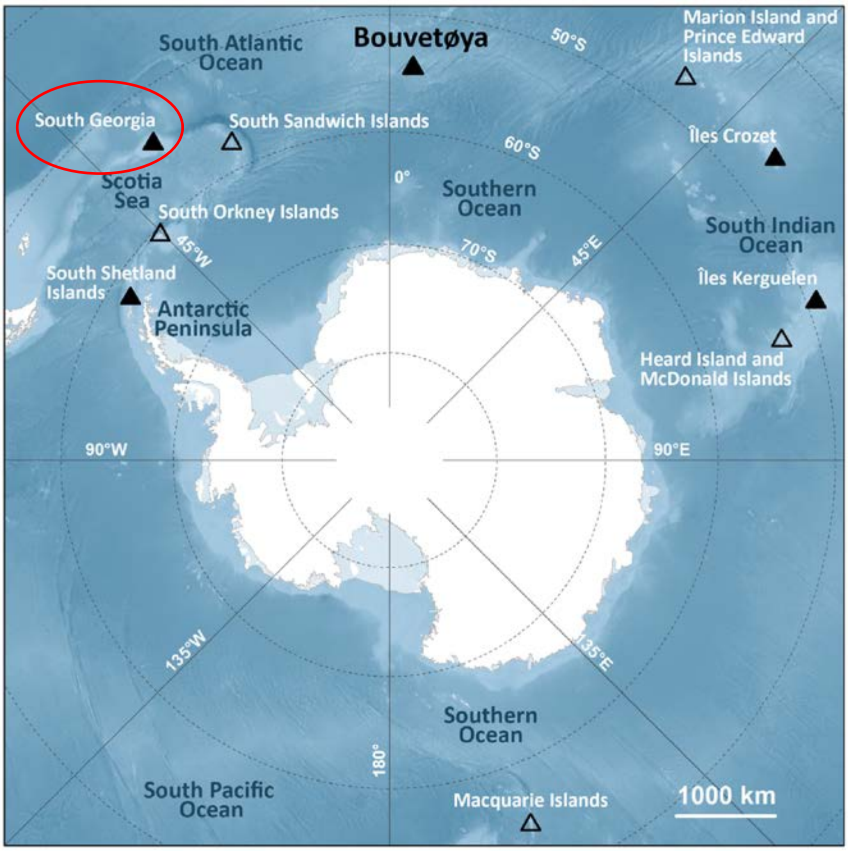

Figure 1.3. Circumpolar distribution of Antarctic fur seal breeding colonies with South Georgia indicated in red (Map modified to highlight South Georgia from Tarroux et al. 2016).

1.7.2. Diet

The Antarctic fur seal diet varies geographically according to different prey assemblages (Forcada & Staniland 2009). Antarctic krill, *Euphausia superba*, dominates the diet in the Atlantic sector of the Southern Ocean, whereas fish are the main prey item in the Indian sector (Forcada & Staniland 2009). However, Antarctic fur seals breeding at South Georgia may switch diets seasonally, indicated by scats on the islands, which contain more fish in winter (mostly mackerel icefish, *Champsocephalus gunnari* and painted notie, *Lepidonotothen larseni*) than summer (Reid 1995). This dietary shift is also apparent in Gentoo penguins, *Pygoscelis papua,* (Williams 1991) and may reflect seasonal variability in krill. Indeed, zooplankton samples collected in waters around South Georgia indicate that krill biomass is lower in winter than summer (Atkinson & Peck 1988). Since the South Georgia Antarctic fur seal population require an estimated 3.84 million tonnes of krill per year (1.85 million tonnes by females and 1.99 million tonnes by males), even with conservative population estimates (Boyd

2002), their krill consumption could have a major impact on the marine ecosystem.

1.7.3. Mating

Selection pressures act on male Antarctic fur seals to grow large to compete for high quality territories, retain them for longer, and increase mating success (Staniland 2005). Adult males are therefore nearly four times heavier than females (133 kg and 34 kg respectively) and 1.5 times longer (180 cm and 129 cm respectively) (Forcada & Staniland 2009) (Fig. 1.4.).

Males establish territories in late October, 2 – 3 weeks before females arrive at breeding beaches (McCann 1980). They acquire and retain territories by vocalising, displaying threat postures, and fighting (Bonner 1968; McCann 1980). They may bite and push each other chest-to-chest, grab and shake their opponents by the fur, or lunge at their opponent's back or fore flippers (McCann 1980). Territories located just above the high water mark are considered higher quality as they attract more females than those at the back of the beach (Staniland 2005). Only the most competitive males will get the chance to reproduce. For example, on a breeding beach at Bird Island, a quarter of pups (out of 600) were fathered by only 12 males (Hoffman et al. 2003), reflecting the intense sexual selection pressure.

Figure 1.4. A large male Antarctic fur seal sat behind a smaller female and her pup, demonstrating the pronounced sexual size dimorphism (Photo: David Vaynor Evans).

1.7.4. Pupping

Adult females are pregnant for about 12 months including 3 months of embryonic diapause, enabling them to give birth around the same time each year in favourable environmental conditions (Boyd 1996). Females have high fidelity to pupping sites (Lunn & Boyd 1991) and give birth from late November to early December, with 90 % of births occurring over a 10 day period (Forcada & Staniland 2009). They mate 6 – 7 days after giving birth (Lunn & Boyd 1991) and may travel through territories to mate with a heterozygous and unrelated bull to increase fitness of their pup (Hoffman et al. 2007). They then alternate foraging at sea for 2 – 10 days with suckling their pup on land for 1 – 4 days until the pup is weaned in April (Staniland & Robinson 2008). This lactation period of 4 months is the shortest among otariids (with that of northern fur seals).

1.7.5. Development

Sexual size dimorphism occurs from birth in Antarctic fur seals, as newborn males are on average 0.5 kg heavier than females (Payne 1979). Pups grow quickly as mothers supply milk to their pups faster than other otariid species (Boyd 1993) and males may grow faster than females when foraging conditions are favourable (Lea et al. 2006; Vargas et al. 2009). As pups develop, the sexes have different growth trajectories: females reach 90 % of their maximum length by age 4, whereas male pups grow at a relatively consistent rate until age 7 (Payne 1979) (Fig. 1.5). Antarctic fur seals become sexually mature at about 4 years of age, but males generally do not establish territories and mate until they are 7 – 8 years old (Payne 1979; Forcada & Staniland 2009). Females live to about 20 years, whereas males only live to an average of 8 years (Forcada and Staniland 2009). The delayed breeding and higher age-specific mortality rate in males is common in sexually dimorphic species that experience intense sexual selection pressures (Trivers 1985).

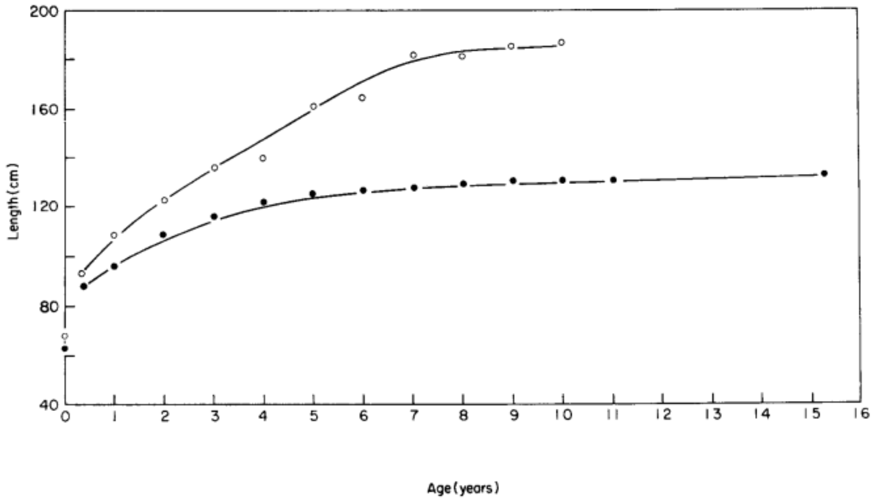

Figure 1.5. Average standard length (nose to tail) of 87 male (open circles) and 284 female (closed circles) Antarctic fur seals at South Georgia from 1972 – 1974 (Payne 1979).

1.8. Sexual Segregation in Antarctic Fur Seals

1.8.1. Pups

Sexual segregation may occur from early life in Antarctic fur seals, as anecdotal observations suggest that male and female pups are more frequently sighted in different habitats. Habitats at Bird Island are cleared delineated as beaches provide open spaces suitable for pup socialisation and learning, water facilitates play in young seals (e.g. Wilson 1974; Wilson and Jones 2018), and tussock grass provides shelter from mortality risks. Mortality risks are high at Bird Island due to predatory seabirds, fighting territorial males and harsh weather conditions (Doidge et al. 1984). Since female pups are smaller than males, they may be more vulnerable to injury and mortality and have a higher preference for safer tussock grass habitats. Sex differences in social behaviour also emerge in pups, as males are engaged in more play-fighting than females (e.g. Gentry 1974; Arnold and Trillmich 1985), which could also contribute to sexual segregation in habitat use. This potential sexual segregation in pups has not yet been quantified, and could offer insights into the initial development and underlying drivers of sexual segregation in general.

1.8.2. Juveniles

Few studies have been conducted on juvenile Antarctic fur seals, so knowledge of any sexual segregation is limited. However, five male and five female weaners were satellite-tracked during their first year of life from Bird Island in 2001 and 2002 respectively (Warren et al. 2006). Both sexes foraged to the east of South Georgia and dispersed away from the continental shelf as winter progressed, but males foraged significantly further from their birth site than females (Fig. 1.6.) (Warren et al. 2006). As juvenile males continue to develop, they may migrate south towards Antarctica as young adult males have been frequently observed at Signy Island and the South Orkney Islands (Waluda et al. 2010). However, there is a considerable gap in knowledge regarding juvenile foraging distributions, as well as extent of sexual segregation and its underlying drivers in this life stage.

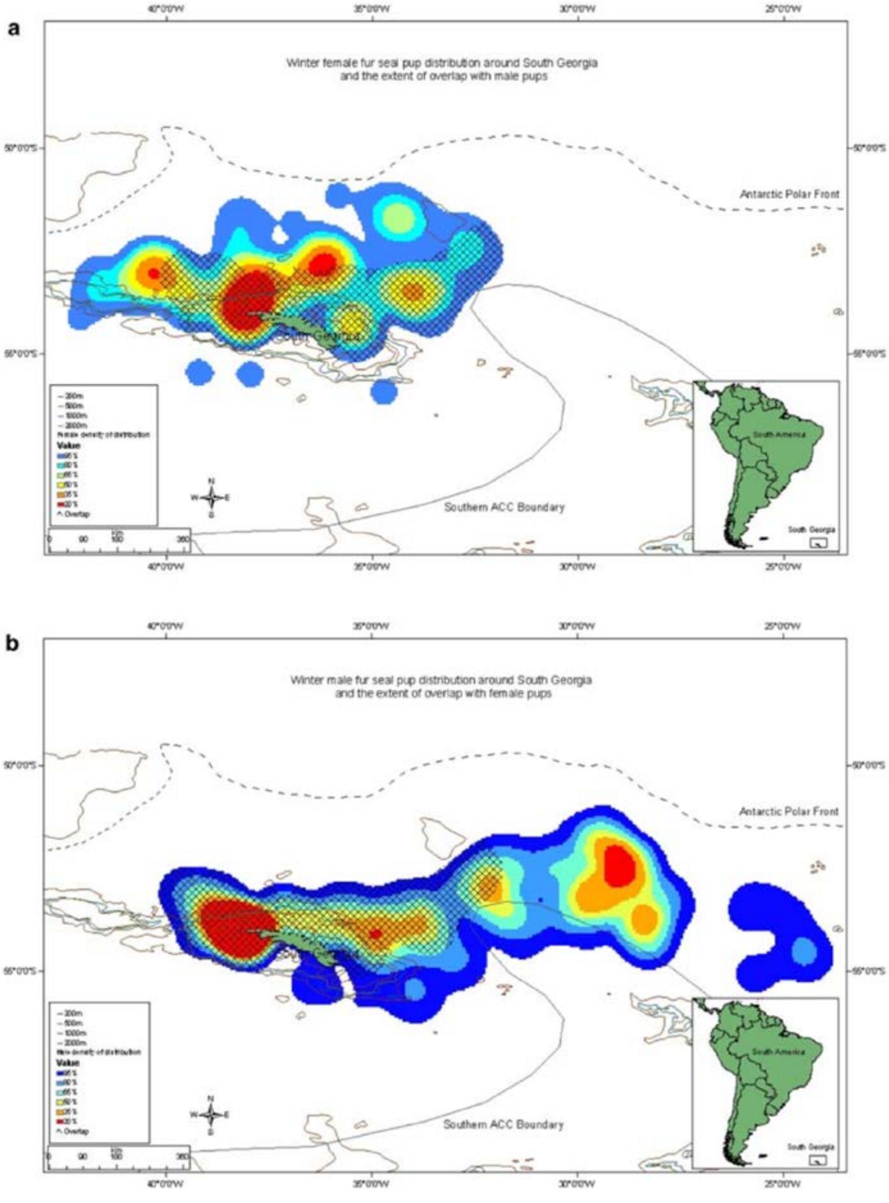

Figure. 1.6. Foraging distributions of (a) five female and (b) five male Antarctic fur seal weaners tracked with Platform Terminal Transmitters (PTTs) during their first year of life from Bird Island, South Georgia (Warren et al. 2006).

1.8.3. Adults

Adult male and female Antarctic fur seals are both present on breeding beaches at South Georgia for about one month during the mating season. At this time, sexual segregation is evident to some degree as males typically dive deeper, closer to the breeding beaches and forage more frequently during the day than females, which dive shallower, further from the breeding beaches and more frequently during the night (Staniland & Robinson 2008; Fig. 1.7.). This sexual segregation may arise from sexual size dimorphism, as larger males have greater diving capabilities than females (Boyd & Croxall 1996). Females may be constrained by the vertical migration of prey in shallow shelf waters, so prefer to exploit krill when it vertically migrates to surface waters at night (Croxall et al. 1985; Staniland et al. 2006), whereas males can exploit deeper prey beyond the limits of female diving abilities (Staniland & Robinson 2008).

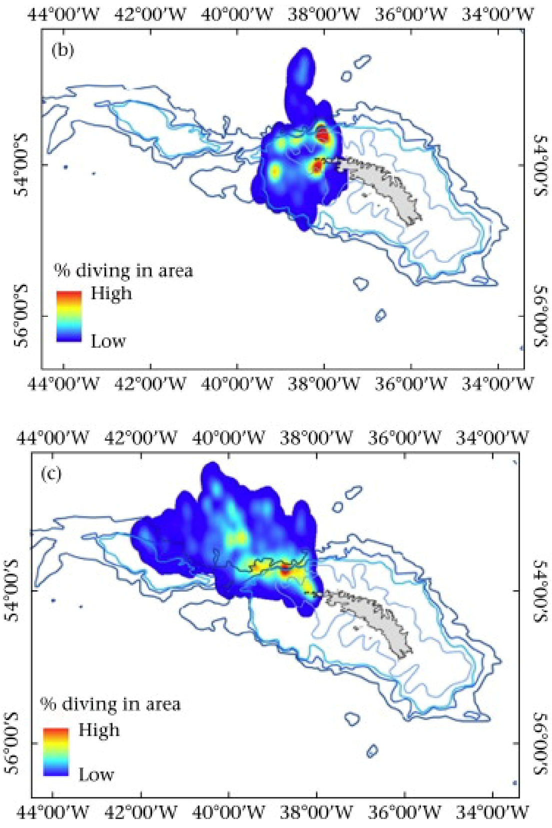

Figure 1.7. Diving locations of (b) 14 males deployed with time depth recorders (TDRs) and satellite tags during November and December 2004 and (c) 41 females deployed with TDRs and satellite tags between December 2003 and February 2004 (Staniland & Robinson 2008).

Sexual segregation may become more pronounced in adults after the mating season. Males depart breeding beaches after most females have been mated in late December (McCann 1980), while females remain in the vicinity of South Georgia to provision their pups (Staniland & Robinson 2008). Few studies have tracked males due to their large size, aggressive nature and unpredictable response to anaesthesia (Staniland & Robinson 2008). However, haul out observations indicate that they migrate south to the Antarctic islands, the Antarctic Peninsula and ice edge (Staniland 2005, Waluda et al 2010; Forcada & Staniland 2009). After weaning their pups in April, females disperse from breeding beaches and remain at sea for almost all of the non-breeding season (Staniland et al. 2012). They either forage in waters around South Georgia or travel thousands of kilometres, as far north as the Patagonian continental shelf or as far south as the Antarctic pack ice (Boyd et al. 2002; Staniland et al. 2012; Arthur et al. 2015; Fig. 1.8.). Gaining further insights into male foraging distributions will be important to quantify sexual segregation, particularly during the non-breeding season.

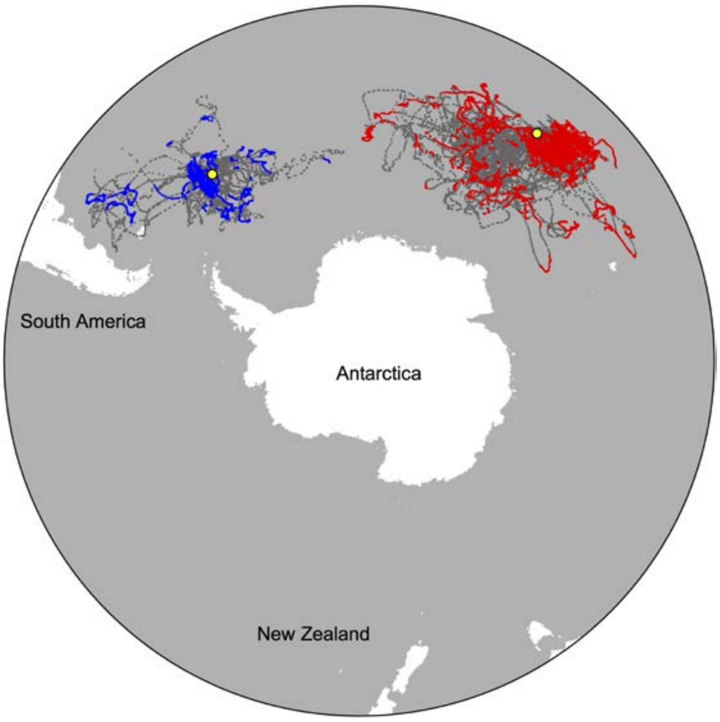

Figure 1.8. Tracks of adult female Antarctic fur seals deployed with GLS loggers during the non-breeding season (April to December 2008 – 2011) from 16 females tracked from Bird Island (blue and grey) and 43 females tracked from Marion Island (red and grey). Red and blue sections represent large-scale foraging behaviour inferred from state space models (Arthur et al. 2015).

1.9. South American Fur Seals

1.9.1. Distribution

South American fur seals are one of the most poorly studied otariid species, despite their extensive range. They breed along rocky coasts and ledges along the Atlantic and Pacific shores of South America, from Peru to southern Brazil, including around the Falkland Islands (Cárdenas-Alayza 2018; Baylis et al. 2019; Iriarte et al. 2020; Fig. 1.9.). The total population size is estimated at ~109,500 mature individuals (Cárdenas-Alayza et al. 2016), with the largest population (36,425 pups counted in 2018) breeding in the Falklands (Baylis et al. 2019). Only a limited number of studies have been conducted on South American fur seals in the Falklands (i.e. Thompson et al. 2003; Laptikhovsky 2009; Baylis et al. 2014; Baylis et al. 2018a; Baylis et al. 2018b; Baylis et al. 2019), so knowledge of their ecology in this region is limited.

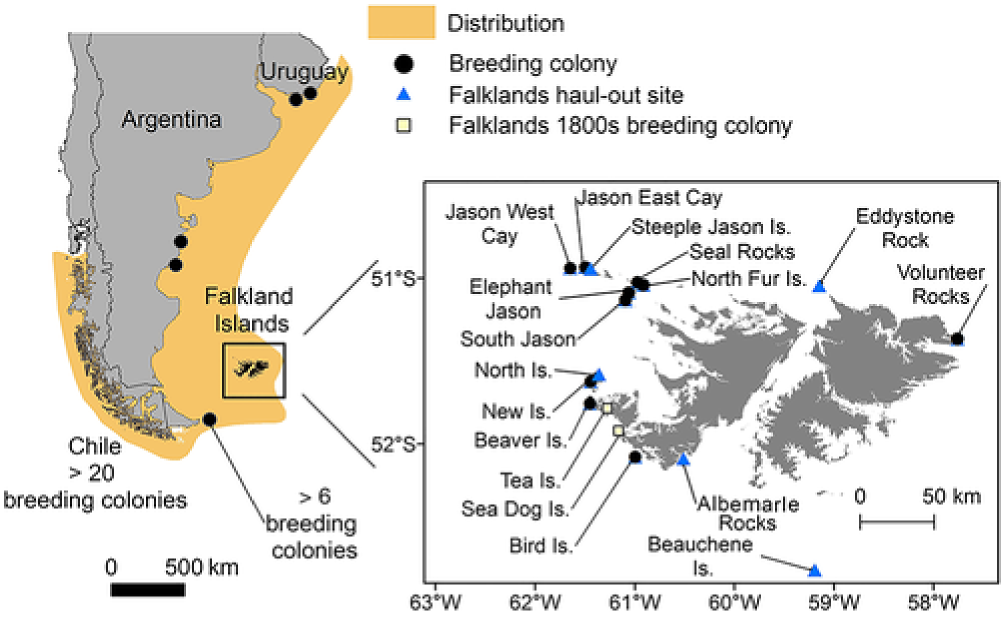

Figure 1.9. Distribution of South American fur seals and their breeding colonies around South America (Baylis et al. 2019).

1.9.2. Breeding Strategy

South American fur seals are polygynous and demonstrate sexual size dimorphism, with adult males measuring 1.3 times longer and 3.3 times heavier than adult females (Cárdenas-Alayza 2018). Adult females are concurrently pregnant during the ~ 10 month lactation period. They therefore incur higher energetic costs of breeding than adult females of otariid species that do not lactate and gestate simultaneously, as they must provide energy to their nursing pup in addition to their growing fetus (Lima & Páez 1995; Fig.1.10.). Adult females are only free from central place breeding constraints for ~ 2 months during the year, differing substantially from adult female Antarctic fur seals.

Figure. 1.10. South American fur seal pup suckling from its mother on a rocky cliff in the Falklands Islands (Photo: Kayleigh Jones).

1.9.3. Maternal Foraging Ecology

Adult female South American fur seals may alter their resource use during pup development from gestation to lactation due to changing pup needs and seasonal changes in prey availability. Previous tracking studies indicate that mothers undertake short foraging trips at the start of lactation when pups may benefit from regular meals, and longer foraging trips towards the end of lactation when pups can withstand longer fasts (Thompson et al. 2003; Fig. 1.11). Individual mothers may also differ in their foraging ecology during gestation and lactation (Rea et al. 2015) due to individual differences in body size, age and experience, which affect diet preference, search efficiency and prey handling ability (Estes et al. 2003; Villegas-Amtmann et al. 2008; Jeglinski et al. 2012; Baylis et al. 2016). Individual pups may also allocate energy differently into their own development, because of their sex, condition and body size (e.g. McDonald et al. 2012a; McDonald et al. 2012b). Investigating changes in maternal resource use throughout pup development, as well as individual differences among mothers and pups, is important to gain new knowledge on South American fur seal ecology.

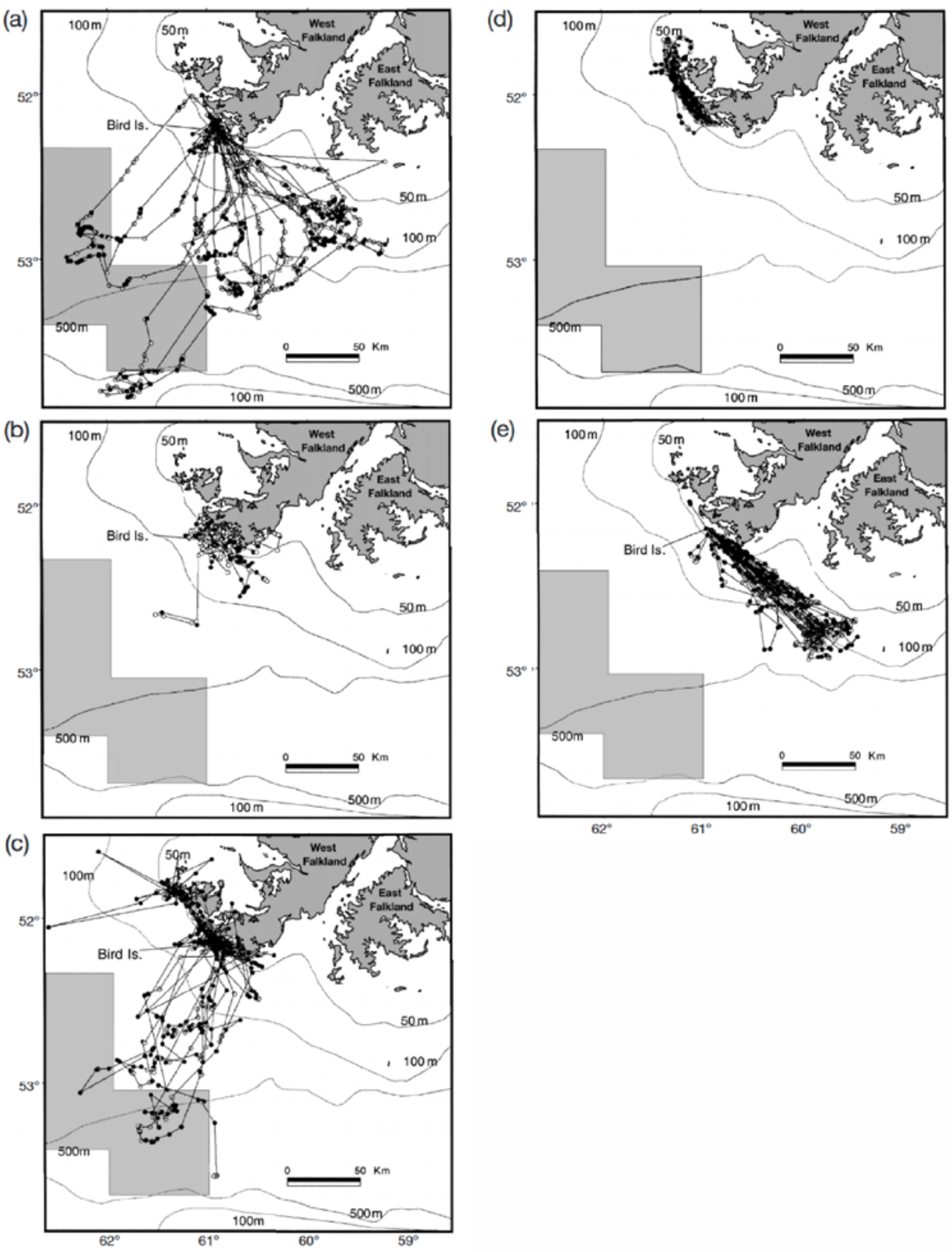

Figure. 1.11. Tracks of 13 adult female and 1 subadult male South American fur seals deployed with satellite transmitters From Bird Island, Falklands, from October 1999 to September 2000: (a) 28 October to 10 January 2000; (b) 28 January to 26 February; (c) 27 February 2000 to late March; (d) 30 April to 31 May 2000. (e) 30 May to 14 September 2000 (Thompson et al. 2003).

1.9.4. Sexual Segregation

Sexual segregation has been documented in South American fur seals in some regions. In Uruguay and Brazil males had higher $\delta^{13}C$ and $\delta^{15}N$ values in their whiskers than females, as they were thought to forage along the southern Brazilian coast where prey are more enriched in ^{13}C (de Lima et al. 2019). Males also had a smaller isotopic niche than females, representing more specialist feeding strategies (de Lima et al. 2019). This sexual segregation may act to reduce intraspecific competition (de Lima et al. 2019). Sexual segregation has not been explicitly identified in the Falkland's South American fur seal population. However, four males and five females were tracked from North Fur Island and four females tracked from Volunteer Rocks from May – December 2015 (Baylis et al. 2018a,b). Males foraged 251 km on average from the island, with mean individual trip duration ranging from 8.6 to 39.2 days (Baylis et al. 2018b). Females from North Fur Island travelled 94 km on average with foraging trips averaging 5.3 days, whereas females from Volunteer Rocks travelled 314 km on average with foraging trips averaging 15.2 days (Baylis et al. 2018a). Female foraging trip distance and duration also increased between May and December, potentially due to changing metabolic requirements or because pups can withstand longer fasts (Baylis et al. 2018a). These findings indicate that the degree of sexual segregation in South American fur seal trip metrics is likely mediated by the local environment and varies among breeding colonies and throughout the year.

1.9.5. Species Comparison

Antarctic fur seals and South American fur seals are closely related otariids but have different characteristics, namely their body size, lactation length, and annual reproductive cycles (Table 1.1.). Sexual segregation and foraging strategies therefore likely manifest differently in these two species.

Table 1.1. Comparison of Antarctic fur seal and South American fur seal characteristics at their largest colonies.

	Antarctic fur seal, ***Arctocephalus gazella***	**South American fur seal,** ***Arctocephalus australis***
Distribution	South Atlantic and Indian sectors of the Southern Ocean	Pacific and Atlantic coasts of South America
Largest colony	South Georgia	Falkland Islands
Common prey species	Antarctic krill, Mackerel icefish, Painted notie	Falkland herring, Patagonian longfin squid, Notothens, Lobster krill
Mean body mass	Adult males 133 kg Adult females 34 kg	Adult males 90 – 160 kg Adult females 60 kg
Lactation length	~ 4 months	~ 10 months
Adult female annual cycle	Give birth late Nov – early Dec Wean April	Give birth Dec Wean Oct
References	Forcada & Staniland 2009	Laptikhovsky 2009; Baylis et al. 2014; Cárdenas-Alayza 2018; Baylis et al. 2019

1.10. Environmental Implications

1.10.1. Climate Change

Climate change can alter predator-prey interactions within marine ecosystems (Draper & Weissburg 2019). The South Atlantic Ocean encompasses an Area of Ecological Significance (AES), where the prey available to marine predators is likely high in diversity and biomass (Hindell et al. 2020). As a result of climate change, sub-Antarctic AESs are projected to expand in area and move southward, meaning some marine predators (particularly central place foragers) may need to use more energy and alter time budgets to forage in regions further afield (Hindell et al. 2020). Changes in the South Atlantic AES is likely to affect the foraging ecology of both South American fur seals and Antarctic fur seals.

The Antarctic Peninsula is one of the fastest warming places worldwide. Here, sea surface temperatures have been rising by ~ 0.54 °C per decade since the 1950s (Turner et al. 2012) and sea ice duration declined by 100 days from 1978 to 2013 (Ducklow et al. 2013). Since larval and juvenile krill depend on sea ice for food and shelter from predation (Constable et al. 2016), low sea ice extent in warm years can reduce krill recruitment (Murphy et al. 2007). Krill availability is also linked to atmospheric variability, particularly the positive Southern Annular Mode (SAM), which has increased in frequency since the early 1990s (Forcada et al. 2008). As a result of these changing conditions, Antarctic krill contracted towards Antarctica between 1926 and 2016 (Atkinson et al. 2019). Changes in krill have already compromised Antarctic fur seal breeding success: numbers of breeding females crashed by 30 % from 2003 – 2012 and fewer pups have been surviving to the end of lactation (Murphy et al. 2007; Forcada & Hoffman 2014). Projections of Antarctic krill also indicate that density will decline in coastal waters around the Western Antarctic Peninsula (Hückstädt et al. 2020). Understanding the requirements of male and female Antarctic fur seals for survival is therefore not only important to gain insights into sexual segregation, but to comprehend the potential impacts of climate change on the species' ecology. The impacts of climate change should not be considered in isolation as other stressors such as fishing pressure and pollution are likely to exacerbate any effects.

1.10.2. Fisheries

Marine predators often co-exist with fisheries, which can lead to competition for prey and incidental mortality in fishing gear. An abundance of fisheries operate in the South Atlantic, mainly targeting finfish and squid (Agnew et al. 2005). South American fur seals have been incidentally caught in a range of fishing gear (including gill nets, bottom-trawlers and long-liners) in Uruguay, Argentina and Chile (Iriarte et al. 2020). In the Falklands, South American fur seals overlap with bottom-trawlers, which led to 137 incidental mortalities during the second Patagonian squid, *Doryteuthis gahi*, season in 2017 (end July – 20 August), prior to effective implementation of Seal Exclusion Devices (Iriarte et al. 2020). Gaining additional knowledge of South American fur seal foraging ecology, in addition to estimating the proportion of Antarctic fur seals that may migrate to this region therefore has relevance for fisheries management.

The Commission for the Conservation of Antarctic Marine Living Resources (CCALMR) manages fisheries in the Southern Ocean and aims to reduce the impact on predator populations. The Antarctic krill fishery is the largest fishery (by tonnage) in the Southern Ocean, catching over 200,000 tonnes per year (Nicol &

Foster 2016). In summer, the fishery is closed at South Georgia to avoid interactions with breeding penguins, flying seabirds and seals, but it still operates further south near Antarctica (Kawaguchi et al. 2009; Nicol et al. 2012). At the start of winter, the fishery operates around the Antarctic Peninsula and South Orkney Islands, potentially overlapping with foraging distributions of adult male Antarctic fur seals that migrate to this region. However, when sea ice advances northward or the fishery reaches its catch limits, vessels operate in waters around South Georgia (outside of the 12 nm no-take zone of the Marine Protected Area). A large proportion of adult females likely remain in the vicinity of South Georgia at this time and may directly compete with the fishery (Staniland et al. 2012). Gaining further knowledge of potential spatial overlap between krill fishing and Antarctic fur seal foraging distributions at progressive life stages is therefore vital to inform ecosystem-based management, particularly in light of recent declines in Antarctic fur seal breeding success.

1.11. Study Aims and Approach

In this study, we ultimately aim to improve understanding of the underlying drivers and ecological consequences of sexual segregation as animals grow and age. By using Antarctic fur seals as an appropriate model species we use a combination of long-term monitoring data, tracking data and stable isotope data to answer three main research questions (Chapters 2 – 4). We additionally aim to improve understanding of South American fur ecology and explore potential sex differences (Chapter 5).

Chapter 2: Is sexual segregation present in pup habitat use?

To explore the influence of sexual size dimorphism, predation risk, and social roles in sexual segregation in early life, we quantify sex differences in habitat use and trip metrics of Antarctic fur seal pups by analysing long-term monitoring data from pups weighed and sexed for over 30 years, as well as GPS data from 35 pups tracked during the 4 month lactation period from Bird Island, South Georgia. We hypothesise that:

(1) Female pups have a higher association with safer habitats than males.

(2) Male pups travel further at sea than females as sexual size dimorphism becomes more pronounced.

(3) The ultimate drivers of any sexual segregation relate back to reproductive roles.

Chapter 3: Where do juveniles forage and is sexual segregation present?

To determine where juvenile Antarctic fur seals forage and whether sexual segregation occurs during a life stage free from immediate reproductive commitments, we analyse GLS logger data from 45 juveniles, estimated as 1 – 3 years of age, tracked from Bird Island, South Georgia. We hypothesise that:

(1) Male juveniles would be larger in body size than females as a result of sexual selection pressures.

(2) Male juveniles use a larger area than females to explore the most productive foraging grounds.

(3) Female juveniles forage closer to the breeding site, as they reach sexual maturity earlier than males.

(4) Any sexual segregation will expose the sexes to different stressors, such as competition with fisheries.

Chapter 4: How does sexual segregation develop and to what extent is it present in adults?

To determine how sexual segregation manifests along a continuous scale in time, and whether it becomes more pronounced as sexual size dimorphism becomes more pronounced, we analyse carbon and nitrogen isotope values along the length of 40 adult Antarctic fur seal whiskers collected at Bird Island, South Georgia. We hypothesise that:

(1) Sex differences in carbon isotope values indicate that males spend more time foraging further south than females.

(2) Ontogenetic niche shifts, reflected in changes in isotopic niches, are more prominent in males than females, as males grow larger and reproduce when they are older.

(3) The ranges of carbon isotope values are greater in females than males, reflecting a wider range of foraging strategies.

(4) Annual patterns in isotope values show consistency in foraging strategies.

Chapter 5: How do stable isotope values change along South American fur seal pup whiskers and how do they differ between sexes and individuals?

To gain insights into foraging ecology of adult female South American fur seals and investigate differences in maternal resource use throughout pup development, between sexes, and among individuals, we analyse stable isotopes along whiskers from 10 South American fur seal pups from Bird Island, Falklands. We aimed to determine:

(1) How stable isotope values change throughout pup development from *in utero* growth to mid-end of lactation
(2) Whether body morphology and stable isotope values differ between the sexes
(3) Whether stable isotope values differ among individuals.

Chapter 6: Conclusion

To improve understanding of the causes and consequences of the ontogeny of sexual segregation we integrate our findings to:

(1) Provide a summary and propose the key drivers for the ontogeny of sexual segregation
(2) Provide a summary on the implications of the ontogeny of sexual segregation
(3) Discuss study limitations and provide recommendations for further research

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Chapter 2. Risk Exposure Trade-offs in the Ontogeny of Sexual Segregation in Antarctic Fur Seal Pups

Short title: Sexual Segregation in Antarctic Fur Seal Pups

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2.1. Abstract

Sexual segregation has important ecological implications, but its initial development in early life stages is poorly understood. We investigated the roles of size dimorphism, social behavior, and predation risk on the ontogeny of sexual segregation in Antarctic fur seal, *Arctocephalus gazella*, pups at South Georgia. Beaches and water provide opportunities for pup social interaction and learning (through play and swimming) but increased risk of injury and death (from other seals, predatory birds, and harsh weather), whereas tussock grass provides shelter from these risks but less developmental opportunities. One hundred pups were sexed and weighed, 50 on the beach and 50 in tussock grass, in January, February, and March annually from 1989 to 2018. Additionally, 19 male and 16 female pups were GPS-tracked during lactation from December 2012. Analysis of pup counts and habitat use of GPS-tracked pups suggested that females had a slightly higher association with tussock grass habitats and males with beach habitats. GPS-tracked pups traveled progressively further at sea as they developed, and males traveled further than females toward the end of lactation. These sex differences may reflect contrasting drivers of pup behavior: males being more risk prone to gain social skills and lean muscle mass and females being more risk averse to improve chances of survival, ultimately driven by their different reproductive roles. We conclude that sex differences in habitat use can develop in a highly polygynous species prior to the onset of major sexual size dimorphism, which hints that these sex differences will increasingly diverge in later life.

Keywords: *behavior; sexual size dimorphism; socialization; habitat use; early-life stages*

2.1.1. Lay Summary

Sexual segregation is common in the animal kingdom, but how it develops is rarely studied. Small sex differences in habitat use occur in Antarctic fur seal pups as males spend more time in riskier habitats than females. Only the “best” males get to reproduce, so they must take risks to gain strength and social skills in preparation for future fights over access to mates. In contrast, females need to prioritize survival and, hence, prefer safer habitats.

2.2. Introduction

Sexual segregation can occur across space, time, diet, and behavior and give rise to resource partitioning, which could reduce intraspecific competition (Schoener 1986). However, such segregation may also expose the sexes to different mortality risks (e.g., from human activities), which could lead to biased sex ratios and cause local extinctions (Ruckstuhl and Clutton-Brock 2005). Understanding how sexual segregation develops and how it relates to sex-specific survival can improve our ability to effectively manage habitats and conserve species (Rubin and Bleich 2005; Ruckstuhl and Clutton-Brock 2005; Wearmouth and Sims 2008).

Sexual segregation has predominantly been studied in the adult life stages of a wide range of taxa, including pinnipeds (Staniland 2005; Wearmouth and Sims 2008). Drivers of sexual segregation in adults are thought to relate to several nonmutually exclusive hypotheses, including size dimorphism, social roles (such as the constraints of parental care), and sensitivity to predation risk (Conradt 2005). However, the initial development of sexual segregation is poorly studied. Investigating the hypotheses for sexual segregation in early life stages could reveal valuable insights as individuals have no reproductive commitments (Salton et al. 2019) and sexual size dimorphism is less pronounced.

Sexual size dimorphism is common in polygynous species, whereby males are usually larger than females (Weckerly 1998). The sexual size dimorphism hypothesis states that the sexes have different energetic requirements as the larger sex has a lower mass-specific metabolic rate and higher digestive efficiency than the smaller sex (Ruckstuhl 2007). This proximate cause of sexual segregation could ultimately be driven by males investing more resources into growth as larger males generally compete for mates more successfully (Isaac 2005), whereas females invest more resources into reproduction (Trivers 1972; Clutton-Brock et al. 1982; Reeve and Fairbairn 2001; Schulte-Hostedde et al. 2001). Although sexual size dimorphism is usually minimal in early life stages, the sexes may differ in body composition and metabolic rate, which could affect their resource use (Arnould et al. 1996; Arnould et al. 2001).

The social roles hypothesis proposes that sexes invest in behaviors to prepare for roles required in their reproductive years (Whiteside et al. 2017). Males are generally more active and physically aggressive to compete for mates, whereas females are more passive and risk averse as their social roles relate to protection and parental care (Pellegrini et al. 2005). This may ultimately be driven by the more variable reproductive success in males than females (Darwin 1871). Early life sex differences in behavior occur in African elephants, *Loxodonta* africana, as females remained closer to their mothers, whereas males engaged in more play with unfamiliar peers (Lee 1986). Male mouflon lambs, *Ovis gmelini*, also demonstrated more sexual and agonistic behaviors than females prior to the onset of sexual size dimorphism (Guilhem et al. 2006). These sex differences may develop in additional species in early life stages.

Animals make decisions reflecting trade-offs between predation risk and energetic and social benefits gained by conducting certain activities (Lima and Dill 1990) or selecting particular patches of habitat (Schoener 1971; Mangel and Clark 1986; Willems and Hill 2009). The predation risk hypothesis states that the more vulnerable sex uses safer habitats under the threat of predation (Croft et al. 2004) as a proximate cause of sexual segregation. Females may favor habitats that maximize the safety of offspring, whereas males select higher-risk habitats to maximize energy reserves and growth rates, which could ultimately improve lifetime reproductive success (Main et al. 1996). For example, female house crickets, *Acheta domesticus*, delayed foraging in the presence of shrew odor, whereas males did not respond to the predation risk (Tanis et al. 2018). During reproduction, female little bustards, *Tetrax tetrax*, selected microhabitats in vegetation that balanced shelter with visibility for predator surveillance, whereas males chose suitable structures to be conspicuous for sexual display (Morales et al. 2008). It is poorly known whether these sex differences in risk avoidance emerge in early life stages.

Pinnipeds are an excellent model for studying the ontogeny (development) of sexual segregation. Most land-breeding species demonstrate striking sexual size dimorphism and polygyny in adulthood (Weckerly 1998; Staniland 2005; Wolf et al. 2005), which are suitable characteristics to explore the size dimorphism and social roles hypotheses. Size and social differences may emerge in male and female pups as pups undergo physical and behavioral changes while transitioning from suckling on land to foraging independently at sea (e.g., Luque et al. 2007). Testing the predation risk hypothesis is also appropriate in early life stages as pups are less able to defend themselves against predators and conspecific aggression (Doidge et al. 1984a). Although juvenile males (hereby, independently weaned individuals) travel further at sea than females in several pinniped species (Warren et al. 2006; Leung et al. 2012; Carter et al. 2017), drivers of this segregation remain poorly understood. However, they may relate to constraints imposed by sex differences in body size (Salton et al. 2019).

Antarctic fur seals are one of the most in-depth studied otariids and adults sexually segregate in foraging distribution (Staniland 2005; Staniland and Robinson 2008). They are highly polygynous, so reproductive success varies substantially among males, which hold harems of 1–27 females at a time (McCann 1980) and will fight to the death to gain access to mates. Only the most competitive males will reproduce; for example, out of 600 pups, a quarter were fathered by only 12 males (Hoffman et al. 2003). The size dimorphism seen in adults occurs from birth as males are (on average) born 0.5 kg heavier than females (Payne 1979) and grow faster than females during the lactation period (Kerley 1985). Socialization is essential in male otariid pups as they frequently play fight (rarely observed in females) and mimic copulatory behavior to prepare for their reproductive roles in later life (Bartholomew 1959; Gentry 1974; Arnold and Trillmich 1985; Warren et al. 2006).

Antarctic fur seal pups must balance trade-offs between developmental needs and exposure to risk. At Bird Island, South Georgia, there is a clear delineation in habitats: beaches, water, and tussock grass. Beaches and water provide opportunities for socialization and learning as the open spaces allow pups to interact and form social groups and water facilitates play in young seals (e.g., Wilson 1974; Wilson and Jones 2018). However, pups are at risk of injury and death from predatory seabirds, fighting territorial males, rebuffs from other seals, and harsh weather conditions (Bartholomew 1959; Doidge et al. 1984a). Areas of tussock grass, *Poa flabellata*, are elevated, densely vegetated regions that provide shelter from these risks but fewer opportunities for social interaction. Indeed, mothers preferentially suckle in safer less disturbed areas of the tussock grass as soon as the pup is physically capable of completing the journey from the pupping beach (Doidge et al. 1984a).

During the 4-month lactation period, mothers alternate foraging at sea (2–11 days) with suckling their pups ashore (1–2 days) (Forcada and Staniland 2009), so pups are alone for the majority of this time. This represents one of the shortest lactation periods among otariids, during which pups must not only grow but also acquire a range of skills to maximize their chances of surviving and breeding in future. There have been few studies on Antarctic fur seal pups other than those related to their growth (Doidge et al. 1984b; Lunn et al. 1993) and acquisition of diving skills (McCafferty et al. 1998), so the development of their behavior and any differences between the sexes are currently unknown.

We studied the habitat use of preweaned Antarctic fur seal pups to test hypotheses for the ontogeny of sexual segregation in early life stages. Using movement data from pups tracked using GPS loggers and counts of pups found on the beach and in the tussock grass, we hypothesized that: 1) female pups have a higher association with tussock grass areas than males as they are more risk averse; 2) male pups travel further at sea than females toward the end of lactation as sexual size dimorphism becomes more pronounced; and 3) the ultimate drivers of this sexual segregation relate back to male and female reproductive roles.

2.3. Methods

2.3.1. Ethical Statement

The procedures in this study were reviewed and approved by the British Antarctic Survey Animal Ethics and Welfare Review Body (AWERB). Procedures adhered to Association for the Study of Animal Behaviour (ASAB) guidelines, Animal Research: Reporting of In Vivo Experiments (ARRIVE) guidelines, and legal requirements of the South Georgia Government. The behavioral response of pups was predictable (based on on-going pup monitoring at the colony) and no pups were injured during handling procedures. It should be noted that the mortality rate of GPS-tracked pups was less than the population average during the study period.

2.3.2. Population-level Sex Differences

Antarctic fur seal pups were captured annually at Main Bay, Bird Island, South Georgia (54.010° S, 38.059° W), as part of a long-term monitoring program. One hundred pups were selected (by convenience sampling), 50 on the beach and 50 in the tussock grass, each month in January, February, and March annually from 1989 to 2018. Each pup was captured by hand, measured, sexed (by examination of genitalia), and weighed to the nearest 100 g (using a hand-held spring balance).

2.3.3. Individual-level Sex Differences

Thirty-five Antarctic fur seal pups, 19 males and 16 females, were GPS-tracked from the beach habitat at Freshwater beach, Bird Island, South Georgia (54.009° S, 38.052° W) between December 2012 and April 2013. To identify individuals, Dalton jumbo roto ID tags were attached to each pup's fore flippers. Pups were sexed, measured, weighed, and equipped with a GPS logger (i-gotU GT-600; 37 g; 46 × 41.5 × 14 mm) and a radio transmitter (Sirtrack V2G-152A; 16 g, 40 × 20 × 10 mm; Figure 2.1). The radio transmitter was glued with quick-set epoxy resin onto the fur on each pup's lower back on the central dorsal line. A rectangle of mesh fabric (40 × 20 mm) was glued between the scapula, and GPS loggers were fixed with cable ties to this mesh, allowing the easy interchange of units when their battery charge had depleted (after ~13 days). GPS loggers were programmed to record locations every 5 min and pups were recaptured and weighed every 3.74 ± 0.076 days until the pups weaned or died. GPS loggers and radio transmitters attached to weaned pups would have detached from their fur during the next molt.

Figure 2.1. Antarctic fur seal pup deployed with a GPS logger on the upper back, radio transmitter on the lower back and ID tag on the right fore flipper at Bird Island, South Georgia (Photo: Hannah Wood).

2.3.3.1. GPS Data Processing

Speed and distance thresholds for each pup were obtained using the 99th percentiles found by the distSpeed function in the diveMove package (Luque 2017) in the software R (R Core Team 2017). These thresholds were used in a speed filter (based on Austin et al. 2003) that removes erroneous locations in a three-stage process as described by Staniland et al. (2012). We then used Correlated Random Walk Library (CRAWL) (Johnson 2017) to fit a state-space model to the data to account for uncertainty in GPS fixes (Johnson et al. 2008) and estimate locations evenly spaced in time (every 5 min). Gaps in data (caused by loss of battery life prior to tag change) were taken into account by removing specified sections of time. Since GPS signals could not be received effectively in water, best-fit tracks sometimes indicated that pups moved over substantial headlands, when they had evidently swum around land. In these cases, tracks were adjusted to prevent implausible movements and CRAWL was rerun to represent the best-fit tracks more accurately. Pups that suffered premature mortality (mostly caused by starvation at the beginning of the lactation period) were not included in analyses as the duration of tracking was short.

2.3.4. Data Analysis

2.3.4.1. Pup Growth

On a population level, to test whether pup growth significantly differed between the sexes with month (indicating stage of pup development), location (beach and tussock grass habitats), and year (to determine any long-term trends from 1989 to 2018) in monitored pups at Bird Island, we used average pup mass as the response variable in a general linear model (GLM). We also tested whether growth rates differed between male and female pups (from January to March) in years when environmental conditions were good and poor in a GLM using gentoo penguin, *Pygoscelis papua*, breeding success (ratio of chicks to nests) at Bird Island (1989–2018) as an indicator of krill availability. Gentoo penguin breeding success was chosen as an appropriate indicator as it is highly sensitive and positively correlated with the proportion of krill in the diet (Waluda et al. 2017), and krill dominates the diet of Antarctic fur seals in the South Atlantic (Forcada and Staniland 2009).

On an individual level, to determine the general trend in mass of male and female GPS-tracked pups with age during the 2012–2013 breeding season, we used pup mass as the response variable in a generalized additive mixed model (GAMM; suitable for nonlinear relationships) using the mgcv package in R (Wood 2017). We specifically used a Gaussian error family and identity link function, with age nested within pup ID as a random factor to account for individual variability. To obtain more accurate mass estimates related to each pup's growth (and not the meal mass of milk consumed), we fitted a generalized additive model to the mass data for each individual pup to smooth regular fluctuations in mass according to whether pups had suckled. We, then, extracted the modeled mass each day for each individual pup, which we used as an explanatory variable (for pup growth) in further analyses.

2.3.4.2. Pup Habitat Use

To test for sexual segregation in pups between beach and tussock grass habitats at the population level, as well as determine any changes in sexual segregation between months and years, we analyzed the pup monitoring data using sex ratio as the response variable in a generalized linear model with a binomial error and logit link function.

To investigate sexual segregation in habitat use at the individual level, we tested whether sex differences occurred between GPS-tracked pups with age and mass using a simplified habitat classification (tussock grass or other) based on multispectral light wavelengths from an aerial image of Bird Island overlaid with the best-fit tracks. For each pup, we determined the proportion of time that pups spent in the tussock grass each day, which we used as the response variable in a GAMM using the mgcv package in R (Wood 2017). We used a Beta error family (suitable for continuous proportional data bounded by 0 and 1; Thomas et al. 2017) and we specified pup ID as a random effect to account for individual variability. Because pup habitat use during the early lactation period is heavily influenced by the mother, the analysis was divided into two sections based on pup ages, that is, 20–40 days (when mothers suckled their pup on the pupping beach) and 41–120 days (when all mothers had led their pup to a new suckling location in the tussock grass). We used 120 days of age as the cutoff point to reduce bias in the analysis because six males and only two females were tracked after this age.

2.3.4.3. Pup Trips at Sea

GPS-tracked pup movements were classed as “trips” if pups ventured at sea further than 300 m away from the mean coordinate of all pup GPS locations (located near the pupping beach). Start and end times of trips were determined according to when pups had left and returned to the pupping beach using the “TimeManager” plug-in (Graser and Alexiou 2011) in QGIS (QGIS Development Team 2017). We calculated the duration and maximum distance traveled from the pupping beach for each trip. Trip metrics were only analyzed for trips taken up to 120 days of age.

GAMMs, implemented using mgcv, were used to test whether the trip distance and trip duration significantly differed between sexes with age and mass. The trip number was nested within pup ID as a random effect to account for deviance among repeated trips made by the same individuals. The maximum trip distance traveled was log transformed to improve model fit. To determine whether the proportion of time that trips occurred at night differed between sexes with age and mass, we assigned each observation to day time or night time (according to sunrise and sunset times) and, then, used a GAMM with a Beta error family and specified pup trip number nested within trip ID as a random effect.

For each analysis, we used Akaike information criterion (AIC) to assess model uncertainty by comparing competing models (Symonds and Moussalli 2011). We included all possible interaction terms in candidate models, including tensor product interactions in GAMMs (Wood 2017). We selected the best-fit model for each analysis according to the lowest AIC. If best-fit models differed by only two AIC, we selected the simplest model with all explanatory variables significantly associated with the response variable. Best-fit models were also checked using the dredge function in the MuMIn package in R, which ranks all candidate models by their fit (Barton 2017). All means are reported with one standard error unless otherwise stated.

2.3.5. Data Overview

2.3.5.1. Pup Monitoring

The sample size for the number of data points for sex ratios of pups during the monitoring period was 180, accounting for the sex ratio in beach and tussock grass habitats over 3 months each year for 30 years (1989–2018). The sample size for the number of data points for average pup mass during the monitoring period was 360, accounting for average pup mass of males and females in each habitat over 3 months for 30 years (1989–2018).

2.3.5.2. Pup Tracking

Thirty-five pups (16 females and 19 males) were GPS-tracked but six pups died during the study period (Supplementary Table S2.1a). This mortality rate of 17.1% was lower than the overall pup mortality rate at Bird Island (23.3%) during the 2012–2013 pupping season. A sample size of 29 pups (13 females and 16 males that survived; Supplementary Table S2.1b) was, therefore, used in the analyses. This included 24 pups (10 females and 14 males) tracked between 20 and 40 days of age and all 29 pups tracked between 41 and 120 days of age.

2.4. Results

2.4.1. Sex Differences in Growth

2.4.1.1. Pup Monitoring

Mass of monitored pups was significantly associated with the interaction between sex, habitat and month, and with year (GLM: adjusted $R^2 = 0.79$, $F_{8, 351} = 170.3$, $P < 0.0001$; sex:habitat:month $F_{2, 351} = 4.3$, $P = 0.01$; year $F_{1, 351} = 52.9$, $P < 0.0001$; Supplementary Table S2.2). Specifically, male pups were heavier than females, pups weighed in the tussock grass (where their mass was affected by meal mass of milk consumed) were heavier than those weighed on the beach, and pups gained mass as they developed from January to March (Figure 2.2.). Sexual size dimorphism became more pronounced as pups developed: on average, males were 0.87, 1.37, and 1.78 kg heavier than females in January, February, and March, respectively. Pup mass of both sexes generally declined by 1.44 ± 0.15 kg from 1989 to 2018. Sex was an important factor in the model as the difference in AIC between the best-fit model and candidate model excluding sex was 113.7.

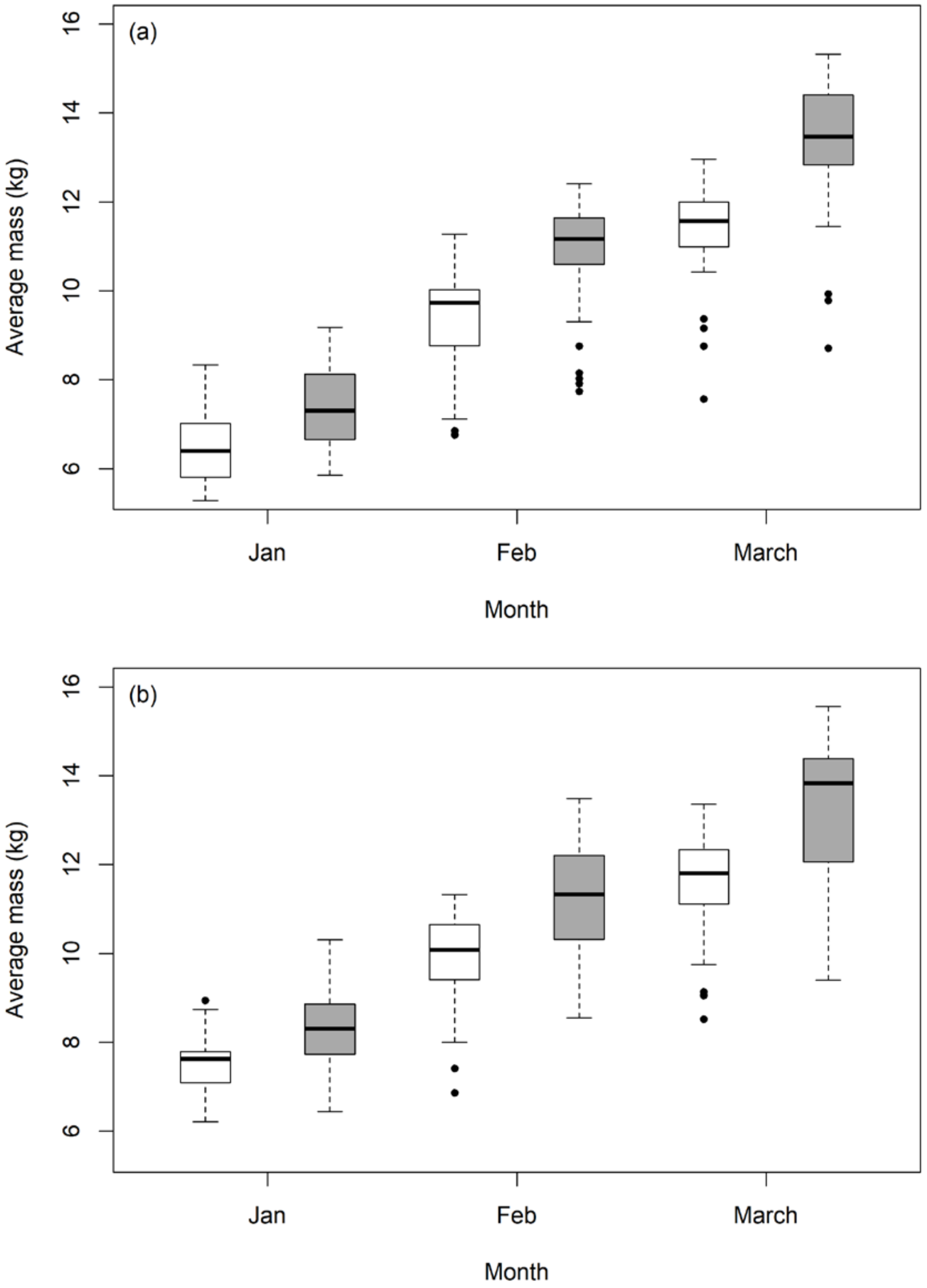

Figure 2.2. Boxplots showing the mass of female (white) and male Antarctic fur seal pups (grey) on the beach (a) and in the tussock grass (b) from long-term monitoring at Bird Island, South Georgia: 100 pups were selected, sexed and weighed, 50 on the beach and 50 in tussock grass, each month in January, February and March each year from 1989 – 2018 (sample size of 360 data points for average pup mass in total). Bold lines are the median values, boxes gives the interquartile range (IQR) and whiskers give 1.5*IQR.

Pup mass each month was significantly associated with sex and gentoo penguin breeding success (used as an indicator of food availability; GLM: adjusted R^2 = 0.80, $F_{6,\ 353}$ = 240.6, P < 0.0001; sex:month:gentoo breeding success $F_{2,\ 353}$ = 3.7, P = 0.03; Supplementary Table S2.3). In years when environmental conditions were inferred as good (gentoo penguin breeding success = 1.6 chicks on average per nest), males grew faster than females and were 2.23 ± 0.22 kg heavier than females by March (Supplementary Figure S2.4). In years when environmental conditions were inferred as poor (gentoo penguin breeding success = 0 chicks on average per nest), males were only 1.25 ± 0.22 kg heavier than females by March (Supplementary Figure S2.4). The difference in AIC between the best-fit model and candidate model excluding gentoo penguin breeding success was 84.3.

2.4.1.2. Pup Tracking

In GPS-tracked pups, mass ranged from 3.6 to 13.8 kg in females and 3.8 to 16.5 kg in males. Mass gain was significantly associated with sex and age (GAMM: R^2 = 0.56, sex and s[age] $F_{7.1,\ 873.9}$ = 343.3, P < 0.0001; Supplementary Table S2.5). Male pups remained 0.71 kg heavier than female pups on average, but the trend in mass was the same for both sexes: pups gained mass at an average of 0.04 kg/day between 0 and 100 days of age and lost mass thereafter at 0.05 kg/day (Figure 2.3). The difference in AIC between the best-fit and second best-fit model (which excluded sex) was 2.3.

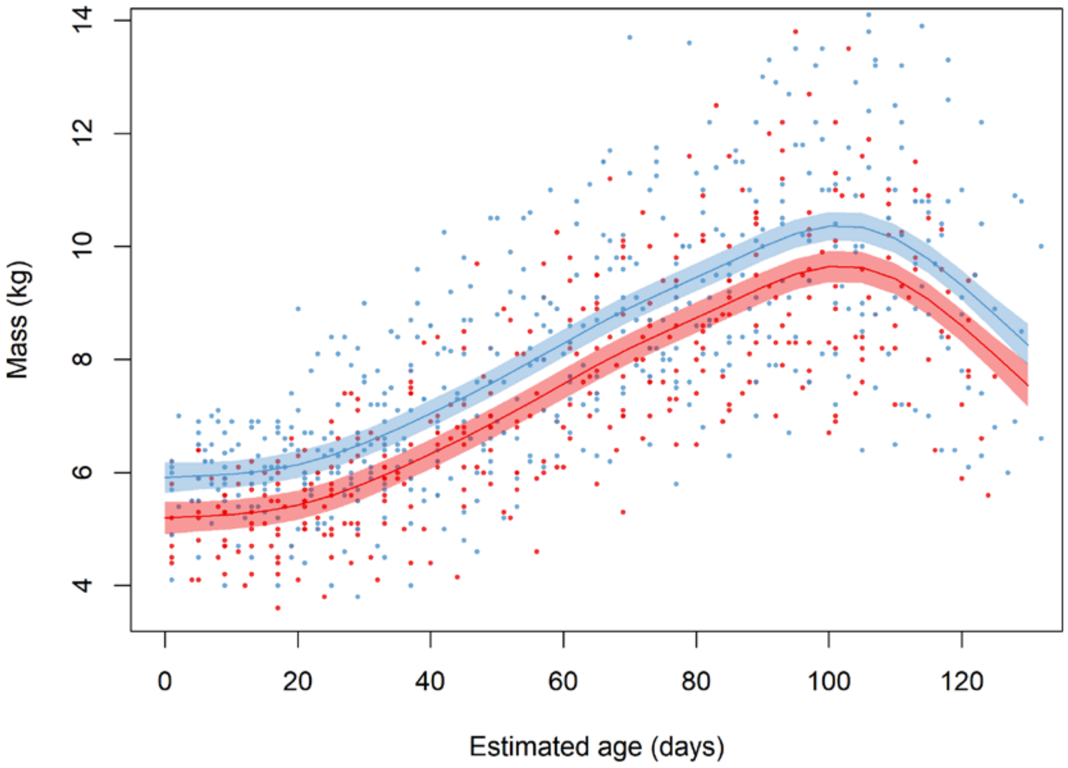

Figure 2.3. Generalized Additive Mixed Model showing the general trend in mass of 16 male (blue) and 13 female (red) GPS-tracked Antarctic fur seal pups with estimated age between December 2012 and April 2013. Points indicate pup mass at each individual weighing, lines indicate modelled averages and shaded areas indicate standard error.

2.4.2. Sex Differences in Habitat Use

2.4.2.1. Pup Monitoring

Sex differences in habitat use were apparent in monitored pups at Bird Island during 1989–2018. Proportion of male to female pups was significantly associated with habitat, month, and year (generalized linear model: pseudo R^2 = 0.18, $F_{3, 176}$ = 0.82, P = 0.49; habitat $P < 0.0001$, month $P = 0.04$, year $P < 0.001$; Supplementary Table S2.6). Addressing each factor, males were more likely to occur on the beach than females (mean proportion of males to females ± SE = 0.52 ± 0.01) and females were more likely to occur in the tussock grass than males (mean proportion of males to females ± SE = 0.46 ± 0.01). Proportion of males to females marginally increased in both habitats from 0.48 ± 0.01 in January to 0.50 ± 0.01 in March (Figure 2.4). Proportion of males to females also significantly increased over the study period from a mean ratio of 0.46 ± 0.01 in 1989 to 0.52 ± 0.01 in 2018. The second best-fit model (within two AIC of the selected model) included the same explanatory variables as the best-fit model but also included an interaction between month and year (which had no significant effect).

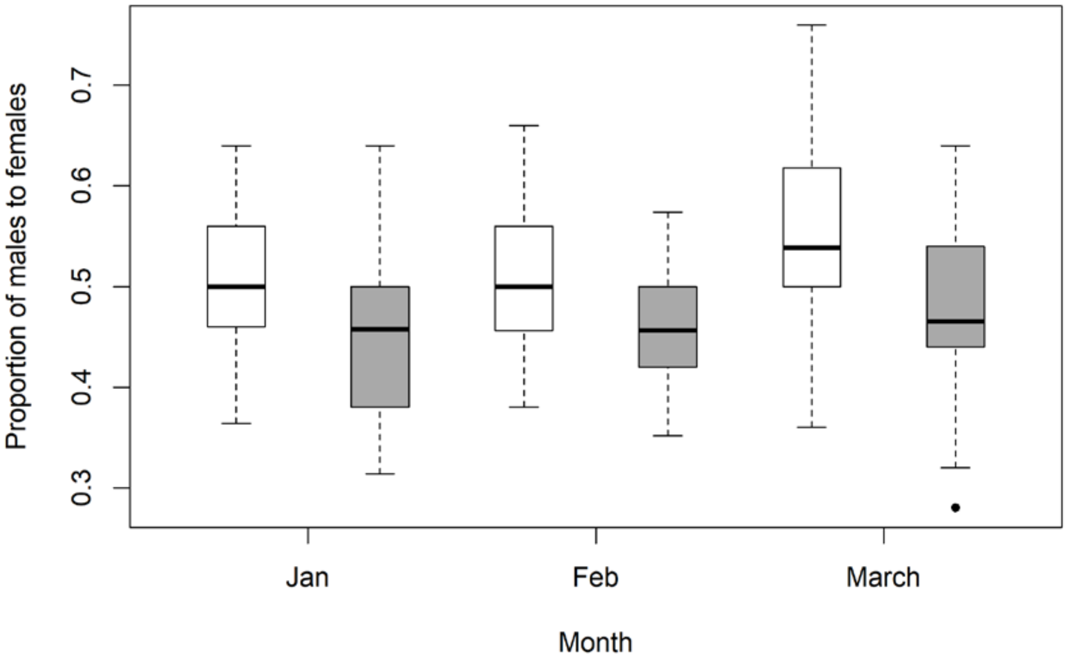

Figure 2.4. Boxplot showing the proportion of male to female Antarctic fur seal pups on the beach (white) and in the tussock grass (grey) during long-term monitoring at Bird Island, South Georgia: 100 pups were selected, sexed and weighed, 50 on the beach and 50 in tussock grass, each month in January, February and March each year from 1989 – 2018 (sample size of 180 data points for sex ratios in total). Bold lines are the median values, boxes gives the interquartile range (IQR) and whiskers give 1.5*IQR.

2.4.2.2. Pup Tracking

From 20 to 40 days of age, 24 GPS-tracked pups (5 out of 29 pups were not tracked over this time) spent a progressively higher proportion of time in the tussock grass and the best-fit model indicated no significant difference between the sexes (GAMM: $R^2 = 0.26$, s[age] $F_{2.5,\ 313.5} = 64.3$, $P < 0.0001$; Supplementary Table S2.7). Pups spent an average of 3.4 ± 1.4% of time in the tussock grass at 20 days of age and 62.1 ± 5.3% of time in the tussock grass at 40 days of age (Figure 2.5). The second best-fit model was within two AIC of the best-fit model and included sex as an additional explanatory variable (which had no significant effect).

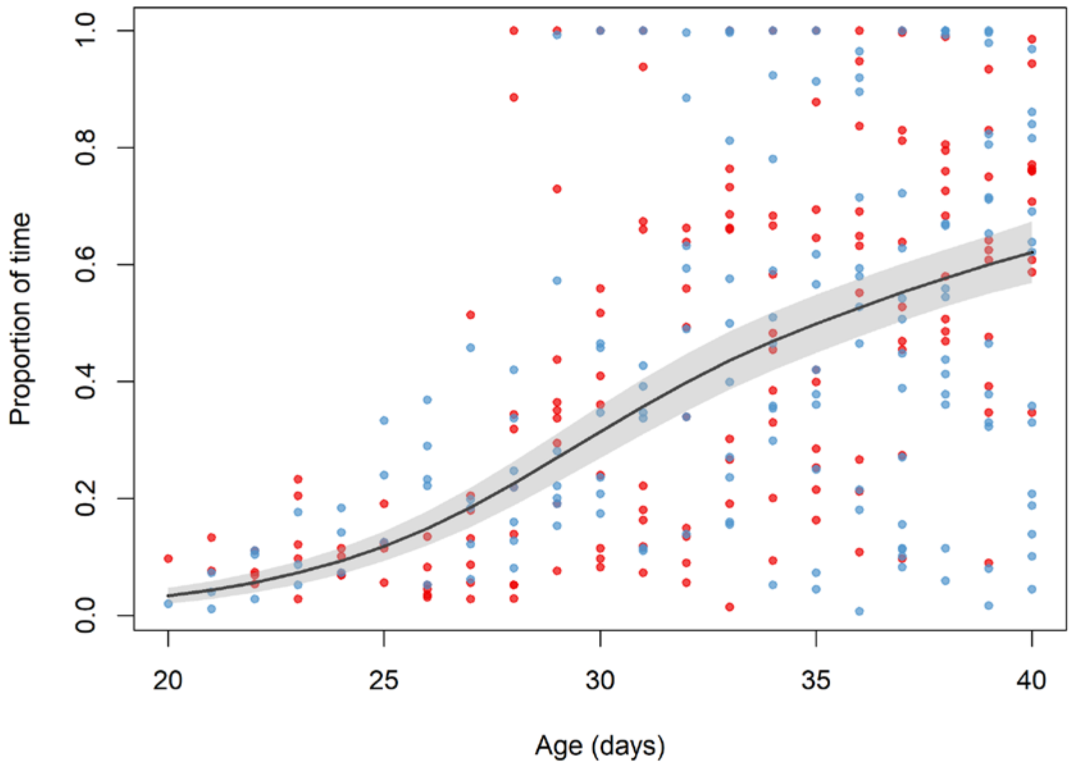

Figure 2.5. Generalized Additive Mixed Model showing the proportion of time that 10 female (red) and 14 male (blue) GPS-tracked Antarctic fur seal pups spent in the tussock grass between an estimated 20 and 40 days of age. Points indicate proportion of time spent in the tussock grass each day by individuals, line indicates modelled average and shaded area indicates standard error.

Between 41 and 120 days of age, the proportion of time that GPS-tracked pups spent in the tussock grass was significantly associated with pup mass and sex, as well as the interaction between pup mass and age (GAMM: $R^2 = 0.04$, s[mass]; $F_{1,\ 1829.1} = 25.7$, $P < 0.0001$; s[mass, by sex]; $F_{1,\ 1829.1} = 25.7$, $P < 0.001$; ti[mass, age]; $F_{6.8,\ 1829.1} = 4.8$, $P < 0.0001$; Supplementary Table S2.8). Specifically, the proportion of time that females spent in the tussock grass was closely associated with their mass (small females spent most time in the tussock grass), whereas the proportion of time that males spent in the tussock grass was more variable with mass (Figure 2.6). Both sexes generally spent less time in the tussock grass as they developed, but lightweight pups (less than 8 kg) spent a high proportion of time in the tussock grass toward the end of lactation (Figure 2.6). Although the effect size of this best-fit model was small, the model had the lowest AIC and explained the most variation out of candidate models. The model excluding sex had a higher AIC (difference of 2.2) and explained less variation ($R^2 = 0.02$).

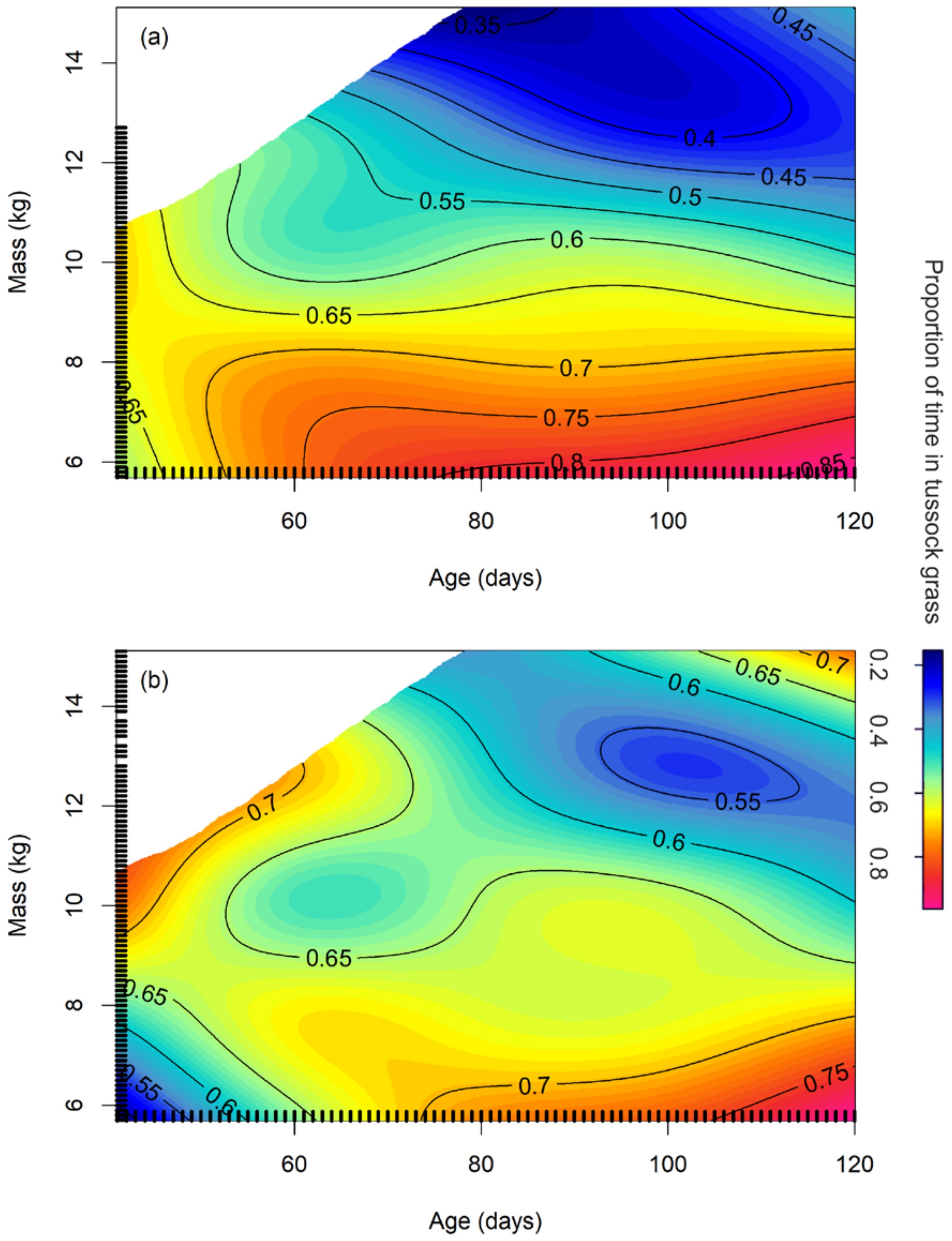

Figure 2.6. Generalized Additive Mixed Model showing the proportion of time that (a) 13 female and (b) 16 male GPS-tracked Antarctic fur seal pups spent in the tussock grass between an estimated 41 and 120 days of age. Rugs (tick marks inside plot) indicate locations of all data points.

Regarding habitat use of pups that died during the study, three pups (two males and one female) remained on the beach for the majority of time during tracking but died of starvation between 17 and 23 days of age. Three additional pups used the beach, tussock, and bay habitats during tracking but died between 39 and 52 days of age: one male and one female died of starvation, whereas the other female drowned in a bog.

2.4.3. Sex Differences in Movements

2.4.3.1. Ontogeny of Movements

Both male and female GPS-tracked pups undertook progressively longer, more distant trips out at sea (from the pupping beach) as they developed. Pups generally returned to previously explored haul-out sites before extending their trip distances. However, occasionally, pups made sudden long-distance trips, such as to the main island of South Georgia, with no prior experience of the area. The first female and male pups that traveled more than 300 m in distance from the mean GPS point near the pupping beach were 48 and 49 days old, respectively. Between 0 and 120 days of age, 522 trips were recorded in total: 222 by 13 females and 300 by 16 males.

Between 20 and 40 days of age, pups mainly spent time on the pupping beach in established suckling locations within the tussock grass or on the immediate coastline (Figure 2.7a,b). Between 41 and 60 days of age, pups had established suckling locations in the tussock grass and traveled to coasts both within and outside Freshwater Bay (Figure 2.7c,d). They further extended their ranges between 61 and 80 days of age (Figure 2.7e,f).

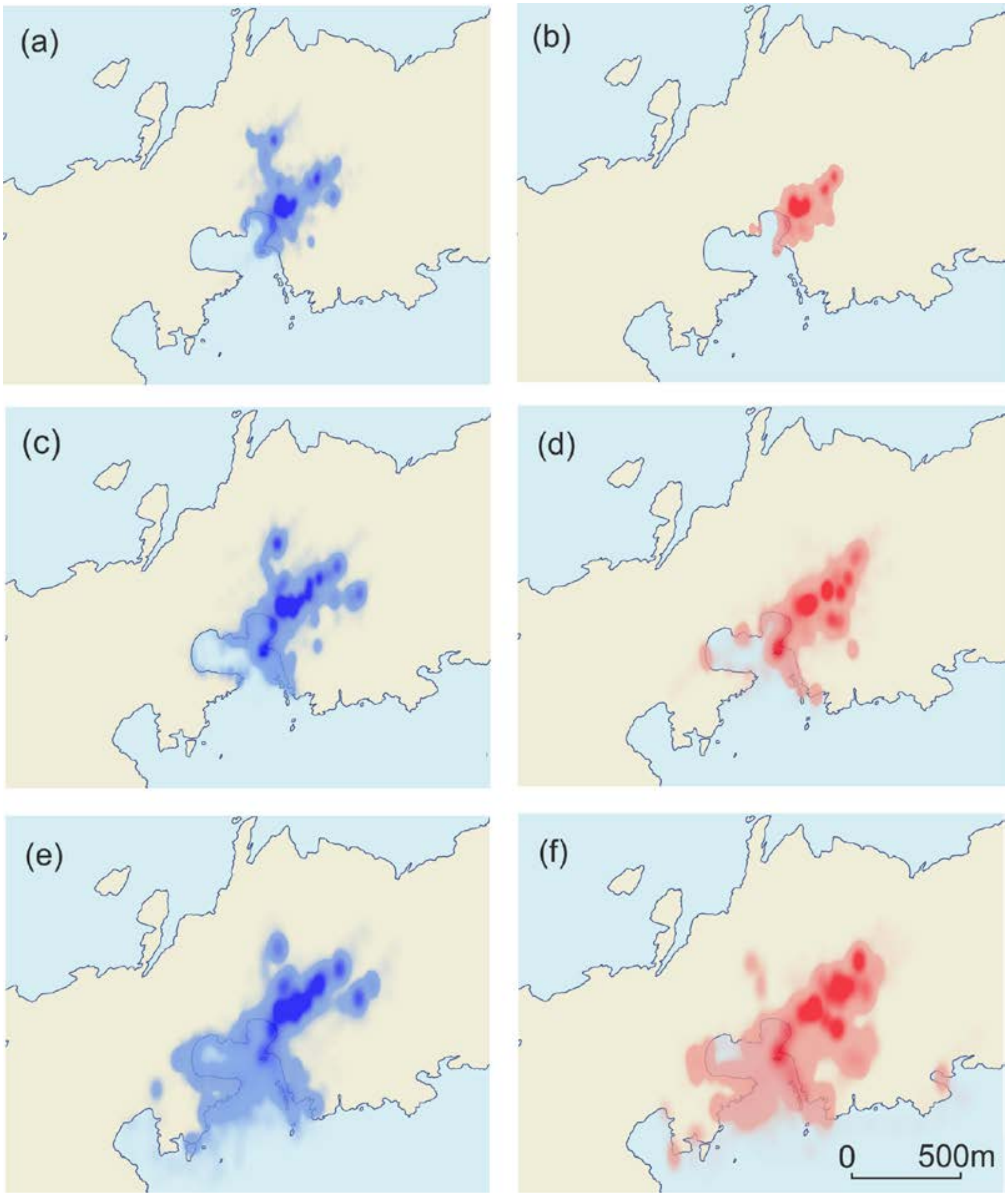

Figure 2.7. Heat maps with 99% of cumulative points showing ontogeny of pup movements and use of land at Bird Island (beige) and sea (light blue) from male (blue) and female (red) pups: (a) 14 males and (b) 10 females between ages 20 and 40 days; (c) 14 males and (d) 10 females between ages 41 and 60 days; (e) 15 males and (f) 13 females between ages 61 and 80 days.

Pups explored the coasts of Bird Island and surrounding islands between 81 and 120 days of age (Figure 2.8). They generally returned to their suckling locations immediately after returning from their trips. One female (w9125) traveled 11 289 m away from the pupping beach at 89 days of age and explored the north-west coast of the main island of South Georgia. This trip distance was 6.5 times greater than the average distance traveled by pups at this age, and the outlier was removed from trip analyses. The female pup also traveled to the south-west of the main island, which was not frequented by any other female pup. Her suckling location was located in the tussock grass behind the research station—notably closer to the breeding beach than those of other female pups. Only one pup (male w9117) traveled to Willis Island (west of Bird Island).

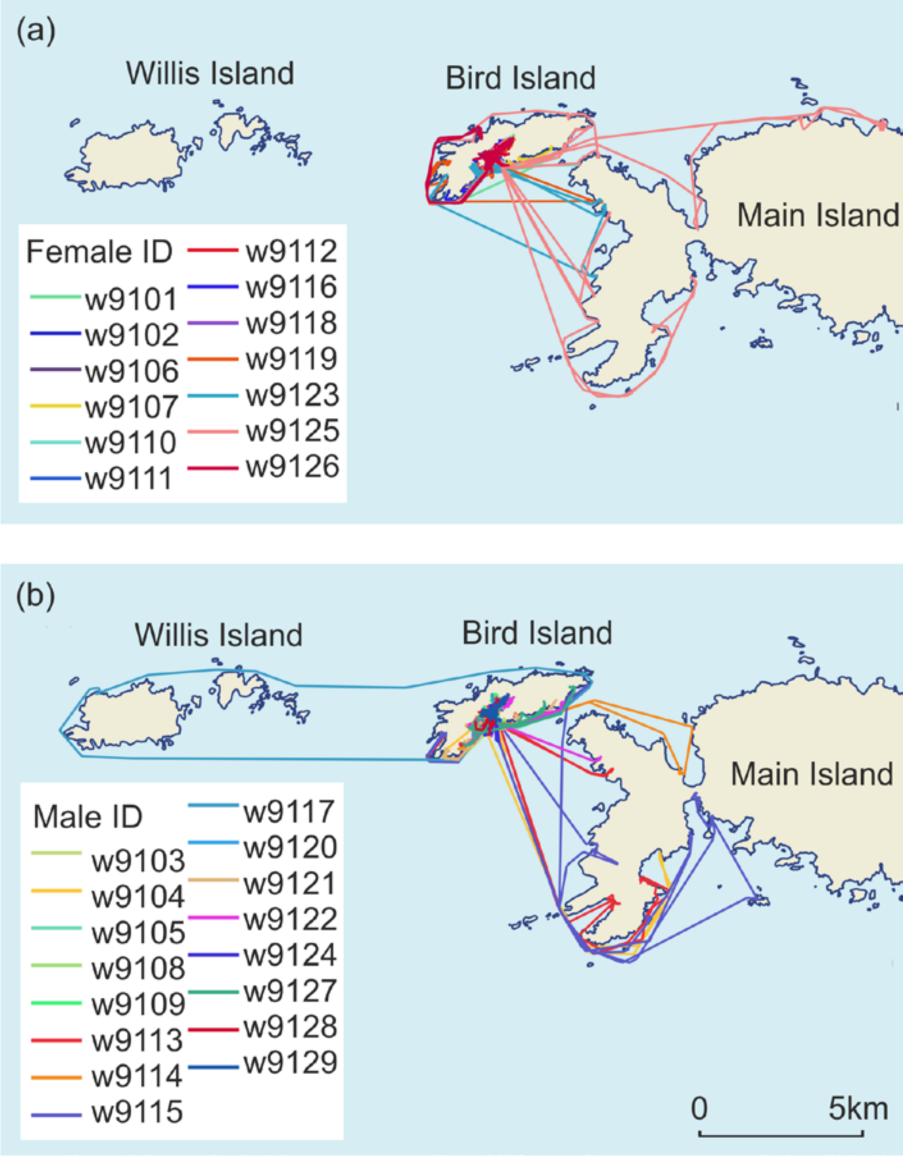

Figure 2.8. GPS tracks of (a) 13 female and (b) 16 male Antarctic fur seal pups between 80 and 120 days of age. Lines represent minimum distance travelled between haul out locations and colours indicate different individuals.

2.4.3.2. Trips at Sea

Maximum distance traveled by GPS-tracked pups on trips at sea was significantly associated with age, mass, and the interaction between age and mass with sex

(GAMM: $R^2 = 0.21$, s[age] $F_{1,\ 515.8} = 80.1$, $P < 0.0001$; s[mass] $F_{1,\ 515.8} = 8.42$, $P = 0.004$; ti[age, mass, by sex]: $F_{2.17,\ 515.8} = 4.7$, $P = 0.01$; Supplementary Table S2.9). Specifically, both sexes traveled further at sea as they aged and gained mass, but males traveled further than females toward the end of the lactation period (Figure 2.9). The second best-fit model was within two AIC of the best fit model and had the same structure with an additional interaction between mass and sex.

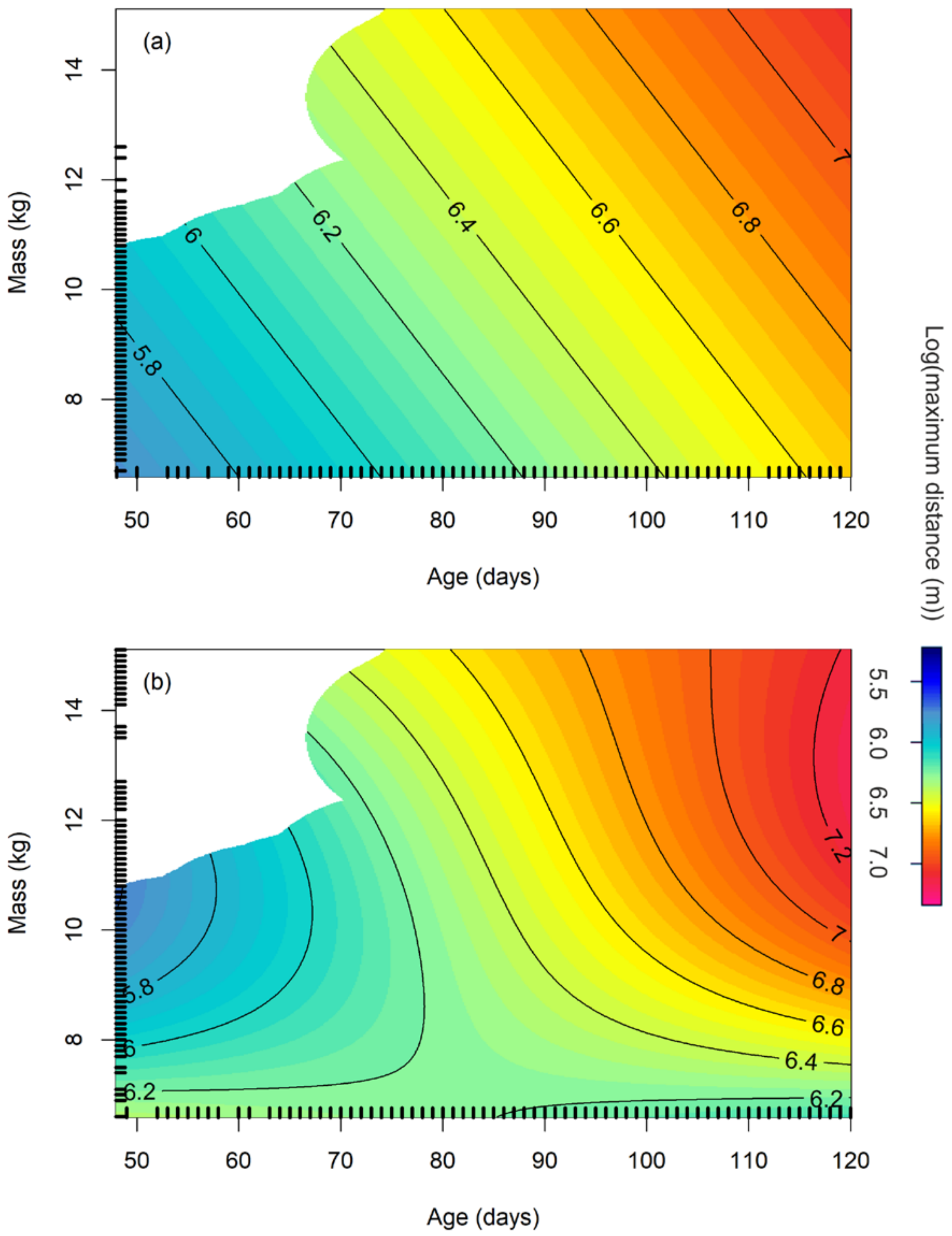

Figure 2.9. Generalized Additive Mixed Model showing log of maximum distance travelled by female and male GPS-tracked Antarctic fur seal pups according to their age and mass based on (a) 221 trips by 13 female pups; (b) 300 trips by 16 male pups. Rugs (tick marks inside plot) indicate locations of all data points.

Trip duration was significantly associated with the interaction between age and mass, but effect size was small (GAMM: R^2 = 0.03, s[age] $F_{1,\ 514.9}$ = 9.2; ti[age, mass] P = 0.003; $F_{4.1,\ 514.9}$ = 6.0, P < 0.0001; Supplementary Table S2.10). Trip duration increased during development, particularly toward the end of the lactation period (Supplementary Figure S2.11). The second best-fit model was within two AIC and also included an interaction between mass and sex (which had no significant effect) and an interaction between age, mass, and sex.

The proportion of time that trips occurred at night was significantly associated with sex and age, but effect size was also small (GAMM: R^2 = 0.03, s[age] $F_{1,\ 518}$ = 8.5, P = 0.004; sex P = 0.006; Supplementary Table S2.12). Between 50 and 120 days of age, the proportion of time that pups spent on trips during the night increased from 25.6 ± 2.3 % to 39.9 ± 3.5 % in males and 31.6 ± 3.1 % to 49.4 ± 4.2 % in females (Supplementary Figure S2.13). The difference in AIC between the best-fit model and second best-fit model (which included sex and mass) was 71.0.

2.5. Discussion

This is one of the few studies to show that small sex differences in habitat use can develop in a highly polygynous species prior to weaning. We found that sexual segregation began to develop in Antarctic fur seal pups at Bird Island, South Georgia, both on land and at sea: 1) analysis of pup counts in beach and tussock grass habitats (from 1989–2018) suggested that female pups had a slightly higher association with tussock grass habitats than males. Small sex differences were found in tussock grass use by GPS-tracked pups (after 40 days of age), which also depended on pup mass—lightweight females spent the most time in the tussock grass. 2) Pups traveled further out to sea as they developed, but males traveled slightly further than females toward the end of the lactation period. We use these findings to investigate the predation risk, social roles, and size dimorphism hypotheses as they relate to early life sexual segregation.

2.5.1. Size Dimorphism

Sexual size dimorphism was present in pups during the monitoring period and in GPS-tracked pups as males remained heavier than females on average. Monitoring data suggested that sexual size dimorphism became more pronounced from January to March, but this trend did not occur in GPS-tracked pups during the 2012–2013 breeding season. In favorable conditions, male Antarctic fur seal growth rates often exceed that of females (Lea et al. 2006; Vargas et al. 2009; present study). This is thought to reflect the need for male pups to attain a relatively large size, which can improve breeding success in later life (Doidge and Croxall 1989; Isaac 2005). When foraging conditions are poor, pup growth is constrained by the mother's milk supply. Our results suggest that foraging conditions during the 2012–2013 breeding season were poor, supported by lower pup growth rates (44 vs. 79 g/day; Doidge and Croxall 1989), a decline in mass after 100 days of age, and an elevated mortality rate (23.3% compared with a 5-year mean of 14%). Monitoring data also showed that pups in the tussock grass were heavier than those on the beach as they had likely suckled more recently (and had more milk in their stomachs).

2.5.2. Sexual Segregation in Habitat Use

Initially, pups are led by their mothers from suckling on the beach to the safer elevated region of tussock grass (Doidge et al. 1984a). Therefore, there was no sex bias in habitat use of GPS-tracked pups in their first 40 days of age as tussock grass use was strongly influenced by the decisions of mothers. Slight sex differences occurred in tussock grass use between 41 and 120 days of age: lightweight females generally spent more time in the tussock grass than heavy females and males of the same mass. This sex difference was supported by long-term monitoring data as males were more commonly found on the beach and females in the tussock grass.

At Bird Island, beach and tussock habitats vary dramatically in risk exposure. Beaches and water provide the best opportunities for pup social interaction. The open spaces allow pups to form social groups, whereas water facilitates playful behavior in young seals (e.g., Wilson 1974; Wilson and Jones 2018). However, the beach is highly populated and pups are at increased risk of injury and death. Adult males fight when attempting to defend, obtain, or expand their territories (McCann 1980), often trampling pups, disturbing the colony and causing mothers and pups to separate (Doidge et al. 1984a). Juvenile animals regularly harass pups, and adult females will bite pups (other than their own) that get too close (Doidge et al. 1984a). Giant petrels, *Macronectes spp.*, brown skuas, *Stercorarius antarcticus,* and sheathbills, *Chionis spp*, also attack pups. Sheathbills peck wounds (Doidge et al. 1984a), which can lead to mortality, whereas giant petrels prey on weak pups or drive swimming pups into deeper water to exhaust and drown them. Beaches are also exposed to wind, rain, snow, and waves, which entail high thermoregulatory and energetic costs. Tussock grass provides shelter and protection from these hazards. Our findings suggest that larger pups are better able to cope with dangers on the beach as they are less vulnerable to predation, hypothermia, and starvation than smaller pups. However, males appear more risk prone than females of the same mass, which indicates that sex differences in social behavior also influence habitat use.

Optimality Theory proposes that animals only perform behaviors if life-history benefits exceed costs (Harcourt 1991a). Generally, males have a higher propensity for risk-taking and dangerous behavior than females (Wrangham 1999). Males tend to be more competitive, energetic, and physically aggressive to develop fighting skills and dominance (Clutton-Brock 1983; Beier and McCullough 1990). Social play in young males can involve mounting and fighting, which mimics adult behavior and enhances skills needed to compete for mates in later life (e.g., Gentry 1974; Smith 1982; Harcourt 1991b). Females are generally less active and aggressive, as their social roles relate better to protecting and provisioning offspring (Pellegrini 2004). They tend to be more risk averse and may avoid vigorous behavior by males (Harpers and Sanders 1975; Pellegrini 2004). Indeed, male Steller sea lion, *Eumetopias jubatus*, and Galapagos fur seal, *Arctocephalus galapagoensis*, pups play fight more frequently than females (Gentry 1974; Arnold and Trillmich 1985). These behavioral differences are driven by perinatal androgens (Goldfoot et al. 1984; Hines and Kaufman 1994; Archer and Lloyd 2002).

Animals must assess reward with the cost of aggregating in areas with high mortality risk (Schoener 1971; Mangel and Clark 1986; Willems and Hill 2009). Play behaviors can be particularly costly. For example, the majority of South American fur seal pups, *Arctocephalus australis*, predated on by Southern sea lions, *Otaria flavescens*, at a colony in Peru were distracted by play at the time of the attack (Harcourt 1991a), suggesting that play came at a cost of vigilance. Despite the risk of early mortality, which is the most severe cost to an animal, pups continued to play in high-risk areas of the beach (Harcourt 1991a). Also, cow elk, *Cervus canadensis,* increased vigilance and decreased feeding in the presence of wolves, whereas bulls (the larger sex) showed neither response—likely unable to pay the associated foraging costs (Winnie and Creel 2007). These sex differences in risk avoidance could explain the small sex differences in Antarctic fur seal pup habitat use.

Male Antarctic fur seal pups may spend slightly more time in the high-risk beach environment to socialize and play fight to gain musculature, experience, and social skills, whereas females spend slightly more time in the safer tussock grass to improve chances of survival. Larger pups are also less vulnerable to injury and predation, so larger males are the most risk prone, whereas small females are the most risk averse. Similar patterns in habitat use have also been reported in guppies, *Poecilia reticulata*, which assorted in size and sex under risk of predation from the Trinidadian pike cichlid, *Crenicichla frenata* (Croft et al. 2004). Males (the brightly colored and more vulnerable sex) preferred safer waters by the riverbank, whereas cryptically colored females preferred deeper (and riskier) waters, and both sexes were longer in mean body length in deeper waters (Croft et al. 2004). Our findings indicate that body size, social roles, and predation risk may all contribute to small sex differences in pup habitat use.

Although our results only explained a low proportion of variation, we were measuring behaviors in a wild population and were unable to control for other influencing factors, such as mother fitness, pup genetics, pup health, time between suckling bouts, location of suckling area (i.e., distance from the pupping beach), weather conditions, and changes in predator assemblages. Despite these limitations, we demonstrated the influence of sex and size on risk exposure at both an individual and a population level.

2.5.3. Sexual Segregation in Trip Metrics

Trip duration at sea did not significantly differ between male and female pups as it is constrained by their mothers' foraging decisions. Although pups are free to explore between suckling bouts, they generally return to their suckling locations before their mothers return from foraging. Our findings suggest that mothers invest the same amount of time suckling male and female Antarctic fur seal pups, which provides support that there is no sex bias in milk consumption (Arnould et al. 1996).

Light level is an important factor in decision-making because it affects the visual abilities of predators and prey (Lima and Dill 1990). Female Antarctic fur seal pups spent a slightly greater proportion of time on trips during the night than males. Although the effect size was low, this result may reflect small sex differences in behavior: females spending slightly more time on trips at night to reduce risk by avoiding aggressive and dangerous attacks by predatory seabirds. This sex difference in trip metric has also been recorded in adults during the mating season as females foraged more frequently during the night time than males, potentially, to reduce diving costs by exploiting prey that vertically migrate to the surface at night (Staniland and Robinson 2008).

Pups traveled further at sea as they aged and gained mass, but males traveled slightly further than females of the same mass toward the end of lactation. As pups developed, they gained the appropriate physiology, locomotor skills, and experience to swim further while their mothers foraged (Salton et al. 2019). Pups also acquire a more slender body shape and larger fore flippers (Luque et al. 2007) and their blood volume and blood oxygen stores increase, which improves their diving capabilities (McCafferty et al. 1998) and subsequent swimming skills (Bowen et al. 1999; Jørgensen et al. 2001). These skills enable pups to catch small prey items approaching weaning age, indicated by traces of crustaceans in their scats (Doidge et al. 1986).

Sex differences in trip distances may be driven by social roles, predation risk, and body dimorphism (Salton et al. 2019). In highly social polygynous mammals, males tend to be more dispersive than females (Greenwood 1980), so males may travel further to prospect sites and evaluate the best foraging areas and potential future mating opportunities, whereas females will return to their natal site to breed and provision offspring. Female pups may also be more risk averse and make shorter distance trips to improve chances of survival. Travelling at sea is risky as small naïve pups explore new regions with different predators (e.g., orcas, *Orcinus orca*, and sixgill sharks, *Hexanchus sp.*) and unpredictable environmental conditions. Pups risk drowning, getting lost, and starving. Males may be more risk prone, gaining experience exploring potential foraging sites to maximize growth rates, as polygynous males are in an energetic race to maximize body condition to compete for mates (Main and Toit 2005). A similar trade-off has been documented in adolescent male long-tailed macaques, *Macaca fascicularis,* which become mostly solitary during several months of high fruit abundance; this increases predation risk but maximizes foraging intake, enabling them to grow rapidly and improve mating opportunities (Watts 2005).

Male and female Antarctic fur seal pups also differ in body composition and physiology. Males direct more energy toward lean tissue growth and females toward accumulating fat stores (Arnould et al. 1996). Females, therefore, have a higher mass-specific metabolic rate (Arnould et al. 2001) and are less efficient at gaining mass than males (Guinet et al. 1999). Females may travel shorter distances to conserve energy or they may be less capable of long trips at sea, as swimming entails energetic costs of physical movement and thermoregulation (and smaller pups have higher costs of maintaining body temperature in frigid waters). Because juvenile otariids with larger body sizes can have higher mass-specific oxygen stores (e.g., Fowler et al. 2007), males may be better divers than females. Their hearts and lungs also constitute a greater proportion of total body mass (Payne 1979). Males may, therefore, develop the physiological capabilities, including greater strength and breath-holding abilities, to travel further than females of the same mass toward the end of lactation—enabling them to take more risks at sea. These findings indicate that sexual segregation will become more pronounced after weaning. Indeed, Warren et al. (2006) found that weaned male Antarctic fur seals traveled substantially further from their birth sites (at Bird Island) than females (maximum distances recorded: 900 and 400 km, respectively).

2.5.4. Environmental Implications

Sexual segregation in Antarctic fur seal pups may depend on the nature of the mortality risk (e.g., predator assemblage and seal density), habitat composition, and prey availability. Pups are more prone to injury and death at beaches with high seal densities (Doidge et al. 1984a), and habitat composition and availability of refuge areas can shape antipredator behaviors (Wcisel et al. 2015). Sexual segregation may be more pronounced in years with high prey availability as sexual size dimorphism will be more extreme. The fact that we detected small sex differences in habitat use even in a year with poor prey availability and minimal sexual size dimorphism suggests that sexual segregation could be a vital aspect of the Antarctic fur seals' life-history strategy. Sex differences in habitat use may manifest differently in pups of other otariid species (e.g., Galápagos sea lions, *Zalophus wollebaeki*; Piedrahita et al. 2014) as a result of different lactation strategies and predictability of environmental conditions.

2.5.5. Drivers of Behavior

Kernaléguen et al. (2016) proposed that size dimorphism and breeding constraints do not directly drive sexual segregation in otariids. However, our findings suggest that the initial development of sexual segregation in Antarctic fur seals may be explained by underlying drivers of behavior, resulting from intense sexual selection pressures. These sexual selection pressures and the coercive behavior of males on females may have originally evolved after sexual size dimorphism and polygyny (Krüger et al. 2014; Cassini et al. 2020). Because reproductive success is more varied in males than females (Darwin 1871), male Antarctic fur seals must gain social skills (e.g., by play fighting) and build muscle mass early in life if they are to successfully reproduce in future. Sexual size and body dimorphism, therefore, occurs even in pups, and male pups may be more risk prone than females, resulting in small sex differences in habitat use.

2.5.6. Conclusions

Investigating the drivers of sexual segregation is key to understanding how the sexes may respond differently to mortality risk. Sexual segregation has predominantly been studied in adults, but studying ontogeny of sexual segregation in early life stages can reveal how this phenomenon initially develops. Our study has improved understanding of these processes by showing that body dimorphism, social roles, and predation risk may all contribute to small sex differences in habitat use and exploratory behavior of Antarctic fur seal pups by influencing risk exposure trade-off decisions. Males may be more risk prone and invest in behaviors to prepare for intense competition for mates, whereas females (particularly small females) may be more risk averse to improve chances of survival, which is ultimately driven by their different reproductive roles. Our findings hint that sex differences in behavior will increasingly diverge in later life, resulting in more pronounced sexual segregation. Life-history strategies play fundamental roles in the ontogeny of sexual segregation and studying sexual segregation in additional species in the initial life stages could underpin species-specific drivers of this phenomenon. Such insights are crucial to understand the requirements of each sex for survival to inform habitat management and species conservation efforts.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Jones et al. (2020).

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2.8. Supplementary Material

Supplementary Table S2.1. Details of GPS-tracked Antarctic fur seal pups that died (a) and survived (b) during the study period in the 2012 – 2013 pupping season at Bird Island, South Georgia.

*Full days of missing data caused by tag failure: w9104=12/03/2013; w9105=27/03/2018 – 29/03/2018; w9108=24/03/2013 – 26/03/2013; w9109=13/02/2013 – 23/02/2013; w9110=09/02/2013 – 23/02/2013; w9111= 22/03/2013 – 24/03/2013; w9118=19/01/2013 – 02/02/2013; w9127=12/03/2013.

(a)

Pup ID	**Sex**	**First tracking obervation**	**Last tracking observation**	**Tracking duration (days)**	**Min–max mass (kg)**	**Date pup died**	**Observation**
atp10	M	27/12/2012	29/12/2012	3	3.9–4.9	29/12/2012	starved, blood in rectum
atp11	F	05/01/2013	16/01/2013	12	4.2–6.3	16/01/2013	starved
atp13	M	21/12/2012	25/12/2012	4	6.5–8	28/12/2012	starved
atp18	F	27/12/2012	31/12/2012	5	6–7.4	31/12/2012	starved, blood in rectum
atp29	M	03/01/2013	22/01/2013	19	5.2–7.4	22/01/2020	starved
atp38	F	10/01/2013	29/01/2013	20	4.8–8.3	03/02/2013	drowned in bog

(b)

Pup ID	Sex	First tracking observation	Last tracking observation	Tracking duration (days)	Min and max mass (kg)	Total number of trips	Max trip duration (mins)	Max trip distance (m)
w9101	F	24/12/2012	29/03/2013	96	4.2-11.6	17	3,600	1,947
w9102	F	24/12/2012	04/03/2013	71	4.7-9.5	15	1,650	1,949
w9103	M	15/02/2013	06/04/2013	51	3.8-10.5	18	1,020	1,682
w9104	M	24/12/2012	25/03/2013	92-1*=91	5.2-11.3	19	2,465	8,215
w9105	M	24/12/2012	07/04/2013	105-3*=101	4.9-11.4	16	2,555	2,702
w9106	F	24/12/2012	22/03/2013	89	4.5-11.9	14	1,930	839
w9107	F	27/12/2012	01/04/2013	96	4.2-10.5	19	1,635	1,717
w9108	M	10/01/2013	07/03/2013	57-3*=54	5.8-12.2	13	730	1,429
w9109	M	27/12/2012	11/03/2013	75-11*=64	5.2-11.1	6	2,010	502
w9110	F	27/12/2012	22/03/2013	86-15*=71	4.5-12.2	17	990	2,321
w9111	F	03/01/2013	06/04/2013	94-2*=92	5-10.8	6	865	532
w9112	F	03/01/2013	14/03/2013	71	5.4-9.5	26	775	840
w9113	M	03/01/2013	19/04/2013	107	5.8-11.3	29	2,415	7,965
w9114	M	15/01/2013	31/03/2013	76	5.4-16.5	25	1,955	5,768
w9115	M	14/01/2013	19/04/2013	96	5.8-13.5	26	5,540	9,428
w9116	F	20/02/2013	02/04/2013	42	3.8-8.1	18	1,690	2,174
w9117	M	03/01/2013	07/04/2013	95	5.2-12.9	19	3,835	12,821
w9118	F	05/01/2013	28/03/2013	83-15*=68	5-10.5	15	1,950	1,462
w9119	F	15/02/2013	26/03/2013	40	3.6-9.6	23	2,055	3,324
w9120	M	10/01/2013	08/03/2013	58	5.2-11	13	1,340	901
w9121	M	05/01/2013	28/03/2013	83	5.9-14.1	20	5,960	2,169
w9122	M	05/01/2013	29/03/2013	84	6.2-13.2	21	2,595	3,333
w9123	F	05/01/2013	19/03/2013	74	5.6-13.8	14	4,735	4,651
w9124	M	14/01/2013	06/04/2013	83	4.5-8.4	32	620	1,029
w9125	F	10/01/2013	08/04/2013	89	4.8-12.7	28	3,260	11,289
w9126	F	21/02/2013	10/04/2013	49	4.5-9.9	10	4,640	2,588
w9127	M	10/01/2013	16/04/2013	97-1*=96	4.7-13.5	17	2,700	2,315
w9128	M	10/01/2013	07/04/2013	88	5.9-10.2	18	830	907
w9129	M	27/02/2013	08/04/2013	41	5-7.6	8	390	472

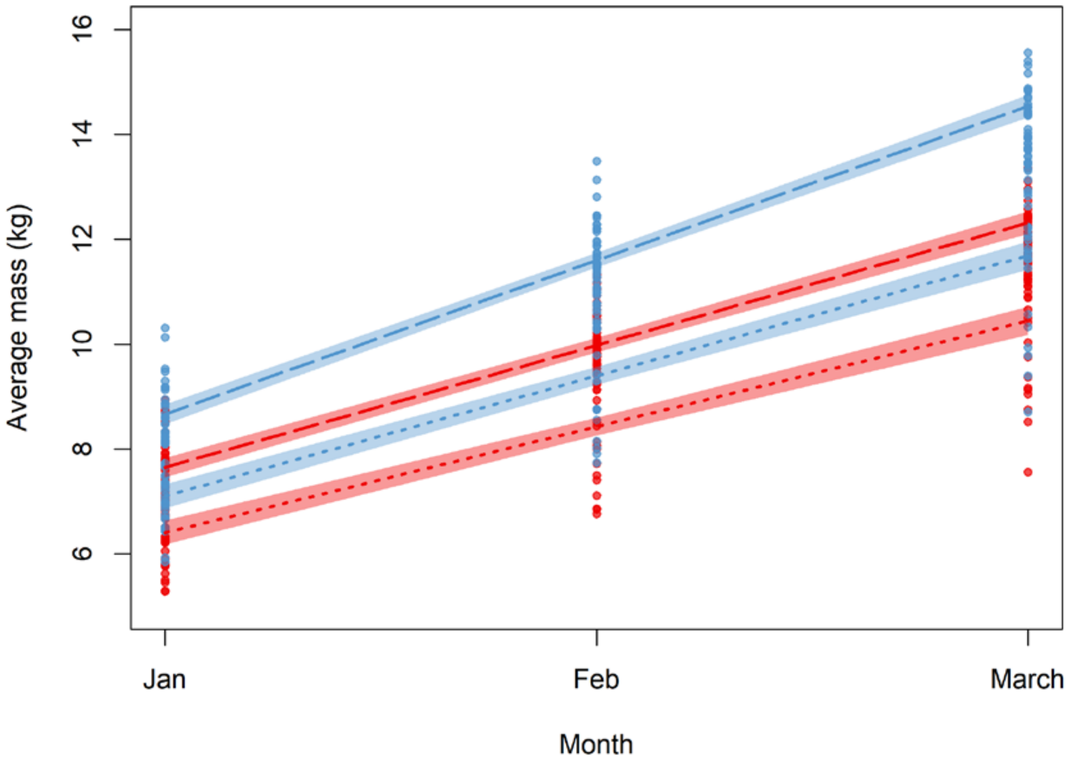
Supplementary Table S2.2. Model comparisons to study the effects of sex, month and habitat (beach or tussock grass) and their interactions on average Antarctic fur seal pup mass at Bird Island, South Georgia, during pup monitoring from 1989 **–** 2018. AIC: Akaike's information criterion; ΔAIC: difference in AIC between candidate model and best-fit model; R^2: proportion of variance explained by predictors; n: number of observations of the response variable. Model parameters are shown for the best-fit model.

Predictors	**AIC**	**ΔAIC**	**R^2**	**n**
sex + habitat + month + year + sex:habitat + sex:month + sex:habitat:month	1112.6	0	0.79	360
sex + habitat + month + year + sex:habitat + sex:month + sex:year + sex:habitat:month	1113.4	0.8	0.79	360
sex + habitat + month + year + sex:habitat + sex:month + sex:year + sex:habitat:month + sex:habitat:year	1116.9	4.3	0.79	360
sex + habitat + month + year + sex:habitat + sex:month	1117.3	4.7	0.79	360
habitat + month + year + habitat:month	1226.3	113.7	0.71	360
	Value	**SE**	**t-value**	**p-value**
Intercept	103.42	13.64	7.58	< 0.0001
sex (male)	0.42	0.44	0.96	0.34
habitat (tussock)	1.38	0.44	3.13	0.001
month	2.40	0.14	16.65	<0.0001
year	-0.05	0.01	-7.28	<0.0001
sex (male): habitat (tussock)	-0.01	0.62	-0.02	0.98
sex (male): month	0.49	0.20	2.39	0.02
sex (female): habitat (tussock): month	-0.40	0.20	-1.96	0.05
sex (male): habitat (tussock): month	-0.45	0.20	-2.19	0.03

Supplementary Table S2.3. Model comparisons to study the effects of sex, month and Gentoo penguin breeding success (as an indicator of prey availability) on average Antarctic fur seal pup mass at Bird Island, South Georgia, during pup monitoring from 1989 **–** 2018. AIC: Akaike's information criterion; ΔAIC: difference in AIC between candidate model and best-fit model; R^2: proportion of variance explained by predictors; n: number of observations. Model parameters are shown for the best-fit model.

Predictors	**AIC**	**ΔAIC**	**R^2**	**n**
sex + month + Gentoo breeding success + sex:month + sex:month:Gentoo breeding success	1093.6	0	0.80	360
sex + month + sex:month	1177.9	84.3	0.75	360
month + Gentoo breeding success + month:Gentoo breeding success	1215.9	122.3	0.72	360
	Value	**SE**	**t-value**	**p-value**
Intercept	4.39	0.37	12.0	<0.0001
sex (male)	0.42	0.30	1.36	0.17
month	2.02	0.18	11.4	<0.0001
Gentoo breeding success	0.58	0.32	1.79	0.07
sex(m):month	0.28	0.18	1.58	0.12
sex(f):month:Gentoo breeding success	0.20	0.16	1.23	0.22
sex(m):month:Gentoo breeding success	0.40	0.16	2.52	0.01

Supplementary Figure S2.4. General linear model showing the growth of female (red) and male Antarctic fur seal pups (blue) during long-term monitoring at Bird Island, South Georgia: 100 pups were selected, sexed and weighed, 50 on the beach and 50 in tussock grass, each month in January, February and March each year from 1989 – 2018. Points show average mass of 100 pups, dotted lines show average growth when krill availability is predicted poor (indicated by gentoo penguin breeding success of 0 chicks per nest) and dashed lines show pup growth when krill availability is predicted good (indicated by gentoo penguin breeding success of 1.6 chicks per nest). Shaded areas indicate standard error.



Supplementary Table S2.5. Model comparisons to study the effects of sex, age and their interactions on mass of GPS-tracked Antarctic fur seal pups at Bird Island, South Georgia. AIC: Akaike's information criterion; ΔAIC: difference in AIC between candidate model and best-fit model; R^2: proportion of variance explained by the predictors; n (N) number of observations of the response variable and number of individuals respectively. Model parameters are shown for the best-fit model.

Predictors	**AIC**	**ΔAIC**	**R^2**	**n (N)**
sex + s(age)	2562.8	0	0.56	883 (29)
s(age)	2565.1	2.3	0.53	883 (29)
sex + s(age by sex)	2587.1	24.3	0.56	883 (29)
Parametric coefficients	**Value**	**SE**	**t-value**	**p-value**
Intercept	7.39	0.25	29.1	<0.0001
sex (male)	0.72	0.34	2.09	0.04
Approximate significance of smooth terms	**edf**	**Ref.df**	**F**	**p-value**
s(age)	7.06	7.06	343.3	<0.0001

Supplementary Table S2.6. Model comparisons to study the effects of habitat (beach or tussock grass), month (January to March), year and their interactions on the proportion of male to female Antarctic fur seal pups at Bird Island, South Georgia, during pup monitoring from 1989 – 2018. AIC: Akaike's information criterion; ΔAIC: difference in AIC between candidate model and best-fit model; pseudo R^2: proportion of variance explained by predictors; n: number of observations of the response variable. Candidate models with ΔAIC < 5 are presented. Model parameters are shown for the best-fit model.

Predictors	**AIC**	**ΔAIC**	**pseudo R^2**	**n**
habitat + month + year	1000.1	0	0.18	180
habitat + month + year + month:year	1001.3	1.2	0.19	180
habitat + month + year + habitat:month	1001.7	1.6	0.18	180
habitat + month + year + habitat:year	1001.9	1.8	0.18	180
habitat + month + year + habitat:month + month:year	1002.9	2.8	0.19	180
habitat + month + year + month:year + location:year	1003.1	3.0	0.19	180
habitat + year	1003.2	3.1		180
habitat + month + year + habitat:month + habitat:year	1003.4	3.3	0.19	180
habitat + month + year + habitat:month + habitat:year + month:year	1004.6	4.5	0.19	180
	Value	**SE**	**t-value**	**p-value**
Intercept	-18.6	5.3	-3.54	<0.001
habitat (tussock)	-0.22	0.05	-4.79	<0.0001
month	0.06	0.03	2.08	0.04
year	0.01	0.003	3.54	<0.001

Supplementary Table S2.7. Model comparisons to study the effects of sex, smooth function of mass, smooth function of age, and their interactions on tussock grass use by GPS-tracked Antarctic fur seal pups from 20 – 40 days of age at Bird Island, South Georgia. AIC: Akaike's information criterion; ΔAIC: difference in AIC between candidate model and best-fit model; R^2: proportion of variance explained by the predictors; n (N) number of observations of the response variable and number of individuals respectively. Candidate models with ΔAIC < 5 are presented. Model parameters are shown for the best-fit model.

Predictors	**AIC**	**ΔAIC**	**R^2**	**n (N)**
s(age)	1005.0	0	0.260	317 (24)
sex + s(age)	1006.2	1.2	0.258	317 (24)
sex + s(mass)	1006.2	1.2	-0.126	317 (24)
s(age) + s(age by sex)	1008.7	3.7	0.267	317 (24)
s(age) + ti(age, mass)	1009.2	4.2	0.250	317 (24)
Parametric coefficients	**Value**	**SE**	**t-value**	**p-value**
Intercept	-0.53	0.19	-2.79	0.006
Approximate significance of smooth terms	**edf**	**Ref.df**	**F**	**p-value**
s(age)	2.46	2.46	64.27	<0.0001

Supplementary Table S2.8. Model comparisons to study the effects of sex, smooth function of mass, smooth function of age, and their interactions on tussock grass use by GPS-tracked Antarctic fur seal pups from 41 – 120 days of age at Bird Island, South Georgia. AIC: Akaike's information criterion; ΔAIC: difference in AIC between candidate model and best-fit model; R^2: proportion of variance explained by the predictors; n (N) number of observations of the response variable and number of individuals respectively. Candidate models with ΔAIC < 5 are presented. Model parameters are shown for the best-fit model.

Predictors	**AIC**	**ΔAIC**	**R^2**	**n (N)**
s(mass) + s(mass by sex) + ti(age, mass)	5650.1	0	0.041	1839 (29)
s(mass) + ti(age, mass)	5652.3	2.2	0.022	1839 (29)
s(age) + s(mass) + s(mass by sex) + ti(age, mass)	5654.4	4.3	0.038	1839 (29)
s(mass) + s(mass by sex)	5654.8	4.7	0.030	1839 (29)
Parametric coefficients	**Value**	**SE**	**t-value**	**p-value**
Intercept	0.67	0.08	7.91	<0.0001
Approximate significance of smooth terms	**edf**	**Ref.df**	**F**	**p-value**
s(mass)	1	1	25.69	<0.0001
s(mass by sex)	1	1	11.11	<0.001
ti(age, mass)	6.90	6.90	4.84	<0.0001

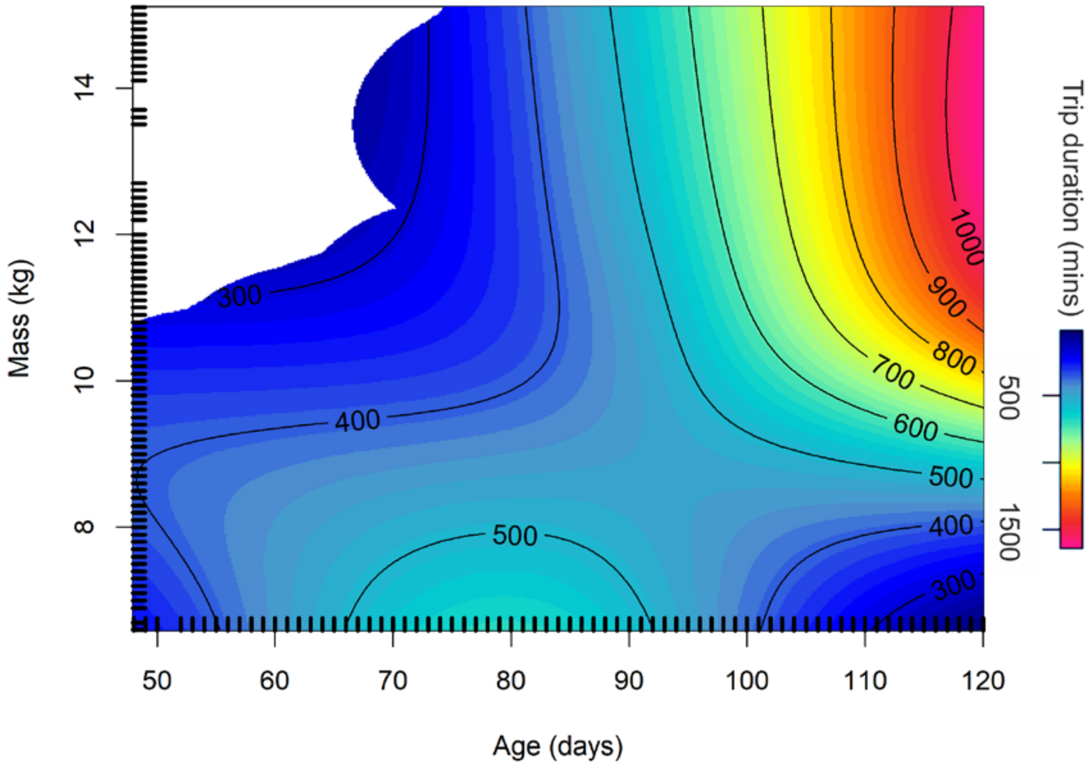
Supplementary Table S2.9. Model comparisons to study the effects of sex, smooth function of mass, smooth function of age, and their interactions on trip distance of GPS-tracked Antarctic fur seal pups at Bird Island, South Georgia. AIC: Akaike's information criterion; ΔAIC: difference in AIC between candidate model and best-fit model; R^2: proportion of variance explained by the predictors; n (N) number of observations of the response variable and number of individuals respectively. Candidate models with ΔAIC < 5 are presented. Model parameters are shown for the best-fit model.

Predictors	**AIC**	**ΔAIC**	**R^2**	**n (N)**
s(age) + s(mass) + ti(age, mass by sex)	769.8	0	0.209	521 (29)
s(age) + s(mass by sex) + ti(age, mass by sex)	769.1	0.9	0.207	521 (29)
s(age) + ti(age, mass)	773.8	4	0.187	521 (29)
Parametric coefficients	**Value**	**SE**	**t-value**	**p-value**
Intercept	6.36	0.03	204.2	<0.0001
Approximate significance of smooth terms	**edf**	**Ref.df**	**F**	**p-value**
s(age)	1	1	80.09	<0.0001
s(mass)	1	1	8.42	0.004
ti(age, mass by sex)	2.17	2.17	4.67	0.009

Supplementary Table S2.10. Model comparisons to study the effects of sex, smooth function of mass, smooth function of age, and their interactions on trip duration of GPS-tracked Antarctic fur seal pups at Bird Island, South Georgia. AIC: Akaike's information criterion; ΔAIC: difference in AIC between candidate model and best-fit model; R^2: proportion of variance explained by the predictors; n (N) number of observations of the response variable and number of individuals respectively. Candidate models with ΔAIC < 5 are presented. Model parameters are shown for the best-fit model.

Predictors	**AIC**	**ΔAIC**	**R^2**	**n (N)**
s(age) + ti(age, mass)	1181.5	0	0.030	521 (29)
s(age) + s(mass by sex) + ti(age, mass by sex)	1183.4	1.9	0.043	521 (29)
s(age) + s(mass) + ti(age, mass by sex)	1183.7	2.2	0.042	521 (29)
s(age) + s(age by sex) + ti(age, mass)	1184.7	3.2	0.028	521 (29)
s(age) + s(mass) + ti(age, mass)	1185.4	3.9	0.030	521 (29)
s(mass)+ ti(age, mass)	1186.4	4.9	0.033	521 (29)
Parametric coefficients	**Value**	**SE**	**t-value**	**p-value**
Intercept	6.13	0.10	62.4	<0.0001
Approximate significance of smooth terms	**edf**	**Ref.df**	**F**	**p-value**
s(age)	1	1	9.22	0.003
ti(age, mass)	4.11	4.11	6.02	<0.0001

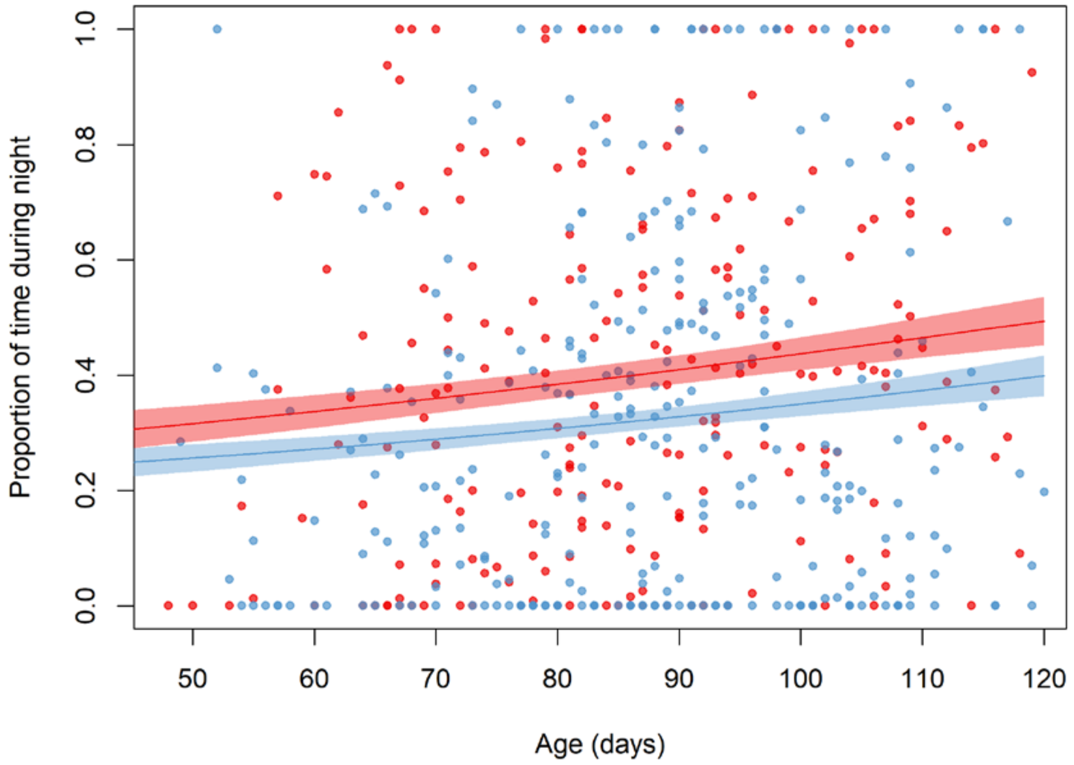
Supplementary Figure S2.11. Generalized Additive Mixed Model showing duration (minutes) of trips taken by both male and female GPS-tracked Antarctic fur seal pups in relation to pup age and mass (221 trips taken by 13 female pups and 300 trips taken by 16 male pups). Rugs (tick marks inside plot) indicate locations of all data points.



Supplementary Table S2.12. Model comparisons to study the effects of sex, smooth function of mass, smooth function of age, and their interactions on the proportion of time that trips of GPS-tracked Antarctic fur seal pups occurred during the night. AIC: Akaike's information criterion; ΔAIC: difference in AIC between candidate model and best-fit model; R^2: proportion of variance explained by the predictors; n (N) number of observations of the response variable and number of individuals respectively. Model parameters are shown for the best-fit model.

Predictors	**AIC**	**ΔAIC**	**R^2**	**n (N)**
sex + s(age)	1562.7	0	0.0279	521 (29)
sex + s(mass)	1633.7	71.0	0.012	521 (29)
s(age) + s(mass by sex) + ti(age, mass by sex)	1664.2	398.5	0.0163	521 (29)
s(age)	1949.8	387.1	0.011	521 (29)
s(mass)	1966.2	403.5	0.000395	521 (29)
s(mass) + s(mass by sex)	1970.7	408.0	-0.0049	521 (29)
Parametric coefficients	**Value**	**SE**	**t-value**	**p-value**
Intercept	-0.32	0.08	-3.79	0.0002
sex (male)	-0.31	0.11	-2.76	0.006
Approximate significance of smooth terms	**edf**	**Ref.df**	**F**	**p-value**
s(age)	1	1	8.51	0.004

Supplementary Figure S2.13. Generalized Additive Mixed Model (with standard error) showing proportion of time that GPS-tracked pup trips occurred during the night in relation to pup age, based on 221 trips taken by 13 female pups (red) and 300 trips taken by 16 male pups (blue). Points indicate proportion of time trips occurred during the night each 24 hrs by individuals, line indicates modelled average and shaded area indicates standard error.



Chapter 3. Sexual Segregation in Juvenile Antarctic Fur Seals, *Arctocephalus gazella*

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3.1. Abstract

Sexual segregation, the differential resource use by males and females, occurs in a wide range of taxa in the animal kingdom. It can have profound implications for conservation, as one sex may be more vulnerable to mortality from environmental and anthropogenic stressors. The drivers of sexual segregation such as sexual size dimorphism, sex differences in breeding constraints and social behaviour, have been well studied in adults, but remain poorly understood in juveniles. To determine how sexual segregation develops in Antarctic fur seals, *Arctocephalus gazella*, which display pronounced sexual size dimorphism in adults, we deployed Global Location Sensors (GLS loggers) on 45 juveniles (26 males and 19 females) of 1 – 3 years of age at Bird Island, South Georgia between 2007 and 2014. Sexual segregation primarily occurred in juvenile foraging distribution, with females foraging closer to South Georgia and the Polar Front, and males foraging further south near the Antarctic Peninsula. Even though juveniles have no immediate reproductive commitments, reproductive selection pressures likely still operate as males may forage in the most productive regions further south to prioritise body growth to attain a large body size, improving future ability to compete for mates. Conversely, females may adopt a more risk-averse foraging strategy and gain sufficient resources to sustain themselves closer to South Georgia and the Polar Front, prioritising survival to fulfil their reproductive potential. As a result of this segregation, males and females may compete or interact with different fisheries that operate in the South Atlantic and Southern Ocean and may respond differently to environmental change, such as the contraction of krill towards Antarctica. This study also highlights the importance of considering the different requirements of sex and age groups in conservation.

Keywords: *geolocation; sexual size dimorphism; early life stages; foraging behaviour*

3.2. Introduction

Sexual segregation, the differential resource use by males and females, has been documented in a plethora of taxa and can be a vital aspect of an animal's life history strategy (Ruckstuhl & Neuhaus 2005; Wearmouth & Sims 2008). The causes of sexual segregation have been studied in adults and include several non-mutually exclusive hypotheses including sexual size dimorphism – whereby the sexes require different resources as one sex is larger than the other (Main et al. 1996; Stokke & Toit 2000); sex differences in predation risk – whereby the more vulnerable sex uses safer habitats (Ruckstuhl & Neuhaus 2005; Croft et al. 2006); sex differences in breeding constraints – such as the constraint of parental care on females (Staniland 2005); and sex differences in social behaviour – individuals investing in behaviours to prepare for their future reproductive roles (Bon & Campan 1996; Pellegrini 2004). However, there has been less attention paid to sexual segregation prior to adulthood. Juveniles are particularly vulnerable to mortality and the two sexes may be exposed to different area-specific stressors (Leung et al. 2012). Juvenile survival also plays a key role in population demography, as low survival can substantially reduce population growth rate (Lindström 1999; Sæther et al. 2013; Benson et al. 2018). Investigating the causes and consequences of sexual segregation in juveniles can therefore gain vital insights into ecology, population dynamics and conservation.

Studying sex-differences in the foraging ecology of juveniles, as opposed to adults, removes the influence of immediate sex-specific breeding constraints such as parental care on females and territory-holding on males, on sexual segregation (Salton et al. 2019). However, intense sexual selection pressures could still influence sexual segregation because sex-specific growth trajectories are geared towards fulfilling future reproductive roles. In polygynous species, males are driven to grow quickly, as larger adult males are generally more successful in competing for mates (Weckerly 1998, Isaac 2005). Males therefore tend to grow faster than females and also grow for longer (Payne 1979; Clutton-Brock et al. 1985; Georgiadis 1985). They must gain enough resources to attain a large body size, as well as to maintain it (Le Boeuf et al. 2000). Males may also require more food as they have higher absolute metabolic demands, whereas females may require better quality food as they have higher mass-specific metabolic needs (Schmidt-Nielsen 1984; Stokke & Toit 2000). Thus, males have been observed foraging over larger areas than females to meet these requirements (Salton et al. 2019), as documented in white-tailed deer, *Odocoileus virginianus* (Hasapes & Comer 2016) and Eurasisn lynx, *Lynx lynx* (Herfindal et al. 2005). Males may also favour foraging strategies that influence growth, whereas females may favour foraging strategies that improve chances of survival as they have more certain reproductive outputs (Trivers 1972; Clutton-Brock et al. 1982; Reeve and Fairbairn 2001; Schulte-Hostedde et al. 2001).

Otariids are ideal taxa to study sexual segregation as they show extreme sexual size dimorphism, which develops early in life (Lindenfors et al. 2002; Payne et al. 1979). Indeed, male pups are born on average 0.5 kg heavier than females and grow faster, weighing nearly four times heavier than females as adults (Payne et al. 1979; Forcada & Staniland 2009). Antarctic fur seals, *Arctocephalus gazella*, are a well-studied species with sexual segregation documented in pre-weaned pups, weaners, and adults. In pre-weaned pups, males have a higher association with riskier habitats than females, which may benefit their ability to gain social skills (i.e. by play-fighting) and compete for mates in future (Jones et al. in 2020a). Toward the end of lactation males also travel further from their birth sites (Jones et al. 2020a) and during the first year of life males have a more oceanic distribution than females (although the sexes were tracked in different years in this study) (Warren et al. 2006). The sexes have different nutritional needs, as males build greater lean tissue stores and females accumulate more fat stores (Arnould et al. 1996). Sex differences in foraging distribution may reflect the drive for males to explore the most productive foraging sites to maximise energy intake to grow and/or the greater physiological capabilities of males to travel further because of their larger body size. The existence of sexual segregation in older juvenile Antarctic fur seals (hereby seals aged 1 – 3 years) is currently limited. However, land-based observations suggest that young adult males are frequently sighted at Signy Island and the South Orkneys (Waluda et al. 2010).

To investigate the existence of sexual segregation in juveniles, we studied the body morphology and movements of 1–3-year-old Antarctic fur seals deployed with GLS loggers. GLS loggers record light intensity, which is used to calculate sunrise and sunset times and infer movement behaviour over several months or years (Joo et al. 2019). We hypothesized that: (1) male juveniles would be larger in body size than females as a result of sexual selection pressures; (2) males would use a larger area than females, exploring wider foraging grounds to maximise energy intake to grow; (3) females would spend more time in proximity to the breeding site, as they become sexually mature earlier than males and must seek out their first mating; (4) the sexes may be exposed to different stressors (e.g. inter-specific competition and fishery interactions) as a result of sexual segregation.

3.3. Methods

3.3.1. Ethics Statement

Animal handling procedures were approved by the British Antarctic Survey Animal Ethics and Welfare Review Body (AWERB) and adhered to the ASAB and ARRIVE guidelines and legal requirements of the South Georgia Government.

3.3.2. GLS Tag Deployment

During austral summers between 4th January 2007 and 13th January 2012, 26 male and 19 female juvenile Antarctic fur seals (estimated as 1 – 3 years of age; Table 3.1) were deployed with GLS loggers at Bird Island, South Georgia (54.01° S, 38.05° W). Each seal was restrained (as described by Gentry & Holt 1982) and a GLS logger developed by the British Antarctic Survey (Mk 4 (25 × 21 × 7 mm, 5 g), Mk 5 (18 x 18 x 6.5 mm, 3.6 g), Mk 9 (16 x 14 x 6 mm, 2.5 g) or Mk 15 (16 *x* 14 *x* 6 mm, 2.5 g)) secured to a Dalton jumbo roto tag, fixed to the trailing edge of a fore-flipper (as described by Staniland et al. 2012). GLS loggers were retrieved (by cutting cable ties around the logger) when seals were opportunistically recaptured. At each capture seal mass, total body length, flipper span and girth were recorded where possible (Committee on Marine Mammals 1967).

3.3.3. GLS Programming

Prior to deployment, GLS loggers were calibrated for at least one month with a full view of the sky at Bird Island. GLS loggers measured light intensity every minute and recorded the maximum light intensity in each 10-minute interval. They also measured salt-water immersion every 3 seconds and recorded the total number of immersion events in each 10 minute interval: a value of 200 shows the

GLS logger was immersed for the entire period, while a value of 0 shows the GLS logger was completely dry. GLS loggers additionally measured sea surface temperature when the logger was immersed for at least 20 mins.

3.3.4. Data Processing

Data was downloaded from GLS loggers using the BasTrak software (British Antarctic Survey, Cambridge, UK). Light data was pre-processed following methods described by Lisovski et al. (2019) using the TwGeos package (Lisovski et al. 2016) in R v3.6.0 (R Core Team 2019). Specifically, the daily sunrise and sunset times (twilight times) were defined as the times when light intensity reaches a pre-determined threshold of 2. Next, the zenith angle (angle between the sun and vertical) and parameters of the error distribution of twilight times, causing uncertainties in location estimates (Lisovski et al. 2012), were determined from the calibration data. These parameters were then used to estimate the movement trajectories using the R Package SGAT (Wotherspoon et al. 2019). The applied Bayesian method makes use of Markov Chain Monte Carlo (MCMC) simulations and allows incorporation of the twilight model (calibration), a movement model and a spatial mask to improve location estimates and estimates uncertainty (Lisovski et al. 2019). A gamma distribution was used to describe the movement model assuming a mean swimming speed of 1 m/s and variance of 0.08 m/s, suitable for relatively slow-moving species and considered an appropriate estimate for mean juvenile Antarctic fur seal speed as mean surface swimming speeds of adult otariids ranges from 0.6 – 1.6 m/s (Ponganis et al. 1990). The spatial mask, consisting of a combined land mask and SST probability mask, was made using a land map and maps of mean daily sea surface temperatures (SST) from the NOAA OI SST V2 High Resolution Dataset. The spatial mask enabled finer accuracy of location estimates by preventing implausible movements of seals across land and by incorporating probability of locations according to mean daily SST and GLS logger SST readings eliminating temperature ranges that were out of the temperature range recorded by the tag' (particularly during 2–3 weeks around the equinox when location estimates are inaccurate using light levels alone). Mk9 tags did not record SST data and hence a land mask was used alone for these seals. The proposals for the MCMC simulations were tuned using 1000 posterior draws and a modified model with relaxed assumptions before running the model with 1000 iterations. Tracks were summarised to produce median tracks and credibility intervals (95 % CRI).

3.3.5. Data Analysis

To identify whether body morphology significantly differed between male and female juveniles, we ran a Principal Components Analysis (PCA) on morphology data, then ran the outputs from Principal Component 1 and 2 (PC1 and PC2) in a student's t-test for PC1 (as variances were equal) and Welch's t-test for PC2 (as variances were not equal). One male seal (w7397) was excluded from this analysis, as its span was not obtained.

To determine whether spatial sexual segregation occurred in juveniles during the annual cycle we used latitude and longitude from 50 randomly selected tracks from each individual as separate response variables in generalised additive mixed models (GAMMs) using the mgcv package in R (Wood 2017). We included day of the year, sex, and their interactions as predictor variables in candidate models. We specified juvenile ID as a random effect to account for variation between individuals and applied a corARMA structure (p=1, q=0) to account for temporal autocorrelation in residuals. Candidate models were ranked according to their Akaike Information Criterion (AIC) and the model with the lowest AIC was considered the best fit model (the simplest model was selected if AICs differed by less than 2. Residual plots were checked for normality and homoscedasticity.

We then tested whether the size of foraging areas differed between male and female juveniles in three key time periods during the year: Dec – Jan (adult males and females are present on breeding beaches); Feb – Apr (adult males have left breeding beaches but adult females are present when suckling their pups); May – Nov (non-breeding period). For each seal and each time period, we used all simulated tracks to calculate a utilisation distribution (UD) by the ad hoc method, using the adehabitatHR package in R (Calenge 2020). The 95 % home range was then deduced from each utilisation distribution, signifying the smallest area where the probability of relocating the individual was 95 %. We log-transformed the home range outputs (to achieve a normal distribution), then used the output as a response variable in a General Linear Model (GLM). We included time period, sex, body size at deployment (indicated by PC1) and their interactions in candidate models and selected the best-fit model as previously described.

3.4. Results

3.4.1. Sample Sizes

Twenty-six males and 19 females were GLS-tracked from Bird Island (Table 3.1). This included 23 males and 14 females tracked in Dec – Jan, 26 males and 19 females tracked in Feb – Apr, and 25 and 16 females tracked in May – Nov.

3.4.2. Size Dimorphism

Juvenile body length, span, girth and mass were highly correlated with Pearson correlation coefficients ranging from 0.62 – 0.91. Male juveniles were larger than females, as indicated by PCA. Specifically, loadings for PC1 were mass (-0.53), length (-0.50), girth (-0.49) then span (-0.48), whereas loadings for PC2 were span (-0.80), girth (0.54), length (0.22) and mass (0.02). PC1 and PC2 explained 86.7 % and 7.0 % of the variability in morphology data respectively. The mean scores significantly differed between males and females by 1.32 for PC1 (Student's t-test: $t = 2.4$ $p = 0.02$), but did not significantly differ between males and females for PC2 (Welch's t-test: $t = 0.53$, $p = 0.60$) (Fig. 3.1).

Table 3.1. Details of GLS logger deployments on juvenile Antarctic fur seals at Bird Island, South Georgia, between 4th January 2007 and 13th January 2012. Body measurements were taken during GLS deployment.

Seal ID/Tag	**Sex**	**GLS model**	**Deployment start**	**Deployment end**	**Mass (kg)**	**Length (cm)**	**Girth (cm)**	**Span (cm)**
W7395	M	Mk5	16/01/2007	25/04/2008	44.2	140	77	113
W7397	M	Mk5	16/01/2007	30/07/2007	45.5	141	91	-
W7398	M	Mk5	16/01/2007	16/12/2007	25.5	121	64	86
W7399	M	Mk5	16/01/2007	12/11/2007	43.8	145	78	115
W7402	F	Mk5	23/01/2007	29/12/2007	21.2	113	63	87
W7404	M	Mk5	23/01/2007	03/01/2008	32.9	128	71	101
W7410	F	Mk5	28/01/2007	20/01/2008	15.5	105	57	87
W7413	M	Mk5	26/02/2007	10/12/2007	24.8	111	67	100
W7530	M	Mk9	09/01/2008	18/08/2008	17.2	101	59	96
W7556	F	Mk9	25/01/2008	30/04/2008	17.7	96	61	92
W7587	F	Mk4	22/02/2008	06/04/2008	15.2	97	56	90
W8376	M	Mk9	12/02/2010	03/01/2011	27.9	109	68	111
W8378	F	Mk9	12/02/2010	09/12/2010	23.5	115	66	105
W8379	M	Mk9	12/02/2010	31/10/2010	36.8	130	80	116
W8381	M	Mk9	28/02/2010	25/09/2010	33.4	122	63	106
W8391	F	Mk9	04/03/2010	08/12/2010	23.4	110	63	113
W8637	F	Mk15	29/03/2011	30/09/2011	21.5	104	54	96
W8640	F	Mk15	29/03/2011	29/12/2011	23.7	101	59	98
W8645	F	Mk15	31/03/2011	12/01/2012	25.6	116	59	106
W8653	F	Mk15	06/04/2011	05/10/2011	21.2	116	56.5	89
W8667	F	Mk15	09/04/2011	08/01/2012	15.6	92	52.5	86
W8582	F	Mk15	10/04/2011	06/10/2011	27.8	112	63	104
W8678	M	Mk15	12/04/2011	09/12/2011	18.7	99	51	96
W8251	F	Mk15	17/04/2011	20/12/2011	28.9	119	65	109
W8687	F	Mk15	13/04/2011	08/01/2012	17	95	53	82
W8690	F	Mk15	13/04/2011	16/02/2012	16.7	99	58	87.5
W8695	F	Mk15	15/04/2011	07/01/2012	27.9	106	68	101
W8902	F	Mk15	17/04/2011	10/11/2011	22.3	99	59	93
W8904	M	Mk15	17/04/2011	24/11/2011	14.3	99	50	88
W8702	M	Mk15	07/01/2012	06/01/2013	25.2	118	59	100
W8706	F	Mk15	09/01/2012	05/02/2012	20	99	60	83
W8708	M	Mk15	10/01/2012	26/10/2014	19.1	99	59	89
W8710	M	Mk15	09/01/2012	06/02/2013	19.9	98	56	98
W8712	M	Mk15	09/01/2012	06/12/2012	42.1	137	69	126
W8714	F	Mk15	09/01/2012	08/01/2013	22.8	101	66	90
W8716	M	Mk15	10/01/2012	06/02/2013	30	118	61	107
W8723	M	Mk15	11/01/2012	28/08/2012	23	108	60	101
W8736	M	Mk15	13/01/2012	03/12/2012	38	124	68	115
W8739	M	Mk15	13/01/2012	16/11/2012	28.8	110	67	104
W8740	M	Mk15	13/01/2012	06/02/2013	35.8	125	71	117
W8686	M	Mk15	13/04/2011	30/01/2012	19.6	103	57	88
W8715	M	Mk15	09/01/2012	13/10/2012	26.4	114	66	106
W8720	M	Mk15	10/01/2012	19/02/2012	15.2	96	54	87
W8709	M	Mk15	09/01/2012	03/09/2012	16.3	99	54	87
W8724	M	Mk15	11/01/2012	05/12/2012	21.9	98	62	97

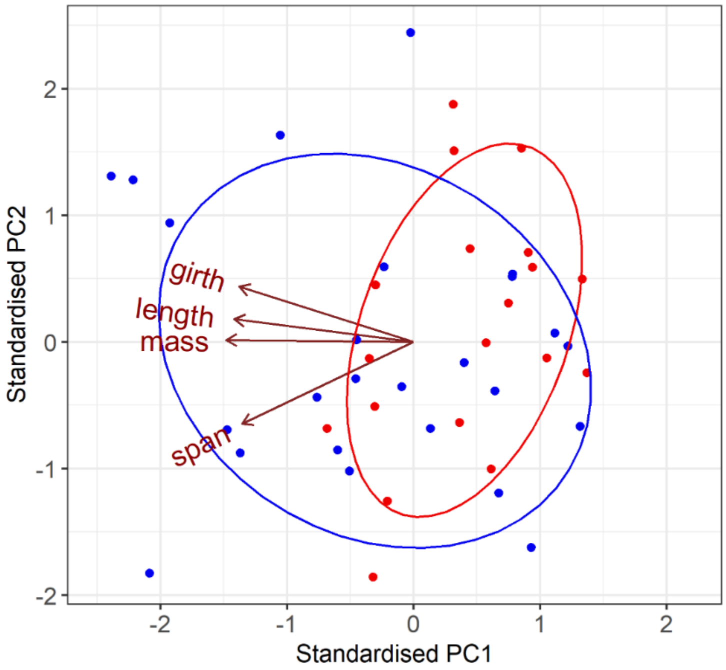

Figure 3.1. Relationship between PC1 and PC2 using morphology data from 19 female (red) and 25 male (blue) juvenile Antarctic fur seals.

3.4.3. Foraging Distribution

Sexual segregation was present in juvenile foraging distribution during the annual cycle. Males generally foraged south of the Polar Front and near the Antarctic Peninsula, whereas females generally foraged closer to South Georgia and north of the Polar Front (with one seal exploring waters surrounding the Falkland Islands) (Fig. 3.2). This sexual segregation predominantly occurred in latitude, as males foraged further south than females on average throughout the year (Fig. 3.3a; Table 3.2a). Patterns in longitude also differed significantly between the sexes, although the effect size was low at 0.08 (Fig. 3.3b; Table 3.2b).

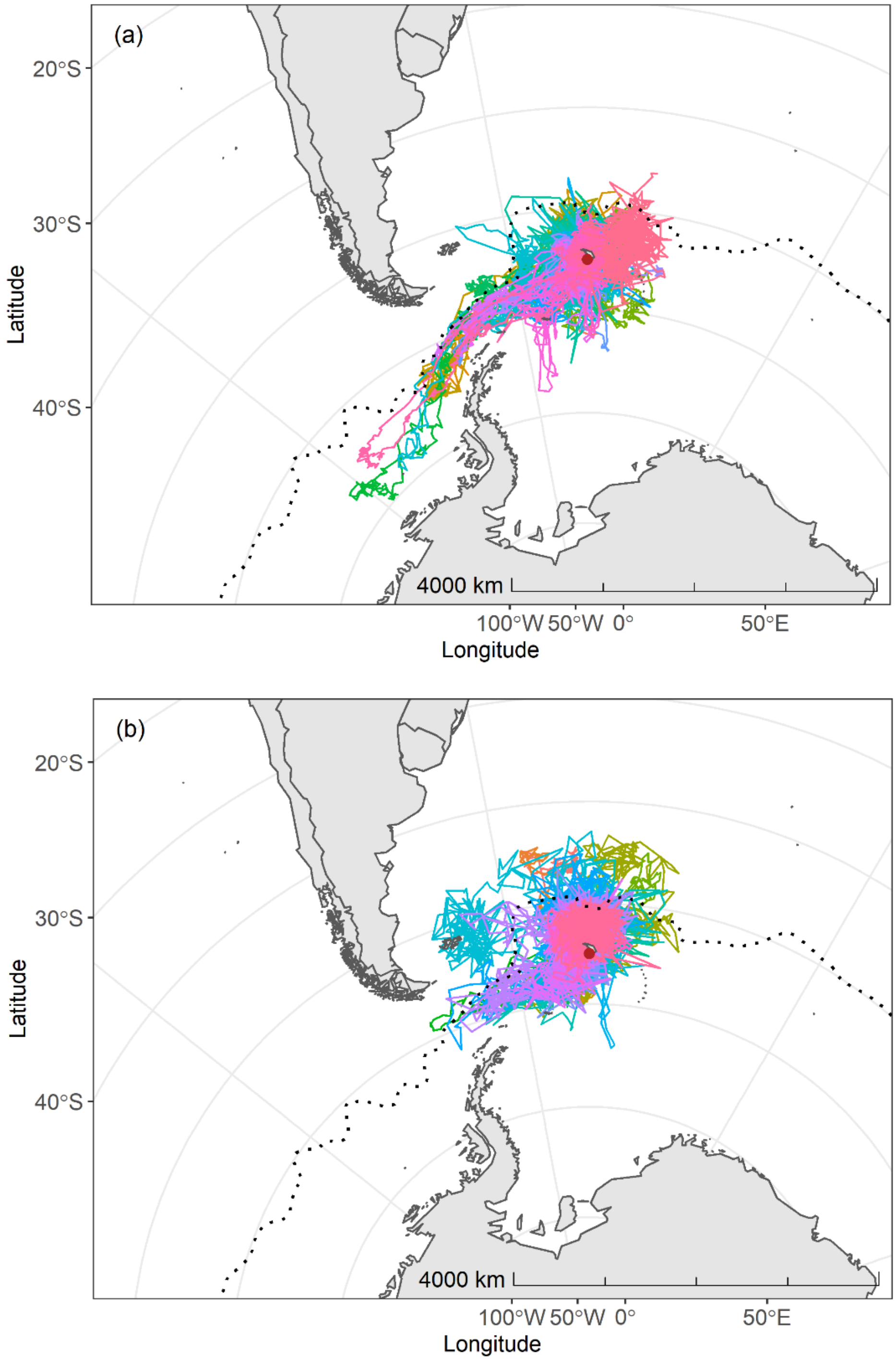

Figure 3.2. Median tracks of (a) 26 male and (b) 19 female juvenile Antarctic fur seals tracked with GLS loggers between 16th January 2007 and 26th October 2014. Grey shaded areas show South America and Antarctica, red dot shows deployment site (Bird Island, South Georgia), dotted line indicates position of the Polar Front, and colours show different individuals.

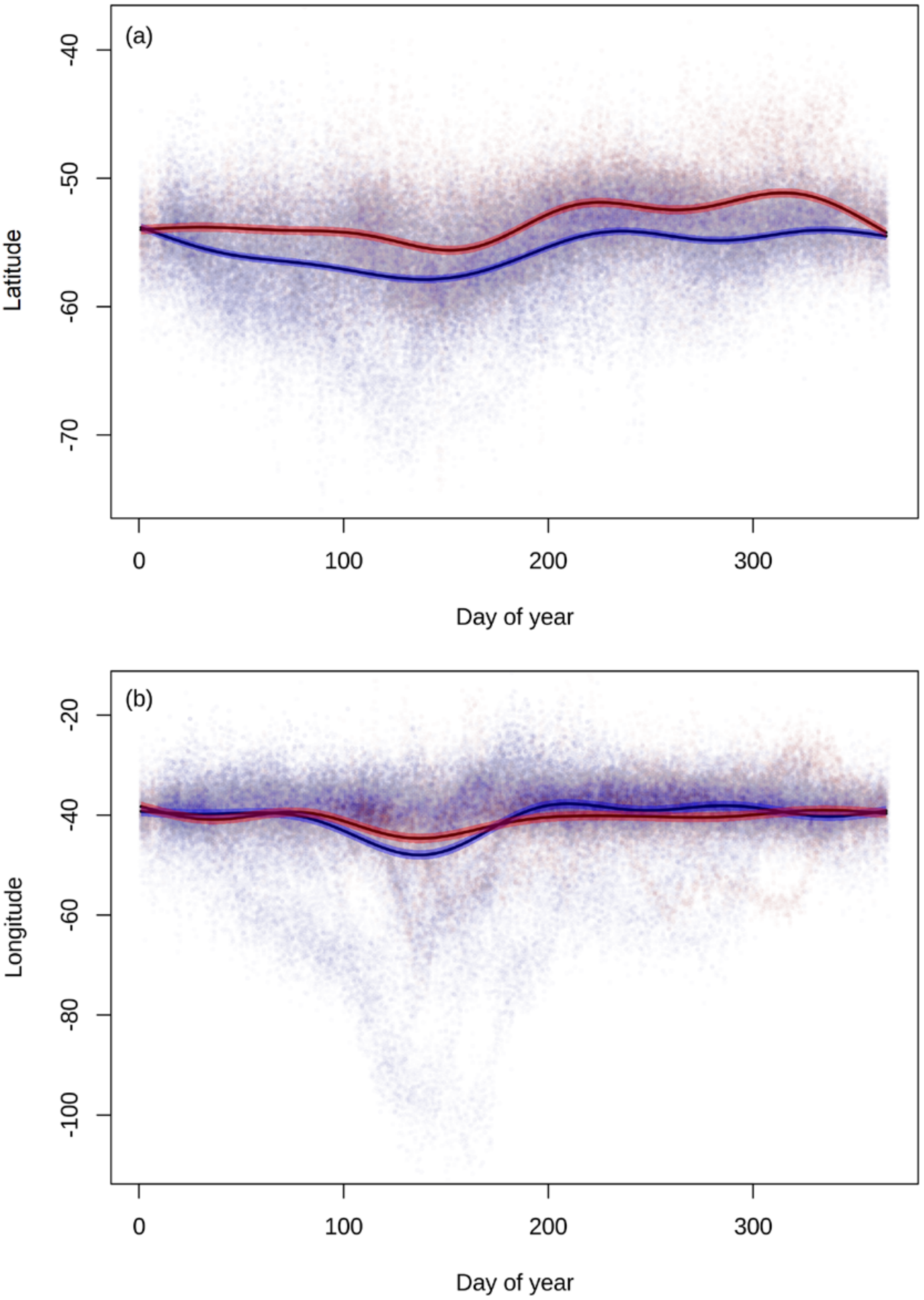

Figure 3.3. (a) Latitude and (b) longitude of GLS-tracked juvenile Antarctic fur seals throughout the year. Black lines indicate fitted values from Generalised Additive Mixed Models, shading represents standard error of fitted values, and

coloured lines show raw data values from 50 randomly selected simulated tracks from each individual: red=females (n=19); blue=males (n=26).

Table 3.2. Generalised Additive Mixed Model selection to study the effect of sex and day of year on latitude and longitude of GLS-tracked juvenile Antarctic fur seals. Akaike's information criterion; ΔAIC: difference in AIC between candidate model and best-fit model; R^2: proportion of variance explained by predictors; n: number of observations of the response variable. Model parameters are shown for the best-fit models.

Model terms	**AIC**	**ΔAIC**	**R^2**	**n**
<u>Latitude</u>				
Sex + s(Day of year, by Sex)	931911.7	0	0.23	182772
s(Day of year, by Sex)	931929.1	17.4	0.14	182772
Sex + s(Day of year)	933175.3	1263.6	0.22	182772
s(Day of year)	933192.3	1280.6	0.14	182772
Sex	962134.5	30222.8	0.10	182772
Parametric coefficients	**Value**	**SE**	**t-value**	**p-value**
Intercept	-53.4	0.36	-148.1	<0.0001
sex (male)	-2.3	0.47	-4.9	<0.0001
Approximate significance of smooth terms	**edf**	**Ref.df**	**F**	**p-value**
s(Day of year, by female)	8.97	8.97	1373	<0.0001
s(Day of year, by male)	8.97	8.97	2311	<0.0001

Model terms	**AIC**	**ΔAIC**	**R^2**	**n**
<u>Longitude</u>				
s(Day of year, by Sex)	1233288	0	0.08	182772
Sex + s(Day of year, by Sex)	1233288	0	0.09	182772
Sex + s(Day of year)	1235989	2701	0.08	182772
s(Day of year)	1235989	2701	0.07	182772
Sex	1257621	24333	0.01	182772
Parametric coefficients	**Value**	**SE**	**t-value**	**p-value**
Intercept	-41.0	0.96	-42.6	<0.0001
Approximate significance of smooth terms	**edf**	**Ref.df**	**F**	**p-value**
s(Day of year, by female)	8.95	8.95	372.7	<0.0001
S(Day of year, by male)	8.99	8.99	2541.8	<0.0001

3.4.4. Extent of Foraging Areas

Extent of foraging areas did not significantly differ between male and female juveniles. However, extent of foraging areas significantly differed between time periods, and larger individuals (with lower PC1 values at deployment) had significantly larger home ranges than smaller individuals (Table 3.3; Fig. 3.4). In Dec – Jan (when both adult males and females were present on breeding sites), both sexes remained in proximity to Bird Island and the average home range area was 1,380,228 ± 49,820 km^2 (± standard error). In Feb – Apr (when adult males have departed from breeding beaches) some males foraged south in maritime Antarctica and most females remained around South Georgia and the average home range area was 1,767,875 ± 122446 km^2. In May – Nov (the non-breeding season), average home range area increased to 2,178,135 ± 137297 km^2.

Table 3.3. General Linear Model selection to study the effect of sex, body size (indicated by PC1) and time period on home range size of juvenile Antarctic fur seals. Akaike's information criterion; ΔAIC: difference in AIC between candidate model and best-fit model; R^2: proportion of variance explained by predictors; n: number of observations of the response variable. Candidate models with ΔAIC < 6 are shown and model parameters are shown for the best-fit model.

Model terms	**AIC**	**ΔAIC**	**R^2**	**n**
Time period + Body size	100.3	0	0.20	120
Time period + Body size + Time period: Body size	101.5	1.18	0.21	
Time period + Body size + Sex	102.5	2.22	0.19	120
Time period + Body size + Sex + Time period: Body size	103.8	3.47	0.20	120
Time period + Body size + Sex + Time period: Sex	103.9	3.56	0.20	120
Time period + Body size + Sex + Body size: Sex	104.5	4.25	0.19	120
Time period + Body size + Sex + Time period: Body size + Time period: Sex	104.7	4.39	0.19	120
Time period + Body size + Sex + Body size: Sex	105.9	5.57	0.19	120
Time period + Body size + Sex + Time period: Sex + Body size: Sex	106.0	5.74	0.19	120
	Value	**SE**	**t-value**	**p-value**
Intercept	27.9	0.06	468.3	< 0.001
Months (Feb – Apr)	0.17	0.08	2.1	0.04
Months (May – Nov)	0.38	0.08	4.7	< 0.001
Body size	-0.06	0.02	-3.13	0.002

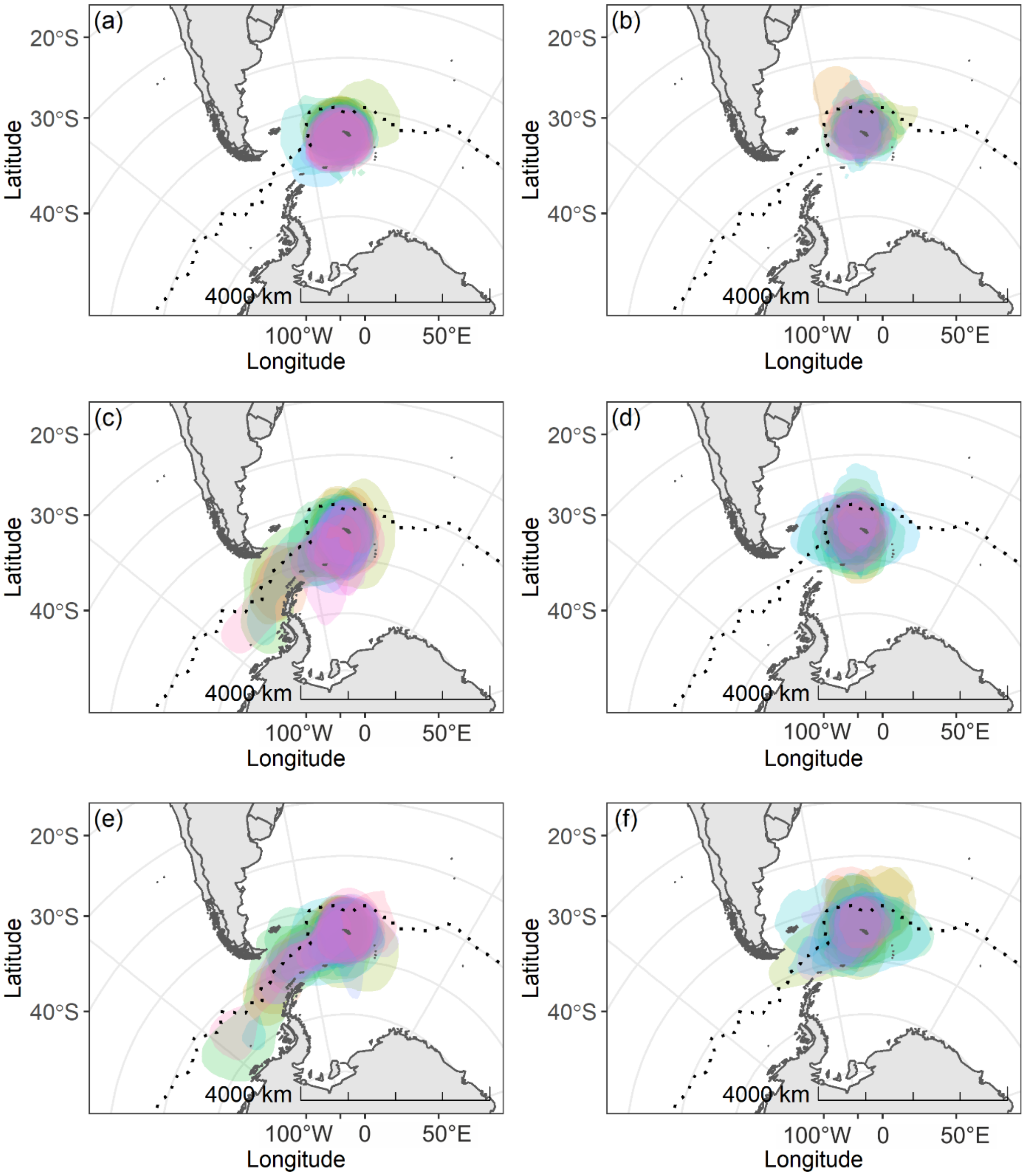

Figure. 3.4. Home ranges (where probability of relocating each individual is 95 %) of (a) 23 males and (b) 14 females in Dec – Jan; (c) 26 males and (d) 19 females in Feb – Apr, and (e) 25 males and (f) 16 females in May – Nov. Colours indicate different individuals.

3.5. Discussion

We found that sex differences in body size and foraging distribution can occur in a highly polygynous species during the juvenile life stage. Male juvenile Antarctic fur seals (1 – 3 years of age at deployment) were significantly larger than females and generally foraged further south near the Antarctic Peninsula, whereas females foraged closer to South Georgia and the Polar Front. Contrary to our prediction, extent of foraging areas did not significantly differ between the sexes. We discuss the underlying drivers and key ecological consequences of these findings.

3.5.1. Sexual Size Dimorphism

Sexual size dimorphism may be driven by sex differences in reproductive success, which is more varied in males that females (Darwin 1871). In polygynous species sexual selection pressures act on males to grow fast, as larger males can compete for mates more successfully (Isaac 2005). This pressure was reflected in the higher mass and body length of juvenile males compared to females (indicated by PC1), as these metrics increase more rapidly in males from birth to 5 years of age (Payne 1979). Males also invest more energy into lean tissue growth (Arnould et al. 1996), as future reproductive success will depend on fighting ability as well as fasting ability (Arnould & Duck 1997). In contrast, females grow more conservatively (Payne 1979) and accumulate greater fat stores (Arnould et al. 1996). This strategy decreases risk of starvation and enables females to invest resources in reproduction earlier than males to maximise lifetime reproductive output at the expense of reduced growth (Mueller et al. 2011).

3.5.2. Sexual Segregation in Foraging Distribution

Juveniles must develop a range of skills to forage independently, including successfully finding, competing for and handling food, as well as escaping predation (Sullivan et al. 1989; Daunt et al. 2007; Carter et al. 2017). Antarctic fur seals predominantly feed on krill, *Euphausia superba,* but also consume squid and fish (e.g. mackerel icefish, *Champsocephalus gunnari*, which is associated with krill aggregations) (Doidge & Croxall 1985; Reid 1995; Reid & Arnould 1996). Since juveniles have no immediate reproductive requirements, they have time to explore and discover the most productive foraging areas (Salton et al. 2019), as matching the distribution of their preferred prey can maximise foraging efficiency (Stephens and Krebs 1986). The juvenile Antarctic fur seals in this study dispersed further at sea than weaners tracked from the same colony in their first year of life (Warren et al. 2006), which is unsurprising as these juveniles were older and larger in body size so had both the experience and physiological abilities to travel further. Sexual segregation was also more apparent in juveniles than weaners, in line with greater sex differences in body size, hinting that sexual size dimorphism likely contributes to the development of sexual segregation in Antarctic fur seals.

Sexual segregation was present, predominantly in latitude, which may result from prey distribution coupled with inter-linking drivers of sexual size dimorphism, sex differences in risk, and sex-specific social roles. Juvenile females foraged near South Georgia and some individuals foraged north of the Polar Front. These female foraging distributions coincided with an Area of Ecological Significance (AES) spanning the Scotia Sea and surrounding waters, where prey available to marine predators is high in biodiversity and biomass (Hindell et al. 2020). Adult females and an abundance of marine predators also forage in this region (Boyd et al. 2002; Staniland et al. 2012; Arthur et al. 2015; Hindell et al. 2020). Hence, competition for resources is likely intense, which could lead to divergent foraging strategies (Schoener 185; Araújo et al. 2008). Indeed, ~ 30 % of adult females may consistently forage north of the Polar Front and consume different prey to ~70 % of adult females that consistently forage to the south of it (Jones et al. 2020b). These divergent foraging strategies could initially develop in juveniles to maximise foraging efficiency. Young female seals may also adopt a more risk-averse strategy and target more predictable environments than males, spending less time searching for prey – as documented in recently weaned grey seal pups, *Halichoerus grypus* (Carter et al. 2019). Indeed, females must prioritise survival to fulfil their reproductive output (Trivers 1972; Clutton-Brock et al. 1982; Reeve and Fairbairn 2001; Schulte-Hostedde et al. 2001; Carter et al. 2019).

Juvenile males mainly foraged in proximity to South Georgia, the Polar Front and Antarctic Peninsula. Their foraging distribution overlapped with the AES (Hindell et al. 2020) and regions of high krill density, west of the Antarctic Peninsula (Atkinson et al. 2019). Male juveniles must consume enough prey to meet their higher energetic requirements and grow quickly. Since adult females (and other predators) may cause local depletion of prey near South Georgia, males may forage more successfully in maritime Antarctica (Boyd et al. 1998), where prey, particularly Antarctic krill, may be more abundant. The ability to forage further from the breeding site in cooler waters may be a function of their larger body size. Indeed, a larger body size can increase travel speed, aerobic limits (i.e. by increasing mass-specific oxygen stores; Fowler et al. 2006) and thermoregulation abilities (Staniland & Robinson 2008). Males are generally also less risk averse than females (e.g. Pellegrini 2004), and may forage closer to Antarctica as the benefits of food availability outweigh the higher costs of thermoregulation and risk of predation (e.g. from orcas, *Orcinus orca*, and leopard seals, *Hydrurga leptonyx*). Young male seals may adopt a more risk-prone foraging strategy than females, spending more time seeking the most productive foraging areas to maximise food intake and obtain a larger body size to improve ability to compete for future mates (e.g. Carter et al. 2019). These sex-specific foraging strategies may develop in juveniles and become more pronounced as sexual size dimorphism becomes more extreme in adults. Indeed, stable isotope values along adult Antarctic fur seal whiskers indicate that males forage further south than females and may spend more time foraging in maritime Antarctica as they grow and develop (Jones et al. 2020b).

3.5.3. Extent of Foraging Areas

Juvenile Antarctic fur seals extended their foraging areas between the breeding and non-breeding seasons, which may relate to presence of adults and seasonal changes in prey. In Dec – Jan adult males compete for mates, and juvenile females may approach breeding beaches to seek mating opportunities, conceiving from 2 years of age (Forcada & Staniland 2009). Juvenile female northern fur seals, *Callorhinus ursninus*, also show greater homing behaviour and fidelity to their natal sites than males likely due to their earlier sexual maturity (Kenyon & Wilke 1953; Zeppelin et al. 2019). In Feb – Apr dominant adult males are absent from breeding beaches, so juvenile males can come ashore to socialise and gain fighting skills with less likelihood of harassment by elders. In May – Nov juveniles extended their foraging areas, similarly to adults. At this time, adult males likely forage in maritime Antarctica (Jones et al. 2020b), whereas adult females are free from breeding constraints and concentrate their foraging efforts within ~500 km of Bird Island, although some females forage north of the Polar Front (1000 km) or south to the northern edge of the Antarctic pack ice (500 km) (Boyd et al. 2002; Staniland et al. 2012). Since juveniles have no immediate breeding constraints, their change in foraging extent may relate to seasonal changes in most common prey. Antarctic krill transports to South Georgia via currents when the Antarctic sea ice retreats in spring (Murphy et al. 2004). In winter, Antarctic krill around South Georgia is smaller in size and less lipid-rich (Reid 1995), so juvenile and adult Antarctic fur seals may forage further afield to exploit krill and/or alternative prey elsewhere. Juveniles potentially follow adults to gain experience of the most productive foraging areas to exploit in future years.

Contrary to our prediction, there was no sex difference in foraging extent. This result contrasts with findings by Bishop et al. (2018), whom found that male juvenile Steller sea lions had larger home ranges than females, attributed to their sexual size dimorphism and higher energetic requirements. The absence of sex-differences in juvenile Antarctic fur seal foraging extent could result from the nature of the prey landscape, or because body size alone (indicated by PC1) was a better indicator of foraging extent than sex. However, we cannot rule out that sex does not drive foraging extents, as body size and sex were confounded and hence difficult to disentangle.

3.5.4. Consequences of Sexual Segregation

Juveniles are vulnerable to mortality, and sexual segregation may expose the sexes to different area-specific stressors (Leung et al. 2012). For example, as a result of sexual segregation, female juvenile New Zealand sea lions, *Phocarctos hookeri*, overlap with trawl fisheries to a greater extent than males, exposing females to higher resource competition and risk of by-catch (Leung et al. 2012). Male and female juvenile Antarctic fur seals may overlap differently with the Antarctic krill fishery – the largest fishery by tonnage in the Southern Ocean (Nicol & Foster 2016). In summer, the fishery operates around the Antarctic Peninsula (and is closed at South Georgia; Government of South Georgia 2020), so fishing effort is more likely to overlap with the distribution of males. In winter, the krill fishery operates around South Georgia (outside of the 12 nm no-take zone; Government of South Georgia 2020), so may overlap with the distribution of both male and female juveniles. Krill fisheries are equipped with mandatory Seal Exclusion Devices that enable seals to escape nets (CCAMLR 2015; Iriarte 2020), so by-catch is likely to be minimal. However, competition may be high, and will likely increase as fishing pressure in the Southern Ocean is expected to intensify (Nicol et al. 2012; Chown & Brooks 2019).

Environmental change is also altering sub-Antarctic and Antarctic ecosystems. It has been suggested that Antarctic krill contracted towards Antarctica between 1926 and 2016 (Atkinson et al. 2019). Antarctic krill density is projected to decline in coastal waters around the Western Antarctic Peninsula (Hückstädt et al. 2020) and sub-Antarctic AESs are projected to expand in area and move southward (Hindell et al. 2020). Juveniles may alter their foraging distributions to match new regions of prey availability, and the sexes may respond differently. For example, males may forage further south to maximise food intake, at the expense of increased thermoregulatory costs, whereas more females may seek alternative foraging strategies (e.g. more individuals may exploit regions north of the Polar Front or forage in new regions further south near Antarctica as ice free areas open up). Given that female survival has a high impact on population dynamics (Boyd et al. 1995), the potential impacts of climate change on females (as opposed to males) will have greater implications for the species.

3.5.5. Conclusion

We found that sexual segregation in foraging distribution can develop in the juvenile life stage of a highly polygynous species. Although juveniles have no immediate breeding constraints, reproductive selection pressures still operate and can drive sexual segregation. Males must prioritise body growth as attaining a larger body size can benefit their future reproductive potential. Male juvenile Antarctic fur seals must therefore discover the most productive areas to maximise foraging intake, which in turn may enable them to forage further from the breeding site in cooler Antarctic waters. In contrast, females must prioritise survival to fulfil their future reproductive output and female juvenile Antarctic fur seals may gain sufficient resources to sustain themselves in waters surrounding South Georgia and the Polar Front. Temporal changes in foraging distributions may cause males and females to overlap with the krill fishery at different times of year, with males more likely to compete with the fishery in summer. Since juvenile survival has a high impact on population demography, understanding the nature of sexual segregation in juveniles of additional species is critical to improve understanding of ecology to develop effective conservation measures.

3.6. References

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Chapter 4. Intra-specific Niche Partitioning in Antarctic Fur Seals, *Arctocephalus gazella*

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4.1. Abstract

Competition for resources within a population can lead to niche partitioning between sexes, throughout ontogeny and among individuals, allowing con-specifics to co-exist. We aimed to quantify such partitioning in Antarctic fur seals, *Arctocephalus gazella*, breeding at South Georgia, which hosts ~ 95% of the world's population. Whiskers were collected from 20 adult males and 20 adult females and stable isotope ratios were quantified every 5 mm along the length of each whisker. Nitrogen isotope ratios ($\delta^{15}N$) were used as proxies for trophic position and carbon isotope ratios ($\delta^{13}C$) indicated foraging habitat. Sexual segregation was evident: $\delta^{13}C$ values were significantly lower in males than females, indicating males spent more time foraging south of the Polar Front in maritime Antarctica. In males $\delta^{13}C$ values declined with age, suggesting males spent more time foraging south throughout ontogeny. In females $\delta^{13}C$ values revealed two main foraging strategies: 70% of females spent most time foraging south of the Polar Front and had similar $\delta^{15}N$ values to males, while 30% of females spent most time foraging north of the Polar Front and had significantly higher $\delta^{15}N$ values. This niche partitioning may relax competition and ultimately elevate population carrying capacity with implications for ecology, evolution and conservation.

Keywords: *sexual segregation; competition; stable isotopes; foraging strategies; ontogeny; sexual size dimorphism*

4.2. Introduction

Competition for resources within a natural population can lead to diversification in resource use, ultimately allowing con-specifics to co-exist[1]. The ecological niche is positioned within an *n*-dimensional hypervolume[2], generally composed of spatial, temporal and trophic axes[3]. Overlap in ecological niches causes competition for resources, which could lead to competitive exclusion[4,5] and consequent niche shifts, whereby the position of a niche alters along the spatial, temporal, and/or trophic axis[6,7]. This niche partitioning commonly arises between sexes, but can also occur throughout ontogeny (hereby over an organism's lifespan) and among individuals within a species[8]. The consequent reduction in intra-specific competition may lead to a greater carrying capacity for the population as a whole[9-11]. Understanding the causes and consequences of intra-specific niche partitioning is therefore a major goal of research into the ecology, evolution and conservation of species[12,13].

Niche partitioning between sexes has been explained by several inter-connected hypotheses: (1) social roles: sexes segregating because they prefer to associate with the same class to benefit from social learning[14,15]; (2) activity budgets: sexes segregating to synchronise activities (e.g. sex-specific behaviours) to enable spatial coherence of the social group as a result of life history strategies[16,17]; (3) life history strategies: including constraint of parental care; and (4) sexual size dimorphism (common in species with polgynous mating systems[18]). The sexual size dimorphism hypothesis has received considerable attention as body size is a key trait influencing fitness[19]. Indeed, males with larger body sizes could compete for mates more successfully[20]. Smaller animals can subsist on sparser resources than larger animals[21,22], but may require higher quality food because of their higher mass-specific metabolic rates[23]. For example, adult female African elephants, *Loxodonta africana*, and their offspring feed in areas with greater plant diversity than larger adult males, which are less selective[24]. Size dimorphism also affects susceptibility to predation[25, 26] and physiological constraints (such as temperature and aerobic dive limits in diving predators[27]).

The above hypotheses relate to animals differently throughout ontogeny. As animals grow their life history priorities change, from maximising growth and survival as juveniles[28] to reproduction as adults[29,30]. Ontogenetic niche shifts may occur as animals grow, become sexually mature and gain more experience with age. They could differ between the sexes, as a result of different life history constraints that affect growth patterns and resulting sexual-size dimorphism. Ontogenetic niche shifts may be particularly pronounced in the larger sex, as larger animals experience a greater diversity of body sizes (and therefore energetic requirements) throughout development[3]. For example, Northern death adders, *Acanthopis praelongus*, predate on frogs and lizards as juveniles, and frogs and mammals as adults, but adult females (the larger sex) consume a greater proportion of mammals than adult males[31].

Niche differentiation can also occur among individuals, when individuals occupy only a subset of the population's niche (individual specialisation)[32]. The optimum strategy for an individual depends on its particular priorities and restraints[33]. Individuals may rank resources differently according to their energy gain per unit time[32] because of their size, age and experience, which affect diet preference, search efficiency and prey handling ability[34,35]. Different foraging strategies may therefore develop within the same sex. For example, female New Zealand sea lions, *Phocarctos hookeri*, have three distinct foraging strategies – a mechanism which could reduce intra-specific competition[36].

Intra-specific niche partitioning may influence population carrying capacity. Theory on habitat selection predicts that as population density and competition increases, animals should distribute themselves relative to habitat profitability[37]. Selection favours behavioural and morphological traits that reduce aggressive encounters and competition for resources[38,39]. Individuals may specialise on particular resources[40] and the population as a whole may exploit a wider range of resources[37]. For example, a population of feral horses, *Equus ferus caballus*, use a greater diversity of resources as population density increases[37]. It is therefore possible that generalist populations are composed of both generalist and specialist individuals[40]. These mechanisms reduce competition, which could increase individual reproductive success and consequently elevate population carrying capacity.

Antarctic fur seals, *Arctocephalus gazella*, are an ideal species to study intra-specific niche partitioning because of their large population size, breeding constraints and pronounced sexual size dimorphism (related to a highly polgygynous mating system). Intra-specific competition may be intense as populations have recovered from near extinction and are now in their millions with ~ 95% breeding at South Georgia, situated in the southern Atlantic Ocean[41] (Fig. 4.1.). The sexes have different breeding constraints, as females arrive at breeding beaches in late November/early December and are spatially restricted for four months while alternating foraging at sea with suckling their pups[27]. Males come ashore from October (peaking in numbers in December), to establish and defend harems (territorial males may fast at this time)[41]. After mating, males have no spatial or temporal constraints and observations suggest they migrate to higher latitudes in January[27, 41-43]. Short-term tracking of individual females has shown that they migrate widely in winter, moving north towards Patagonia, south towards the Antarctic pack-ice and within waters around South Georgia[44-46]. However, it is unknown if these movement patterns are consistent across years and/or individuals.

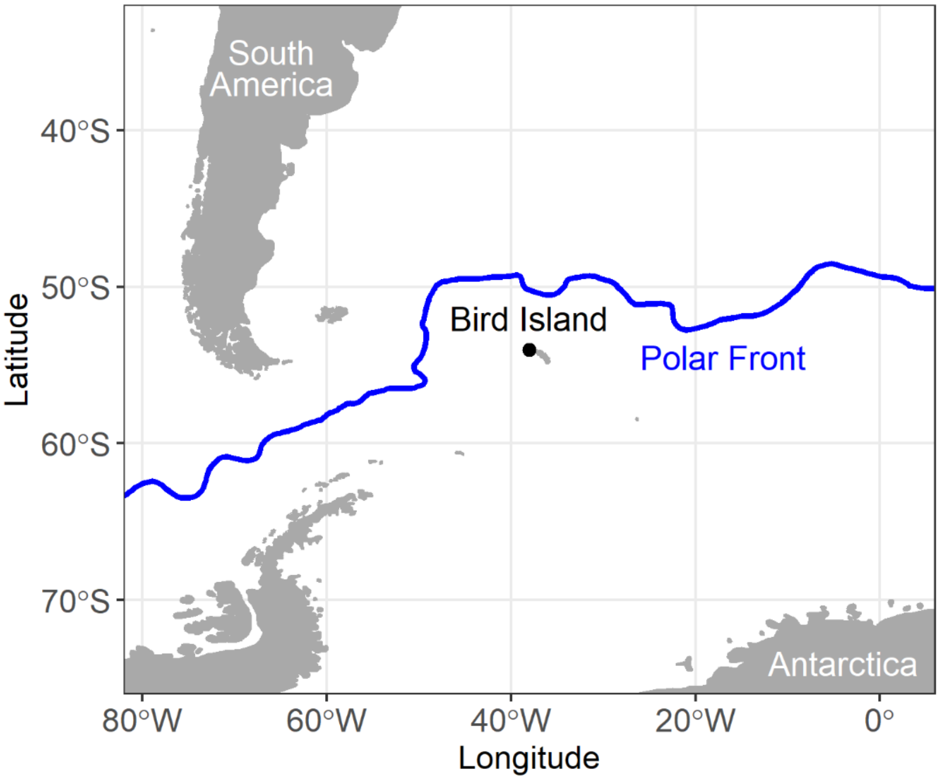

Figure 4.1. Map showing location of Bird Island, South Georgia, in relation to South America, Antarctica and the Polar Front. Map was created using R software (v3.6.1; https://www.R-project.org/).

The sexes have different growth trajectories that may facilitate ontogenetic niche shifts: females reach 90% of their maximum body length and become sexually mature by age four, while males grow to age seven (weighing up to four times more than females) and may not establish territories until age seven or eight[41,47]. Niche partitioning between sexes and throughout ontogeny has been determined in Antarctic fur seals breeding at Kerguelen[48]. However, Antarctic fur seals breeding at South Georgia may show different patterns in niche partitioning as a result of different environments, diets (i.e. Antarctic krill, *Euphausia superba*, predominates the diet at South Georgia[41], while myctophids dominate at Kerguelen[49]), and the higher competitive pressure associated with a higher population density.

Stable isotope analysis can provide quantitative insights into intra-specific niche partitioning[48,50] as stable isotope values are represented in delta-space as the ‘isotopic niche’[51]. Stable isotope values of a consumer’s tissues in part reflect its diet, plus an added trophic discrimination factor (TDF) signifying the offset in stable isotope values between the tissue and the consumer’s food[52]. This offset occurs as a result of physical and biological processes involved in assimilating resources[53]. Nitrogen isotope ratios ($^{15}N/^{14}N$ expressed as $\delta^{15}N$) are used as a proxy for trophic position, as the ratio increases stepwise with trophic level[54,55]. In marine systems carbon isotope ratios ($^{13}C/^{12}C$ expressed as $\delta^{13}C$) indicate the geographic source of prey as they vary with offshore versus inshore regions, pelagic versus benthic regions, and notably latitude[56,57]. The $\delta^{13}C$ values in particulate organic carbon in the oceans generally decline from the tropics to the poles[58,59] and can be distinct between water masses separated by frontal zones, reflected in $\delta^{13}C$ values of marine predators in sub-Antarctic regions[60-64].

To investigate the existence and development of intra-specific niche partitioning and its role in reducing competition we analysed $\delta^{15}N$ and $\delta^{13}C$ values along the length of adult Antarctic fur seal whiskers. These are ideal tissues to study ontogeny and individual specialisation as they are metabolically inert once formed, grow continuously, and are retained for years so can reflect the animal’s foraging over long time periods. We hypothesise that for Antarctic fur seals within the world’s largest breeding colony: (1) Males will have lower $\delta^{13}C$ values along their whiskers as they spend more time in maritime Antarctica than females; (2)

Males will show greater ontogenetic changes in their isotopic niche as they exhibit greater growth than females and do not breed until they are older; (3) Females will show greater variation in $\delta^{15}N$ values and $\delta^{13}C$ values, reflecting a wider range of post-breeding migration strategies; (4) Consistent annual patterns in the isotopic values will show that these migration strategies are consistent between years.

4.3. Results

4.3.1. Seal Age

Average age of adult males, obtained from external growth ridges in canines, was 8.94 ± 0.89 years for all 34 males and 8.70 ± 0.73 for 20 randomly selected males. These age determinations were in close agreement between any two readers, with 92.1% of all readings showing a 0 or ± 1 year difference. Age determinations were fairly consistent among all three readers, as the Index of Average Percentage Error (IAPE) was relatively low at 4.3%. Average minimum age of adult females at capture was 7.45 ± 2.17 years according to whisker growth rates.

4.3.2. Whisker Growth Rates

Whisker length significantly differed between males (mean =25.75 cm, SD= 6.95) and females (mean =16.29 cm, SD= 4.53, excluding the whisker root ~ 0.5 cm in length) (Mann-Whitney U test, U=42, $p < 0.001$). Male whiskers also grew significantly faster (0.096 ± 0.026 mm/day) than female whiskers (0.063 ± 0.013 mm/day), assuming oscillations corresponded to annual migrations (Welch's t-test, t=5.29, $p < 0.001$) (e.g. Figure 4.2; Supplementary Fig. S4.1). The calculated growth rates suggest that male whiskers were grown over an average of 6.93 ± 2.03 years and females an average of 7.18 ± 1.20 years.

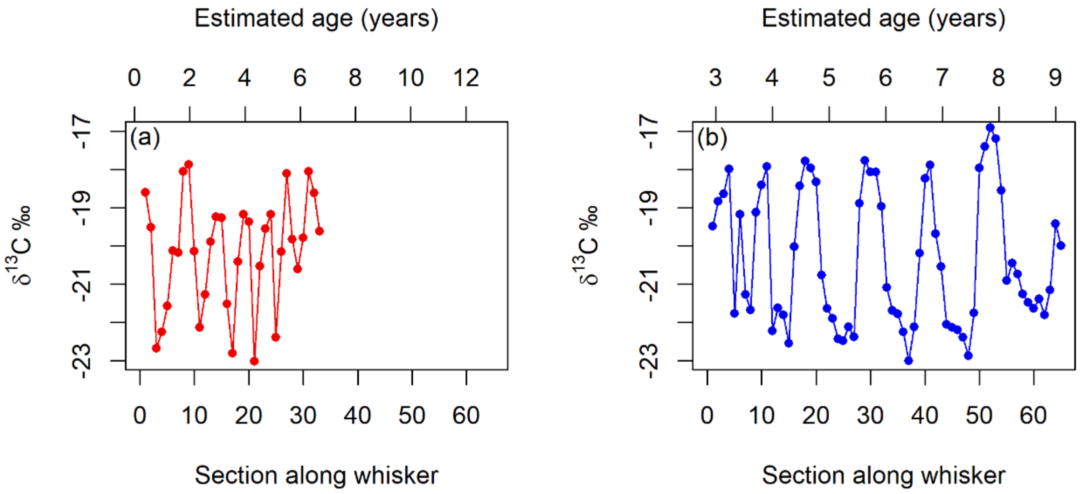

Figure 4.2. Oscillations in δ^{13}C values along the length of (a) a female Antarctic fur seal whisker (ID=w8859) and (b) a male Antarctic fur seal whisker (ID=w8821) from the distal to the facial end. Points are δ^{13}C values of samples taken every 5 mm along the length of each whisker and lines join these points. Figure was created using R software (v3.6.1; https://www.R-project.org/).

4.3.3. δ^{13}C Value of Polar Front

When seals foraged at the Polar Front we estimated that δ^{13}C values in their whiskers were about -18.92 ‰. This value was calculated from the average δ^{13}C value of prey species (myctophids and krill) collected at the Polar Front in 2009 (-20.98 ‰) (Supplementary Fig. S4.2), added to the estimated TDF for Antarctic fur seal whiskers (2.06 ‰ ± 1.79 for δ^{13}C). The variation in δ^{13}C values along each whisker suggested all 20 females and only six males foraged north of the Polar Front at any point during their lives (as their maximum δ^{13}C values exceeded -18.92 ‰) (Supplementary Table S4.3 and Table S4.4). Stable isotope bi-plots (Fig. 4.3.) revealed two isotopically distinct groups of females, separated by estimated δ^{13}C values of whiskers at the Polar Front: 14 individuals (female Group 1) had lower mean δ^{13}C values (using all δ^{13}C values along the whisker) than -18.92 ‰ and 6 individuals (female Group 2) had higher mean δ^{13}C values than -18.92 ‰.

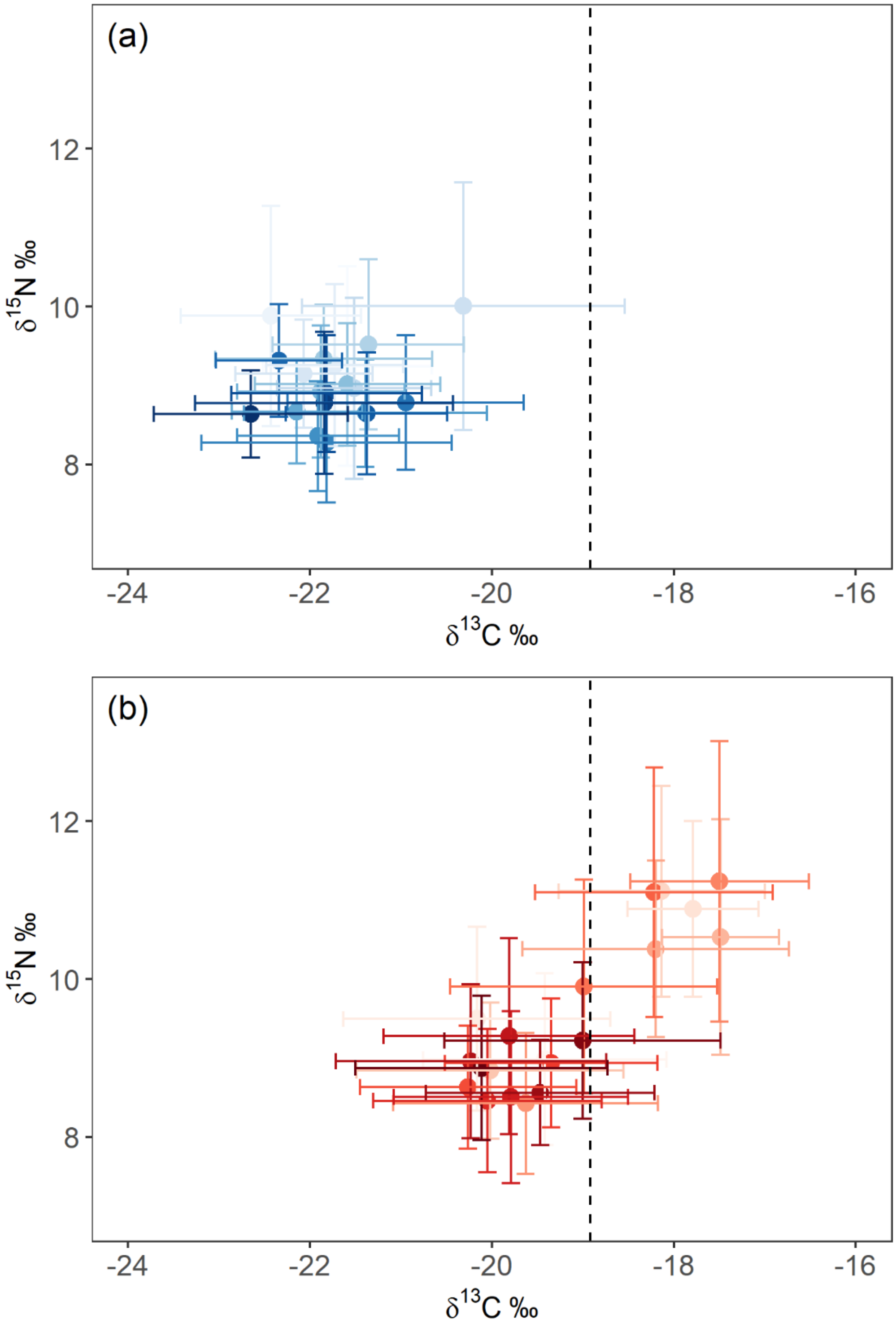

Figure 4.3. Bi-plots showing the means (points) and standard deviations (lines) of $\delta^{13}C$ and $\delta^{15}N$ values in whiskers of (a) 20 male and (b) 20 female Antarctic fur seals breeding at South Georgia. Dashed line indicates estimated $\delta^{13}C$ value of whiskers when seals foraged at the Polar Front. Figure was created using R software (v3.6.1; https://www.R-project.org/).

4.3.4. Sex-specific Niche Partitioning

Sexual segregation occurred primarily in foraging distribution (along the carbon axis), but not in trophic position (along the nitrogen axis). Mean $\delta^{13}C$ values were substantially lower in males than females (-21.68 ‰ ± 1.20 and -19.22 ‰ ± 1.58 respectively), while mean $\delta^{15}N$ values were similar in males and females (8.98 ‰ ± 1.04 and 9.47 ‰ ± 1.45 respectively). Females occupied a larger isotopic niche than males as Standard Ellipse Areas (SEAs) were 5.39 for females (Bayesian Standard Ellipse Area (SEA_B) mode: 5.49 with 95 % credibility interval 5.00 – 5.82), and 3.72 for males (SEA_B mode: 3.83 with 95 % credibility interval 3.50 – 3.96) (Fig. 4.4a.). Isotopic niches were distinct between the sexes, as male and female SEAs only overlapped by 1.2% (1.1% using Bayesian inference with 95 % credibility interval 0.089 – 2.37).

4.3.5. Isotopic Differences within Females

Female Group 1 mainly foraged at higher latitudes on potentially lower trophic level prey than female Group 2, as both mean $\delta^{15}N$ and $\delta^{13}C$ values were lower in female Group 1 than female Group 2 (means of each group: 8.96 ‰ ± 1.06 and 10.89 ‰ ± 1.46 respectively for $\delta^{15}N$; -19.71 ‰ ± 1.44 and -17.89 ‰ ± 1.13 respectively for $\delta^{13}C$). Female Group 1 occupied a slightly larger isotopic niche than female Group 2 as SEAs were 4.21 for female Group 1 (SEA_B mode: 4.20 with 95 % credibility interval 3.85 – 4.58) and 3.61 for female Group 2 (SEA_B mode: 3.62 with 95 % credibility interval 3.11 – 4.21). These female groups were largely distinct as SEAs overlapped by only 4.5% (3.1% using Bayesian inference with 95 % credibility interval 1.01 – 9.17) (Fig. 4.4b.). Males likely competed more with female Group 1 (SEAs overlapped by 5.1%; 4.8 % using Bayesian inference with 95 % credibility interval 3.26 – 6.77) than female Group 2 (SEAs did not overlap).

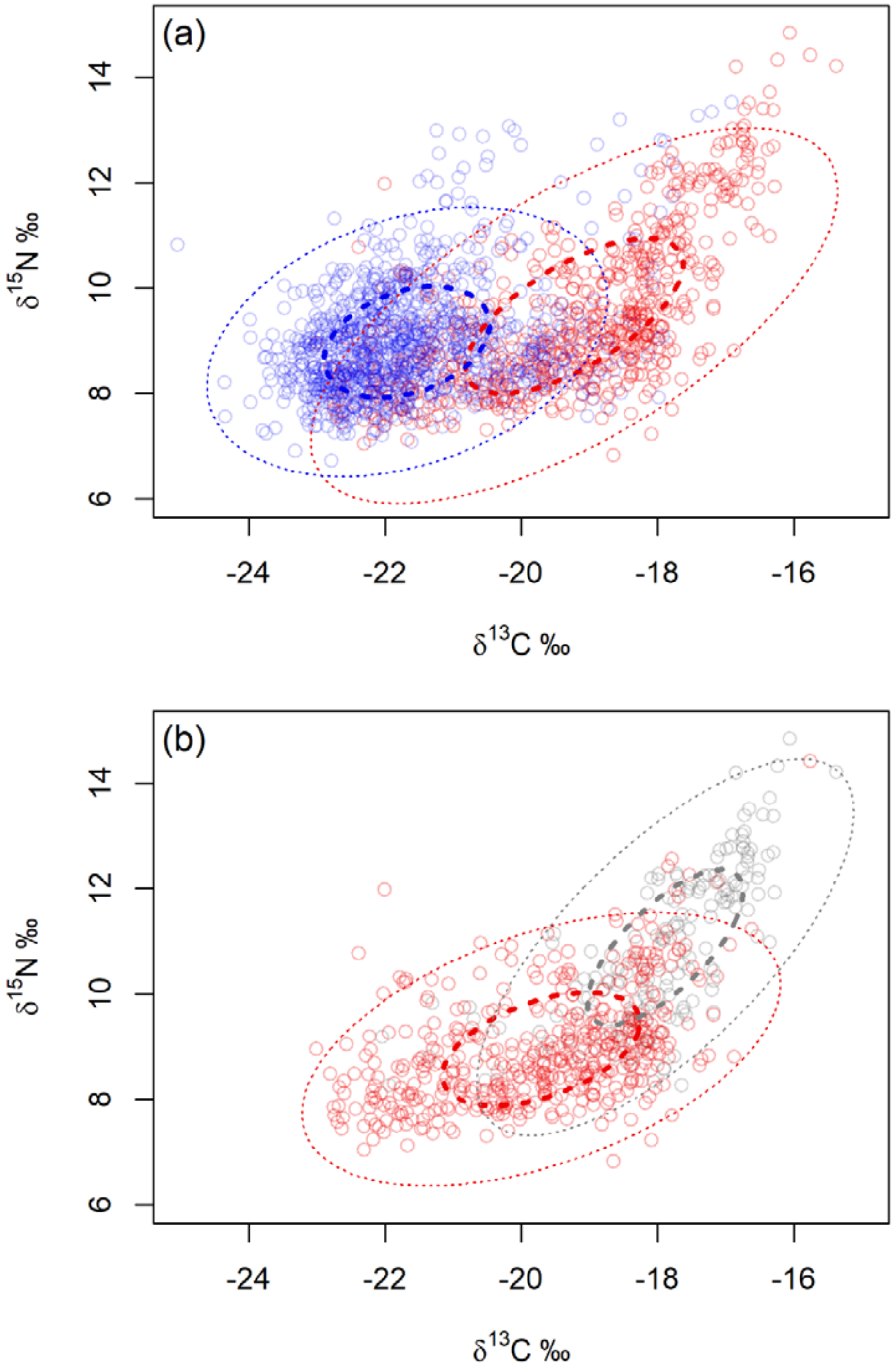

Figure. 4.4. Standard Ellipse Areas (SEAs) representing the isotopic niches of (a) 20 male (blue) and 20 female (red) Antarctic fur seals by $\delta^{13}C$ and $\delta^{15}N$ values in their whiskers and (b) isotopic niches of females according to the estimated $\delta^{13}C$ value of whiskers at the Polar Front (-18.92 ‰): female Group 1 (red) consists of 14 individuals with mean $\delta^{13}C$ values below -18.92 ‰; female Group 2 (grey) consists of 6 individuals with mean $\delta^{13}C$ values above -18.92 ‰. Points are isotopic values of each whisker sample, bold dashed ellipses use 40% of data

points and dotted ellipses use 95% of data points. Figure was created using R software (v3.6.1; https://www.R-project.org/).

4.3.6. Body Size Differences within Females

Females in Group 1 were significantly smaller than females in Group 2, as indicated by principal components analysis (PCA). Specifically, loadings for principal component 1(PC1) were highest for mass (-0.57), span (-0.52), length (-0.50) then girth (-0.40), while loadings for principal component 2 (PC2) were highest for girth (0.84), length (-0.47), span (-0.25) then mass (0.04). PC1 and PC2 explained 73.9% and 18.2% of variability in morphology data respectively. The mean scores between the two female groups differed by 1.97 for PC1 (Welch's t-test: t = -2.70, p = 0.02) and 0.98 for PC2 (Welch's t-test: t = 3.11, p = 0.01) (Supplementary Figure S4.5).

4.3.7. Ontogeny of Sexual Segregation in Isotopic Niche

Ontogenetic niche shifts were present in males on an annual scale. SEA increased between ages 0.5 – 2 years (although there were only 6 samples for males aged 0.5 – 1), then generally declined with age thereafter (Fig. 4.5; Supplementary Table S4.6). Overlap in isotopic niche between males of different age classes and SEA of female Group 1 increased from males aged 0.5 – 3 years, then declined with increasing male age until only 0.0015% of overlap occurred when males aged 6 – 7 years and no overlap in SEA occurred thereafter (Fig. 4.6; Supplementary Table S4.7). No overlap in SEA occurred between any male age group and female Group 2.

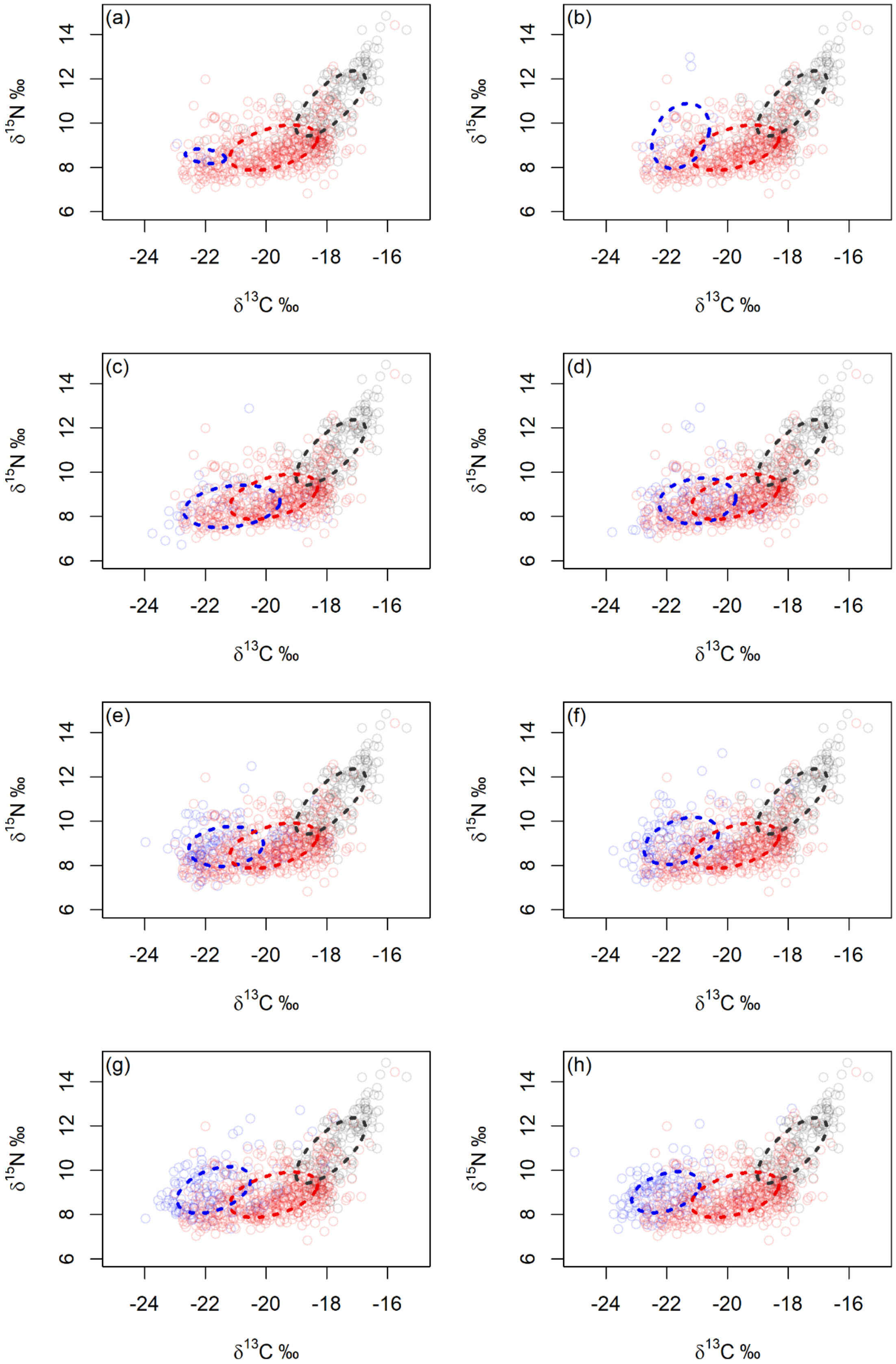

Figure 4.5. The ontogeny in isotopic niche of male Antarctic fur seals (blue) as they age compared to Standard Ellipse Areas (SEAs) of female Group 1 (red) and female Group 2 (grey). Males are aged (a) 0.5 – 1 year; (b) 1 – 2 years; (c)

2 – 3 years; (d) 3 – 4 years; (e) 4 – 5 years; (f) 5 – 6years; (g) 6 – 7 years; (h) 7 – 8 years. Points are isotopic values of each whisker sample and bold dashed ellipses represent SEAs using 40% of data points for each group: blue represents the isotopic niche of males; red SEA represents the overall isotopic niche of female Group 1 (females with lower mean δ^{13}C values than estimated δ^{13}C value of whiskers at the Polar Front) and grey SEA represents the overall isotopic niche of female Group 2 (females with lower mean δ^{13}C values than estimated δ^{13}C value of whiskers at the Polar Front). Figure was created using R software (v3.6.1; https://www.R-project.org/).

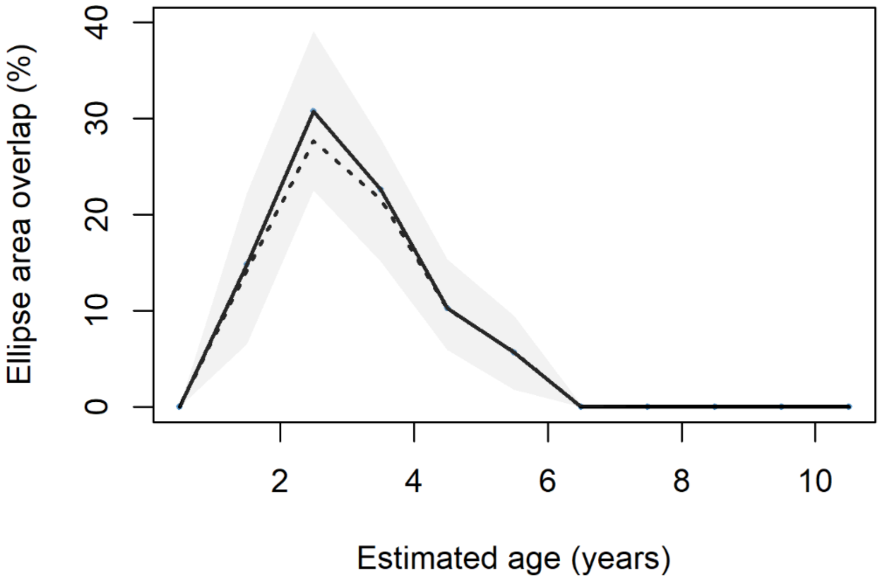

Figure 4.6. Percentage overlap in Standard Ellipse Area (SEA) of male Antarctic fur seals as they age with female Group 1 (females with lower mean δ^{13}C values than estimated δ^{13}C value of whiskers at the Polar Front). Bold line shows overlap in SEA using maximum likelihood, dotted line shows mode overlap using Bayesian inference, and grey shaded region shows 95% credibility interval around this mode. Figure was created using R software (v3.6.1; https://www.R-project.org/).

4.3.8. Contributions of Sex, Age and Individual to Isotopic Niche Differentiation

The δ^{13}C values along the length of whiskers, indicating changes in foraging distribution throughout ontogeny, were best explained by group (males, female Group 1 and female Group 2) and age (linear mixed model; likelihood ratio test LR = 76.4, p < 0.001; conditional R-squared = 49.3%). The δ^{13}C values significantly differed among all three groups and values declined as seals aged

(Table 4.1; Fig. 4.7a). Foraging distribution was highly generalised within the sample population, as the individual specialisation value was 0.89.

The estimated portion of time that seals spent north of the Polar Front (based on $\delta^{13}C$ values in sampled whisker segments and estimated $\delta^{13}C$ value of whiskers when seals foraged at the Polar Front) was best described by group alone (Generalised linear mixed model; likelihood ratio test LR = 90.4, df = 2, $p < 0.001$). Female Group 2 spent the highest percentage of time north of the Polar Front (mean = 85.8% ± 8.7), followed by female Group 1 (mean = 32.6% ± 14.4) and males (mean = 2.6% ± 6.6).

The $\delta^{15}N$ values along the length of whiskers, indicating changes in trophic position, throughout ontogeny, were best explained by group and age (linear mixed model; likelihood ratio test LR = 7.72, p = 0.006; conditional R^2 = 43.4%). Trends in $\delta^{15}N$ values significantly increased with age for all groups and $\delta^{15}N$ values significantly differed between males and female Group 2 but not female Group 1 (Table 4.1; Fig. 4.7b). Individuals were slightly less generalised in trophic position than foraging distribution within the sample population, as the individual specialisation value was 0.76.

Table 4.1. Results of best-fit linear mixed models explaining the change in $\delta^{13}C$ and $\delta^{15}N$ values along the length of Antarctic fur seal whiskers: males, female Group 1 (females with lower mean $\delta^{13}C$ values than estimated $\delta^{13}C$ value of whiskers at the Polar Front) and female Group 2 (females with higher mean $\delta^{13}C$ values than estimated $\delta^{13}C$ value of whiskers at the Polar Front).

Fixed effects	**Intercept Value**	**Degrees of freedom**	**p-value**
$\delta^{13}C$			
Male (Intercept)	-21.61	1596	<0.001
Female Group 1	1.66	37	<0.001
Female Group 2	3.56	37	<0.001
Age	-0.30	1596	<0.001
$\delta^{15}N$			
Male (Intercept)	9.00	1596	<0.001
Female Group 1	-0.07	37	0.69
Female Group 2	1.93	37	<0.001
Age	0.15	1596	0.0038

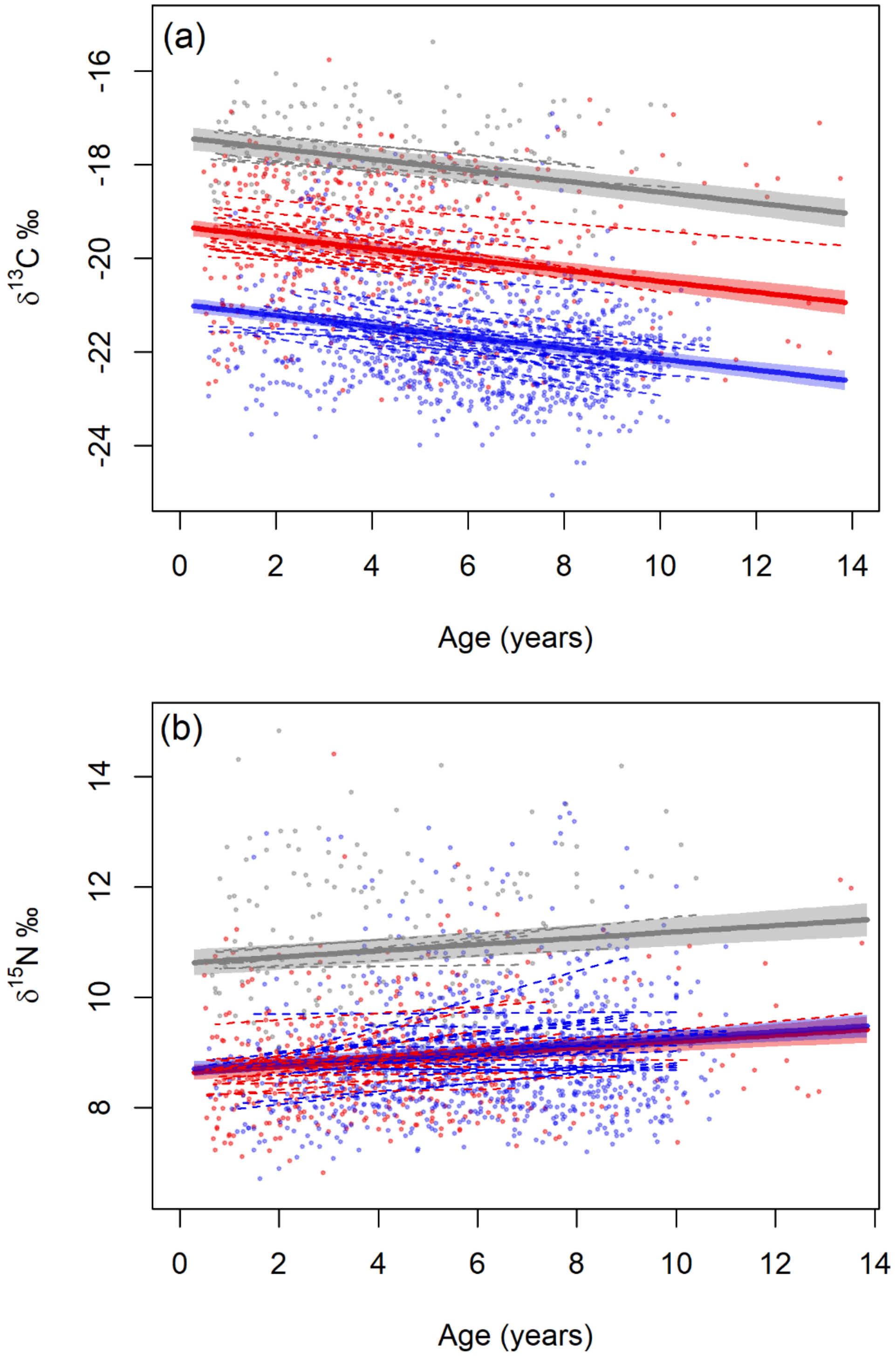

Figure 4.7. Best-fit linear mixed models explaining the change in (a) δ^{13}C and (b) δ^{15}N values along Antarctic fur seal whiskers with estimated age of males (blue) and minimum estimated age of females: female Group 1 (red; females with lower mean δ^{13}C values than estimated δ^{13}C value at the Polar Front) and female Group 2 (grey; females with higher mean δ^{13}C values than estimated δ^{13}C value of whiskers at the Polar Front). Points are isotope values of each whisker sample, dashed lines are fitted slopes explaining trend for each individual seal, bold lines

are fitted trends for each group and shaded areas indicate standard error. Figure was created using R software (v3.6.1; https://www.R-project.org/).

4.4. Discussion

Niche partitioning plays a fundamental role in ecology by reducing competition for resources. This study revealed that the behaviour of Antarctic fur seals in the world's largest breeding colony show distinct niche partitioning between sexes, throughout ontogeny and among individuals, which may help facilitate the high population density on South Georgia and the recovery of this population post-sealing. By analysing stable isotopes along whiskers we found strong support that (1) Males spend more time foraging in maritime Antarctica than females; (2) Males progressively spend more time foraging in maritime Antarctica during each annual cycle as they age; (3) Females demonstrate two main foraging strategies with 70% of females (female Group 1) mainly foraging south of the Polar Front and the remainder (female Group 2) mainly foraging to the north of it; (4) Migration strategies remained consistent between years. We discuss the potential underlying drivers of these findings and propose their key ecological consequences.

4.4.1. Methodological Considerations

Prior to interpreting results there are several caveats of our study to consider. The estimated whisker $\delta^{13}C$ value when Antarctic fur seals foraged at the Polar Front was based on only one season of prey data and the proportion of each species' contribution to the diet was unknown. Our estimated value was very close to -19 ‰: estimated by Cherel et al. (2009)[62] and used by Kernaléguen et al. (2012)[63] for Antarctic fur seals breeding at the Crozet Islands. It also closely aligned with isotope values in blood of seabirds foraging at the Polar Front from South Georgia[61]. However, the location and width of the Polar Front is not constant as a result of high variability in mesoscale meanderings, eddies and ring formations[61,65]. The value can therefore vary spatially and temporally and should only be considered as a broad indicator of foraging distribution. Baseline isotope ratios also change in time and space with sources of organic matter[66]. We could not account for these changes due to uncertainties inferring fine-scale foraging locations at set points in time from the isotope data, coupled with the lack of comprehensive isoscapes available for the geographical area (which vary seasonally and annually). The available isoscapes for the Antarctic Peninsula region revealed that $\delta^{13}C$ values in particulate organic matter showed high annual variation (standard deviation of 2.9 ‰) in February each year between 2013 and 2016, but no general trend over time[67]. It is unlikely that trends in our results reflect changes in baselines, as there is currently no evidence of simultaneous trends in baseline isotope values in the Southern Ocean[68].

The isotope data also presented additional sources of variation. In females, the exact point that whiskers were cut likely differed (within ~ 2 mm) among individuals, which may slightly affect the minimum ages of females. Since only minimum female age could be determined, we could not assess changes in isotope values with exact age. In males, we were unable to account for fasting during the breeding season. Fasting enriches $\delta^{15}N$ values in organisms by 0.5 ‰ on average and has no signficiant effect on $\delta^{13}C$ values[69]. However, male Antarctic fur seals will also forage during the breeding season[27], so we were unable to determine the length of fasting by each male each year (as well as determine the enrichment in nitrogen, which may depend on seal age, size and health). Although this short period of fasting may have slightly increased the values of some data points, it is unlikely that this explains patterns in our results.

4.4.2. Niche Partitioning between Sexes

Sexual segregation occurred along the spatial and temporal axis of the niche: male Antarctic fur seals had lower $\delta^{13}C$ values than females, indicating they spent more time foraging further south in maritime Antarctica during each annual cycle than females, supporting hypothesis (1). This sexual segregation might be partially driven by breeding constraints, as females are restricted in the distance they can travel from pupping beaches when foraging to provision their pups, while males have no temporal or spatial limitations post-mating so can forage further afield[27,70]. Indeed, three Antarctic fur seal adult males tracked with satellite transmitters migrated south post-mating[44] and young males marked with flipper tags have been re-sighted further south at Signy Island[43].

There may also be a link between sexual size dimorphism and foraging niche. Lower $\delta^{13}C$ values (indicating more southerly foraging) in males than females have also been reported in sexually dimorphic albatrosses and giant petrels breeding at South Georgia, but not in monomorphic burrowing petrels[61]. According to optimal foraging theory[71] larger animals should prefer spatially clustered resources to decrease foraging costs[72], as they have higher energetic needs[20,21]. For example, Albrecht et al. (2018) found that larger birds (of over 80 species) sampled along Mount Kilimanjaro foraged on plants with higher resource density than smaller birds. Male Antarctic fur seals require an estimated 3.8 tonnes of krill per year – twice as much as females[73] and may therefore exploit the most productive areas available[48]. Krill density tends to be higher near the Antarctic Peninsula than South Georgia (1996 –2016[74]) and there is large inter-annual variability in krill abundance and availability in the Scotia Sea[75], which has been associated with sporadic declines in breeding success and population sizes of predators at South Georgia[76-78]. Males may exploit the greater density and predictability of krill near the Antarctic Peninsula to maintain a large body size. The Antarctic Peninsula and nearby islands appear to be less suitable for females to provision pups, as shown by the low numbers that breed there (e.g. [77,79,80]) relative to South Georgia.

Males and female Group 1 had similar $\delta^{15}N$ values, indicating they likely competed for the same prey. They are likely opportunistic foragers, as the individual specialisation index for $\delta^{15}N$ values showed greater generalisation than specialisation. Males potentially forage more successfully in the absence of females[42,44,70], which reduces intra-specific competition. Spatial segregation between the sexes also occurs in grey seals, *Halichoerus grypus*, as males primarily use the continental shelf and females the mid-shelf, which the authors suggest acts to maximise fitness by reducing intersexual competition[81]. Shifting habitat, as opposed to diet, may be a more effective strategy to reduce competition[6]. By migrating south, male Antarctic fur seals could also reduce inter-specific competition with millions of breeding seabirds that congregate at South Georgia in summer. However, males likely increase spatial overlap with the krill fishery (largest fishery by tonnage in the Southern Ocean[82]), which operates at the Antarctic Peninsula in summer: a time when it is closed at South Georgia.

4.4.3. Niche Ontogeny

Individual niches are not fixed and can differentiate throughout an animal's life[26,28,29]. We found that $\delta^{15}N$ values and therefore trophic level of prey in male and female Antarctic fur seal whiskers gradually increased with age. Similar patterns have been documented with increasing body size in striped dolphins, *Stenella coeruleoalba*[50] and great white sharks, *Carcharodon carcharias*[83]. This pattern may result from development of a larger mouth gape[84], greater physiological capabilities (e.g. travel speed and aerobic dive limits[27]) and foraging experience, enabling larger individuals to handle larger higher-trophic-level prey with greater nutritional value. Alternatively, the increasing $\delta^{15}N$ values may relate to changes in prey availability over time, such as declines in krill abundance as a result of climate change[74;85]. Indeed, Tarroux et al. (2016)[68] attributed increasing $\delta^{15}N$ values in blood and plasma of Antarctic fur seals breeding at Bouvetøya (from 1997 – 2015) to a shift in diet towards greater consumption of higher-trophic-level prey (replacing krill). This best explains trends in $\delta^{15}N$ along Antarctic fur seal whiskers at South Georgia, as $\delta^{15}N$ values did not level when adults reached maximum body size.

Distinct ontogenetic niche shifts were present in males, supporting hypothesis (2). The $\delta^{13}C$ values declined as males aged, indicating they progressively spent more time south during each annual cycle. This trend in $\delta^{13}C$ values was also apparent in growth layers of male Antarctic fur seal teeth[86]. As males age they gain experience of the best foraging areas and may exploit abundant resources in maritime Antarctica to meet their growing energetic needs. A larger body size and better body condition will improve a male's ability to gain and retain high quality territories with greater mating opportunities[42]. Larger body sizes also facilitate better heat retention[87], enabling larger males to withstand the higher thermoregulatory costs of foraging in colder environments. Thermal tolerance also influenced sexual segregation in the most sexually dimorphic bird species: great bustards, *Otis tarda*[88], and could be an overlooked factor driving sexual segregation.

Trajectories in ontogenetic niche shifts may differ between the sexes, as females reach maximum body size and become sexually mature earlier than males. Kernaléguen et al. (2016)[48] found that female Antarctic fur seals breeding at

Kerguelen had a similar isotopic niche to adult females by age 2. We could not assess whether this pattern occurred in females breeding at South Georgia, as we could only determine minimum female age since body length was a poor indicator of age (varying substantially among individuals; see Forcada & Hoffman 2014[78]). However, trends in $\delta^{13}C$ values along female whiskers suggest a more continuous change in isotopic niche, which requires further investigation.

Ontogenetic niche shifts can reduce intra-specific competition[11,89], as only a subset of individuals will compete with one another at a specific time[29,90]. Sample sizes for males aged under 2 years were small (as a result of whisker wear). However, throughout the remainder of male Antarctic fur seal development, the greatest isotopic niche overlap (indicating competition for resources) occurred between female Group 1 and males aged 2 – 3 years. This overlap may result from similarities in body size[47] and energetic requirements. Isotopic niche overlap gradually declined between the sexes as males grew and aged, showing progressive development of sexual segregation as ontogenetic shifts in males freed up resources available to females. This mechanism (which may occur in other sexually dimorphic species) substantially reduces intra-specific competition, which potentially increases female survival, reproductive rates and ultimately elevates population carrying capacity.

4.4.4. Niche Partitioning within Females

Female Antarctic fur seals occupied a broader isotopic niche (SEA 1.5 x larger) than males, supporting hypothesis (3). This concurs with tracking studies whereby females migrated north to the continental shelf east of Patagonia[45,46], south to the northern tip of Antarctic pack ice[45], or remained within the vicinity of South Georgia[44-46]. However, stable isotope analysis allowed us to quantify foraging strategies into two main groups supporting hypothesis 4. The consistency of these foraging strategies within the two groups highlights the potential of familiarisation with a foraging area allowing individuals to maximise net energy gain[46].

Size dimorphism may be a cause or consequence of divergent foraging strategies, as female Group 1 and Group 2 differed in body size: a phenomenon also observed in female loggerhead turtles, *Caretta caretta*[91]. Size dimorphism could lead to distinct foraging strategies as larger animals are generally less susceptible to predation and have greater competitive abilities than smaller animals[91]. They tend to have lower stroke frequencies[92] and lower mass-specific maintenance costs[93], enabling them to migrate over greater distances than smaller animals using the same amount of energy. This size dimorphism could stem from early life e.g. size of tadpoles at metamorphosis affects size of adult frogs[94]. However, foraging strategies were consistent in female Antarctic fur seals and body mass and girth were the most important components in PC1 and PC2 respectively, suggesting body dimorphism was more likely a consequence of divergent foraging strategies. These strategies may initially develop when pups disperse after weaning and explore potential foraging sites[95]. Pups with bolder personalities could show greater exploration than shyer individuals, as documented in wandering albatrosses, *Diomedea exulans*[96]. Female Group 2 may discover better foraging opportunities north of the Polar Front, resulting in their larger body size. Indeed, loggerhead turtles that migrated further foraged in more productive waters were significantly larger than other turtles – potentially investing more resources into growth[91].

According to Schoener (1974)[3], competition should result in overdispersion of niches. Marginal value theorem[97] also predicts that an animal should leave a patch of resources and search for another when rate of resource gain falls under expected mean rate. Competitive interactions and low resource availability could have alternatively initiated the longer foraging trips by female Group 2. For example, at high population densities some three-spined stickleback, *Gasterosteus aculeatus,* become more opportunistic while others form novel dietary groups[98] and when resource availability is limited some female parasitic wasps, *Pachycrepoideus vindemmiae*, immediately retreat from a resource patch, while others remain and are more involved in competitive interactions[99]. Female Group 2 may minimise intra-specific competition with males and Female Group 1, while gaining nutritional benefits that outweigh the energetic costs of locomotion[100]. Since Antarctic krill is almost exclusively distributed south of the Polar Front[101], female Group 2 must predominantly feed on alternative species such as squid, myctophids and other fish – as found in the diet of Antarctic fur seals breeding at Kerguelen, Heard Island and Marion Island[49,102,103]. They are likely more susceptible to competition and interaction with an abundance of squid jiggers, longliners and benthic trawlers that operate in the South Atlantic. Prey consumption by female Group 2 (satisfying potentially 30% of the female population) could result in a greater impact on the South Atlantic marine ecosystem than previously realised.

4.4.5. Conclusion

Stable isotope analysis (complimented with findings from short-term tracking studies) enabled us to reveal niche partitioning in the world's largest Antarctic fur seal colony. Analysing stable isotopes along progressively growing tissues may be more practical, more cost-effective and less invasive than using short-term tracking methods alone[36]. We propose that the Antarctic fur seal colony breeding at South Georgia is generalist as a whole (indicated by individual specialisation indices), as seals could inhabit a range of environments, from warmer South Atlantic waters to colder Antarctic waters. However, the population is composed of more specialised strategies that may develop as a function of body size (with males experiencing a large range of body sizes and energetic requirements throughout ontogeny and female size differing according to foraging strategy). These strategies relax intra-specific competition, which may benefit population stability and carrying capacity, as well as the behavioural plasticity of the colony to adapt to changing environmental conditions. Intra-specific niche partitioning therefore has implications for ecology, evolution and conservation and is important to study in other species.

4.5. Methods

4.5.1. Ethics Statement

The animal handling procedures in this study were reviewed and approved by the British Antarctic Survey Animal Ethics and Welfare Review Body (AWERB). The procedures adhered to the ASAB guidelines, ARRIVE guidelines and legal requirements of the South Georgia Government. The behavioural responses of adult females during restraint were predictable (given previous research conducted within the colony) and all efforts were made to minimise stress to individuals.

4.5.2. Sample Collection

Whiskers were collected from 30 freshly dead adult male and 25 live adult female Antarctic fur seals from September 2016 – February 2017 during the breeding season at Bird Island, South Georgia (54.010° S, 38.059° W). Dead males are regularly found ashore during the mating season: a reflection of the intense competition among males to gain access to females[104]. For males the two longest whiskers were pulled from both sides of the face, body length and girth measurements were recorded (fresh dead males only), an ID tag was applied to the skull, and after decomposition an upper canine was extracted from the jaw. An upper canine was extracted from an additional four dead males (34 teeth total), in which whiskers could not be obtained because of prolonged decomposition. Females rarely die ashore and no dead females were observed during this period. For each live female, the single longest whisker was cut from the right side of the face (as close to the skin as possible) during restraint (enabling whiskers to regrow). Females were weighed and body length (nose to tail), flipper span and girth measurements recorded. The longest whisker (representing the longest period of growth) on the right side of the face was chosen from 20 randomly selected males and 20 randomly selected females for sample preparation.

4.5.3. Sample Preparation

Whiskers were washed with a sponge and Ecover detergent, transferred to a water bath for five minutes to remove contaminants (i.e. blood and dirt), then dried in an oven at 70 °C. Adhesive measuring tape was placed along each whisker and clear thin plastic positioned on the alternate side to ensure samples could be cut with accuracy and remained enclosed (to secure samples during cutting). Samples weighing a target weight of 0.7 mg were cut at the start of every 5 mm segment along the length of each whisker (most samples were 1 – 2 mm in length). Each 5 mm segment represented approximately 1.5 – 2.8 months of whisker growth based on growth rates calculated by Kernaléguen et al. (2016)[48]. Samples were removed from the tape using tweezers and placed in glass vials with a 2:1 chloroform:methanol solvent to remove any lipids and tape residue stuck to the whisker to leave clean keratin[105]. Samples were dried in a fume hood overnight then weighed into 3 x 5 mm tin capsules for mass spectrometry. Total sample sizes were 1011 for males and 642 for females.

4.5.4. Mass Spectrometry

Tin capsules were loaded into the autosampler of an Elementar (Hanau, Germany) Pyrocube Elemental Analyser, which converted carbon and nitrogen in the samples to CO_2 and N_2 gases. The ratios of carbon and nitrogen isotopes in these gases were measured on a Thermo-Fisher-Scientific (Bremen, Germany) Delta XP Plus Isotope-Ratio Mass Spectrometer. The internal reference materials (mean ± SD) were GEL (gelatin solution, $\delta^{13}C$= -20.09 ± 0.19 ‰, $\delta^{15}N$= 5.59 ± 0.12 ‰), ALAGEL (alanine-gelatine solution spiked with ^{13}C-alanine, $\delta^{13}C$= -8.69 ± 0.17, $\delta^{15}N$= 2.22 ± 0.08 ‰), and GLYGEL (glycine-gelatine solution spiked with ^{15}N-alanine, $\delta^{13}C$= -38.35 ± 0.13 ‰, $\delta^{15}N$= 23.19 ± 0.22 ‰), each dried for two hours at 70°C. Four USGS 40 glutamic acid standards[106,107] were used as independent checks of accuracy. Delta values were corrected for instrument drift (changes in isotopic composition of gases through the mass spectrometer) and linearity (variability in sample masses). Stable isotope ratios were expressed in parts per thousand (‰) deviation from the international standards (Vienna Pee Dee Belemnite for carbon and AIR for nitrogen), according to the equation:

$$\delta X = [(Rsample/Rstandard) - 1]$$

where X is ^{15}N or ^{13}C and R is the corresponding ratio ($^{15}N/^{14}N$) or ($^{13}C/^{12}C$). Stable isotope ratios were reported as $\delta^{13}C$ values for carbon and $\delta^{15}N$ values for nitrogen.

4.5.5. Age Determination

Each male seal was aged by three readers by counting external growth ridges on the extracted upper canine. These ridges, formed from annual deposition of dentin, are prominent in male Antarctic fur seals[108]. The modal ages were assumed for each individual. Precision in age determination was estimated using the IAPE, as described by Beamish and Fournier (1981)[109] according to equation:

$$IAPE = \frac{1}{N} \sum_{j=1}^{N} \left[\frac{1}{R} \sum_{i=1}^{R} \frac{|X_{ij} - X_j|}{X_j} \right] \text{x } 100$$

N is the total number of individuals aged, R is the number of times each individual is aged, and X_{ij} is the *i*th age determination of the *j*th individual. A smaller IAPE indicates more precise age determinations. Females were first aged according to their measured body length by extrapolating age from a modelled body length-to-age curve (Figure 1d in Forcada & Hoffman 2014[78]). Age was not estimated for five females, as body lengths exceeded modelled lengths in the growth curve.

Whisker growth rates were calculated using wavelet analysis, which can assess the degree of periodicity in stable isotope values along the length of whiskers (as described by Kernaléguen et al. 2012[63]). For each seal whisker the wavelet transform was applied and a power spectrum produced using the 'WaveletComp' package[110] in R[111]. The power spectrum specified significant periodicity in $\delta^{13}C$ values, which were used to reconstruct the original time series by 'denoising' the series and retaining the smooth components. These reconstructed time series were used to calculate the growth rate of each whisker, assuming oscillations corresponded to annual migrations. Since whiskers of four females and four males demonstrated no clear periodicity in $\delta^{13}C$ values, the average growth rates of all female and male whiskers were applied respectively for these individuals. For each of the 20 male seals, age was estimated along the length of the whisker using whisker growth rate and seal age (obtained from external growth ridges in canine) by back-tracking along the whisker (facial end to whisker tip). This method was repeated for the 20 females using the estimated ages obtained from body length. However, age estimates are highly variable with body length[78] and body length substantially underestimated female age at capture (by 3.5 years on average) according to female age determined by whisker growth rates. Whisker growth rates were considered more reliable (since oscillations in $\delta^{13}C$ values likely correspond to annual migration patterns) and were used alone to determine minimum female age along the length of each whisker for following analyses. Exact female ages could not be determined as a result of whisker wear/breakage at the tips and because whisker growth rates were not definite. Characteristic peaks in $\delta^{15}N$ values at the tips of six female whiskers likely corresponded to suckling patterns, suggesting these whiskers had not broken. In these cases, $\delta^{15}N$ peaks were lined up and age was estimated along the whisker (whisker tip to facial end) using the calculated whisker growth rates.

4.5.6. Data Analysis

To broadly determine Antarctic fur seal foraging distribution using stable isotope values we approximated the $\delta^{13}C$ value for whiskers when seals foraged at the Polar Front (convergence between cold Antarctic waters and warmer sub-Antarctic waters). We first determined the TDF for Antarctic fur seal whiskers using the SIDER package[112] in R[111]. SIDER estimates the TDF for a particular consumer and tissue (in which controlled feeding studies are impractical) using a phylogenetic regression model, fitted using Bayesian inference to a compiled dataset of TDF values of phylogenetically and ecologically related species[112]. We secondly added this TDF to the average $\delta^{13}C$ value of prey items (myctophids and krill) collected at two locations at the Polar Front (50.0632° S, 34.0287° W and 49.9357° S, 34.2078° W) during research cruise JR200 (British Antarctic Survey) in Autumn 2009. The resulting $\delta^{13}C$ value for Antarctic fur seals whiskers when seals foraged at the Polar Front was then overlayed on stable isotope bi-plots to assess differences in foraging distributions between and within the sexes. Since bi-plots revealed two isotopically distinct groups of females, with average $\delta^{13}C$ value of each individual falling lower or higher than the estimated $\delta^{13}C$ value of whiskers when seals foraged at the Polar Front, females were split into two groups (female Group 1 and female Group 2 respectively) for subsequent analyses. To test whether body morphology significantly differed between female Group 1 and Group 2, we ran a PCA on body mass, length, span and girth measurements, and used the output from PC1 and PC2 as separate response variable in Welch’s t-tests.

To compare male and female isotopic niche areas we used the SIBER package in R[43,113] to calculate SEAs (encompassing 40 % of data points) according to maximum-likelihood estimation, as well as SEA_Bs according to Bayesian inference to account for uncertainty in ellipse areas. The Bayesian Standard Ellipse Areas were calculated using 100,000 posterior draws and the mode and 95% credibility intervals reported. The proportions of overlap between male and female prediction ellipse areas, and between female Group 1 and Group 2 ellipse areas, were calculated to quantify isotopic niche differentiation between these groups – first using maximum-likelihood estimation, then using Bayesian inference with 100,000 posterior draws. This method was repeated to quantify ontogeny of isotopic niche differentiation on an annual scale in males (from 0 to

11 years of age) and to assess overlap among these niches and overall SEAs of female Group 1 and 2.

Since sexual segregation can also occur along the $\delta^{13}C$ and $\delta^{15}N$ axes separately, $\delta^{13}C$ and $\delta^{15}N$ values were used as separate response variables in linear mixed models[36]. We tested whether $\delta^{13}C$ and $\delta^{15}N$ values significantly differed among males, female Group 1 and female Group 2 using a global model, refined by backward-stepwise deletion and likelihood ratio tests using the ‘nmle’ package[114] in R. Each global model included group (males, female Group 1 and female Group 2), age, and the interaction between group and age as fixed effects. Age was used as a random intercept and slope to account for variability in $\delta^{13}C$ and $\delta^{15}N$ values among individuals as they aged and a corARMA structure (p=2, q=0) was used to account for temporal autocorrelation in residuals. We additionally tested whether males, female Group 1 and female Group 2 differed in time spent north of the Polar Front as they aged by calculating the proportion of time spent north of the Polar Front (based on whether $\delta^{13}C$ values exceeded estimated $\delta^{13}C$ value of whiskers when seals foraged at the Polar Front), which was used as the response variable in a generalised linear mixed model with a Beta error family, refined as above. Individual specialisation indices were determined, corresponding to the average similarity among individuals and the population[115]. The variance components were partitioned from each best-fit model and the within individual component (WIC) was divided by trophic niche width (TNW). An individual specialisation index of 0 indicates individuals are complete specialists, while a value of 1 indicates individuals use the whole range of the sample population’s niche[116,117]. All results were reported as means plus standard deviations unless stated.

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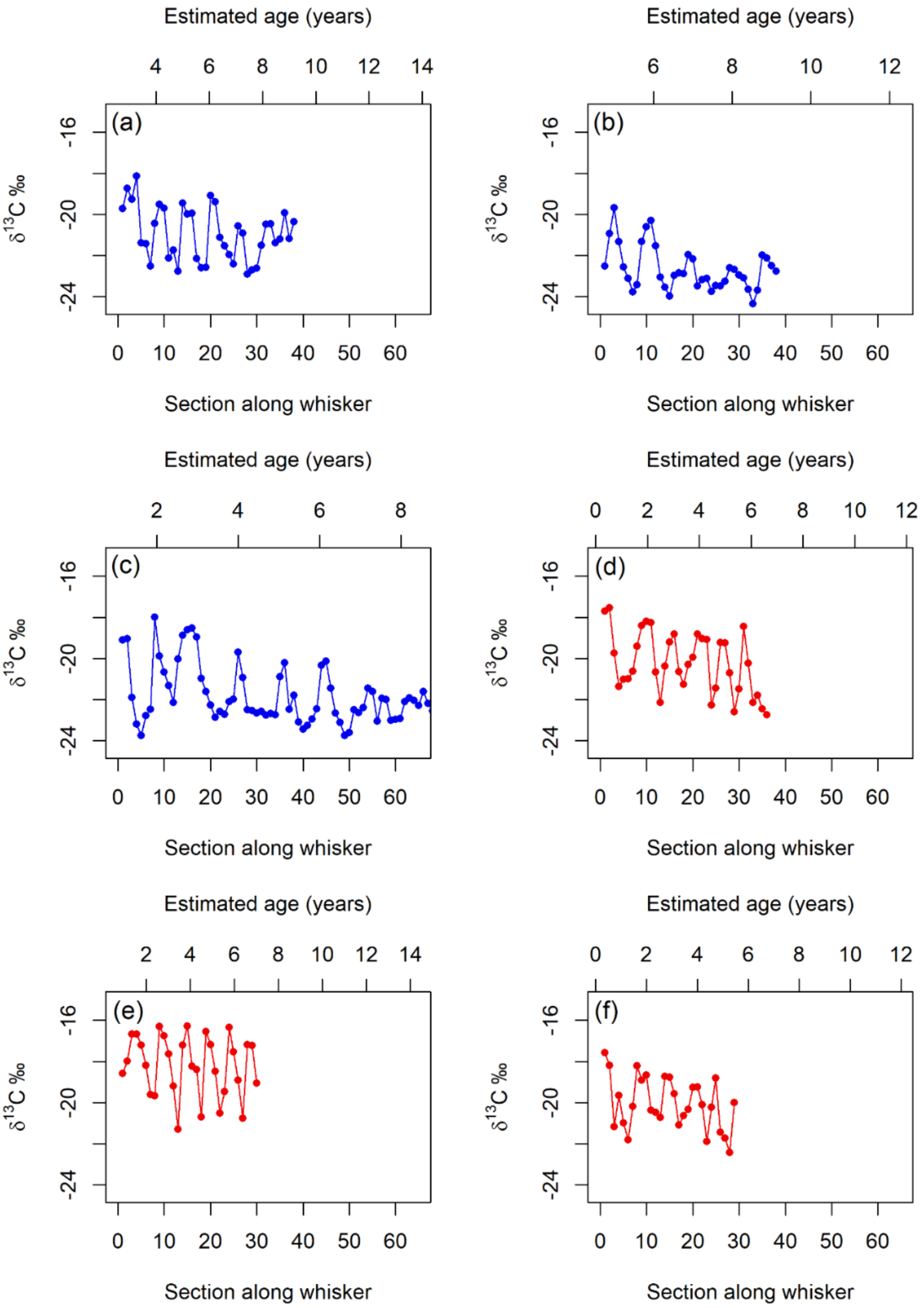
4.8. Author Contributions

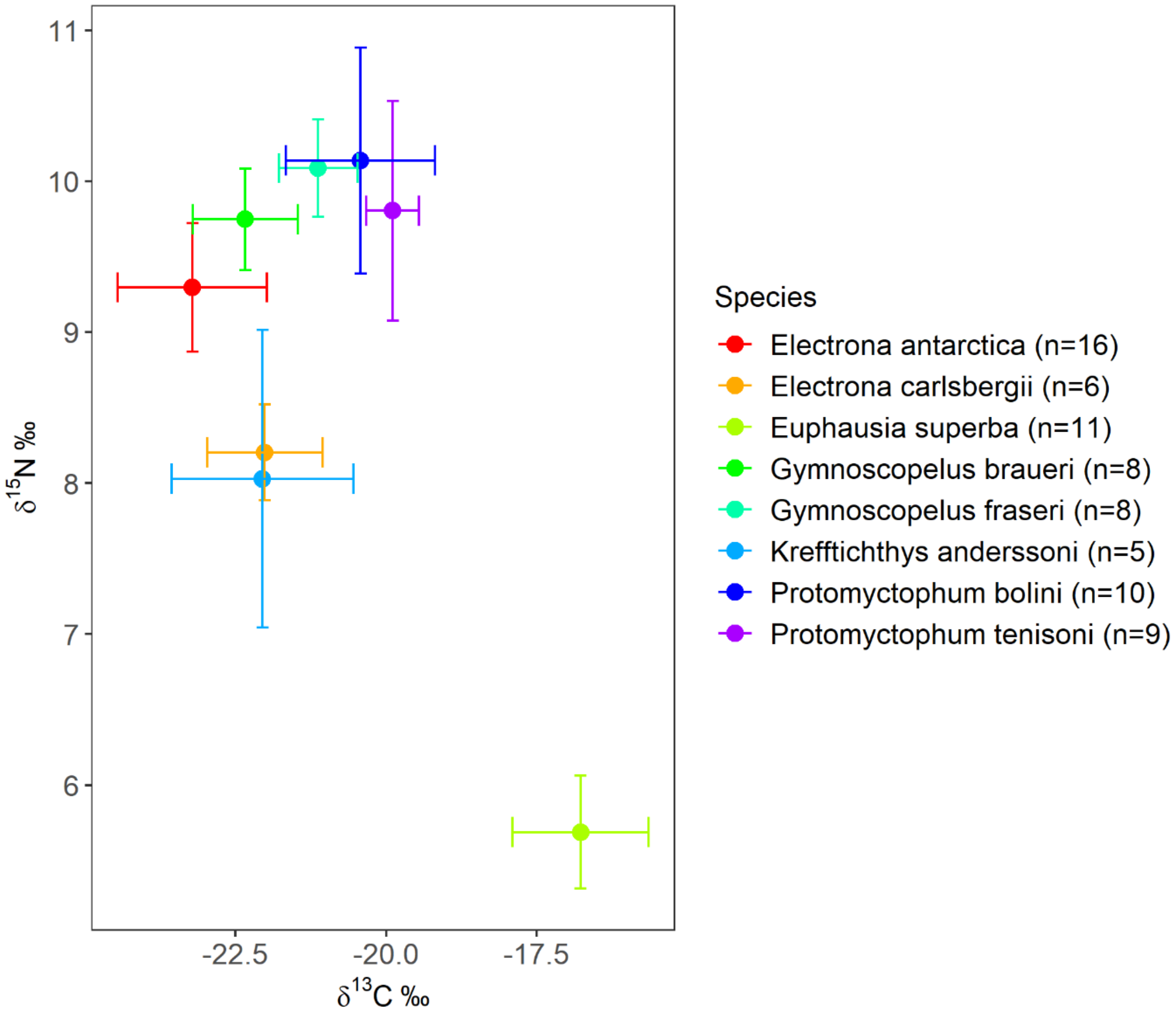
Study design: IJS. Fieldwork: JF and JD. Laboratory work: KAJ, JN and GS. Contributed data: GS. Advised data analysis: IJS, NR and SV. Analysed data: KAJ. Drafted manuscript: KAJ. All authors reviewed the manuscript.

4.9. Supplementary Material

Supplementary Figure S4.1. Oscillations in δ^{13}C values along the length of whiskers (from the distal to facial end) in (a–c) three male Antarctic fur seal whiskers (IDs = w8315, w8580 and w8675 respectively) and (d–f) three female whiskers (IDs = w8868, w8858 and w8870 respectively). Points are δ^{13}C values of samples taken every 5 mm along the length of each whisker and lines join these points. Male age was determined by external growth ridges on canines and minimum female age was determined by whisker growth rates.



Supplementary Figure S4.2. Bi-plot showing the mean (points) and standard deviation (lines) of $\delta^{13}C$ and $\delta^{15}N$ values of each prey species (Antarctic krill, *Euphausia superba*, and myctophids (remainder of species)) collected at two sample locations at the Polar Front (50.0632° S, 34.0287° W and 49.9357° S, 34.2078° W) in Autumn 2009.



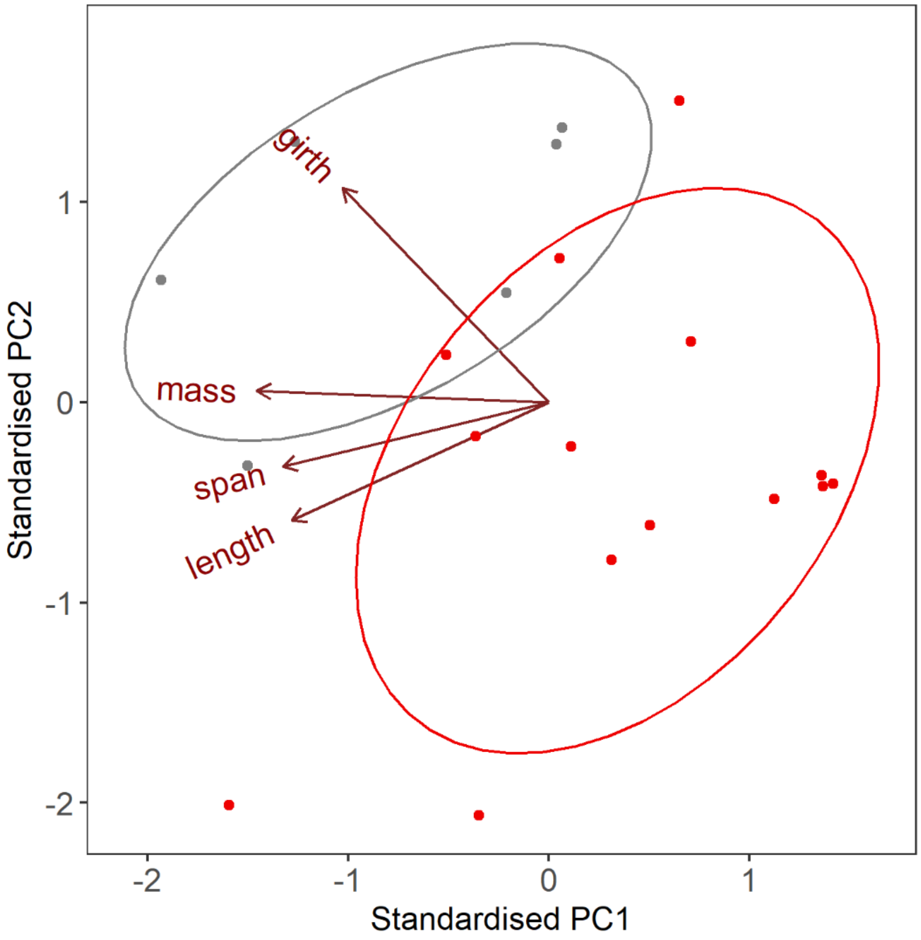
Supplementary Table S4.3. Length of the longest whisker on the right side of the face of 20 live adult female Antarctic fur seals, as well as body length, estimated age based on body length alone, minimum estimated age based on oscillations in $\delta^{13}C$ values along each whisker and minimum and maximum $\delta^{13}C$ and $\delta^{15}N$ value along each whisker. Asterisks indicate that a weaning signal (characterised by high $\delta^{15}N$ values followed by a drop) was present at the distal end of the whisker.

ID	**Whisker length (cm)**	**Body length (cm)**	**Estimated age using body length**	**Min age using oscs. in $\delta^{13}C$ (%)**	**Min $\delta^{13}C$ (%)**	**Max $\delta^{13}C$ (%)**	**Min $\delta^{15}N$ (%)**	**Max $\delta^{15}N$ (%)**
w8851	17.4	130.5	Unknown	7.7	-22.18	-17.98	6.83	10.46
w8852	16.0	128	Unknown	7.4	-21.80	-15.76	7.72	14.42
w8854	14.4	118.75	3	5.6	-22.21	-18.18	7.35	10.39
w8855	13.3	126	6	7.0	-19.32	-16.38	8.80	12.63
w8856	11.4	119.5	3	4.0	-21.94	-16.72	8.27	13.08
w8857	16.6	128.5	Unknown	10.4	-22.04	-16.06	8.80	14.84
w8858	15.0	123	4	6.8	-21.31	-16.28	8.36	12.69
w8859	16.5	120.25	4	6.6*	-23.01	-17.87	7.79	11.51
w8860	13.0	134	Unknown	8.6	-19.02	-16.51	8.27	12.74
w8862	16.6	125.5	6	7.6	-22.70	-17.92	7.44	10.03
w8863	30.6	124.5	5	13.7	-22.60	-16.62	7.23	12.13
w8864	16.8	121.25	4	8.2	-20.35	-15.38	8.53	14.32
w8865	25.7	131.75	Unknown	10.2	-22.57	-17.49	7.04	10.81
w8867	12.9	126	5	5.6*	-22.74	-17.98	7.61	10.68
w8868	18.0	117	3	6.4*	-22.75	-17.53	7.61	12.26
w8869	15.5	122	4	6.8*	-22.14	-17.75	7.12	10.74
w8870	14.6	120.75	4	5.3*	-22.43	-17.58	7.37	10.93
w8871	14.3	118	3	6.1*	-22.62	-17.74	7.49	12.42
w8874	11.0	119.25	3	6.0	-22.23	-18.12	7.66	11.32
w9150	16.1	112	3	8.8	-22.20	-16.87	7.31	11.19

Supplementary Table S4.4. Length of the longest whisker on the right side of the face of 20 dead adult male Antarctic fur seals, as well as body length, estimated age based on external growth ridges in the upper canine and minimum and maximum $\delta^{13}C$ and $\delta^{15}N$ value along each whisker. Body length could not be measured for decomposed males.

ID	Whisker length (cm)	Body length (cm)	Estimated age using canine	Min $\delta^{13}C$ (%)	Max $\delta^{13}C$ (%)	Min $\delta^{15}N$ (%)	Max $\delta^{15}N$ (%)
w8278	15.6	181	10	-23.30	-20.86	7.93	11.11
w8313	19.0	172	8	-22.92	-18.13	7.24	11.70
w8328	41.5	169	9	-23.47	-19.53	7.11	10.26
w8429	31.0	180	9	-23.02	-19.43	7.22	10.25
w8522	26.3	181	10	-23.47	-19.23	7.82	11.79
w8525	28.2	182	9	-23.09	-19.08	7.37	10.82
w8580	19.1	173	8	-24.36	-19.67	7.79	10.36
w8610	17.2	177.5	9	-25.05	-20.56	7.75	12.98
w8614	30.3	-	9	-23.80	-18.48	7.30	11.74
w8627	22.6	183	8	-23.21	-20.23	7.84	11.65
W8640	24.7	168	9	-23.67	-19.00	7.59	10.81
w8675	36.5	177	8	-23.75	-17.98	6.72	10.39
w8730	22.2	179	8	-23.16	-19.00	7.62	11.07
w8737	22.1	178	9	-23.21	-20.07	7.94	10.34
w8787	30.6	182	8	-23.37	-19.30	7.70	13.07
w8820	23.5	-	8	-24.35	-18.73	7.56	10.34
w8821	34.2	-	8	-23.00	-16.91	7.59	13.52
w8853	25.1	-	9	-23.38	-19.83	7.51	10.01
w8901	28.8	-	10	-23.32	-19.61	6.90	12.98
w9034	16.5	192	8	-23.33	-18.34	8.22	10.91

Supplementary Figure S4.5. Relationship between Principal Component 1 (explaining 73.9 % of variability) and Principal Component 2 (explaining 18.2 % of variability) of morphology measurements taken from 14 female Antarctic fur seals (red; Group 1; those with lower mean $\delta^{13}C$ values than estimated whisker $\delta^{13}C$ value at the Polar Front) and 6 female Antarctic fur seals (grey; Group 2; those with higher mean $\delta^{13}C$ value than estimated whisker $\delta^{13}C$ value at the Polar Front).



Supplementary Table S4.6. Standard Ellipse Areas (SEAs) and Bayesian Standard Ellipse Areas (SEA_Bs) quantifying the isotopic niches of 20 male Antarctic fur seals throughout ontogeny using $\delta^{15}N$ and $\delta^{13}C$ values along whiskers.

Male age (years)	**SEA**	**SEA_B mode**	**SEA_B 95% confidence interval**	**No. of males**	**No. of male whisker samples**
0.5 – **1**	0.640	0.562	0.177 – 2.123	2	6
1 – **2**	5.710	5.610	3.947 – 7.745	4	17
2 – **3**	3.800	3.756	2.951 – 4.837	10	47
3 – **4**	3.611	3.601	2.988 – 4.328	17	92
4 – **5**	3.310	3.311	2.774 – 3.880	19	128
5 – **6**	3.916	3.898	3.286 – 4.629	19	131
6 – **7**	3.256	3.259	2.745 – 3.824	20	140
7 – **8**	3.813	3.814	3.219 – 4.506	20	141
8 – **9**	2.573	2.576	2.185 – 3.002	20	145
9 – **10**	1.914	1.873	1.525 – 2.403	12	87
10 – **11**	1.488	1.421	0.922 – 2.373	6	42

Supplementary Table S4.7. Standard Ellipse Areas (SEAs) and Bayesian Standard Ellipse Areas (SEA*B*s) quantifying the overlap in isotopic niches of 20 males with 14 females in female Group 1 (those with lower mean δ^{13}C values than estimated whisker δ^{13}C value at the Polar Front) throughout male ontogeny using δ^{15}N and δ^{13}C values along whiskers.

Male age (years)	SEA overlap	SEA*B* overlap mode	SEA*B* overlap 95% confidence interval	No. of males	No. of male whisker samples
0.5 – **1**	0	0	NA	2	6
1 – **2**	14.832	14.203	6.586 – 22.212	4	17
2 – **3**	30.785	27.687	22.562 – 39.125	10	47
3 – **4**	22.600	21.611	15.138 – 27.873	17	92
4 – **5**	10.321	10.258	5.959 – 15.371	19	128
5 – **6**	5.675	5.792	1.857 – 9.473	19	131
6 – **7**	0.00154	0.001	0.000 – 0.224	20	140
7 – **8**	0.000	0.001	0.000 – 0.021	20	141
8 – **9**	0.000	0.000	NA	20	145
9 – **10**	0.000	0.000	NA	12	87
10 – **11**	0.000	0.000	NA	6	42

Chapter 5. Stable Isotope Values in South American Fur Seal Pup Whiskers as Proxies of Year-round Maternal Foraging Ecology

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5.1. Abstract

Natural selection should favour strategies that maximise reproductive success. Females may use different resources during progressive stages of reproduction according to energetic demands, behavioural constraints and prey availability. We used South American fur seal, *Arctocephalus australis australis*, pup whisker isotope values as a proxy for maternal diet and habitat use to determine; (1) how this resource use changes throughout pup development from *in utero* growth to mid-end of lactation and (2) how it differs among individuals. The longest whisker was cut from five male and five female fur seal pups (of approximately 8 months of age) at Bird Island, Falkland Islands, in 2018 and δ^{15}N values and δ^{13}C values were analysed every 5 mm along the length of each whisker. Patterns in δ^{13}C values indicated that mothers used different habitats during the annual cycle, likely coinciding with seasonal shifts in prey availability or distribution. The individual specialisation index based on δ^{13}C values was 0.34, indicating that adult females used different habitats, which could reduce intra-specific competition and ultimately enhance pup growth and survival. An increase in δ^{15}N values occurred along every pup whisker from pup birth to mid-end of lactation, which likely reflected trophic enrichment related to suckling and fasting by pups, overriding the maternal isotopic signature. Pup whisker stable isotopes are a convenient proxy of maternal foraging ecology. However, physiological processes complicate interpretations by altering δ^{15}N values. Interpreting these values therefore requires additional knowledge of the species' ecology and physiology.

Key words: *offspring, gestation, lactation, habitat use, diet, fasting, physiology*

5.2. Introduction

In mammals, gestation and lactation have different energetic requirements that influence maternal resource use (Gittleman & Thompson 1988). During gestation, female mammals must grow and maintain foetal, uterine, placental and mammary tissues, which is particularly demanding toward the end of gestation when the foetus is large (Gittleman & Thompson 1988; Hückstädt et al. 2018). During lactation, maternal metabolism dramatically increases as nutrients are transferred to the mammary glands to produce milk for offspring (Crocker et al. 1998). Some otariid (eared seal) species are concurrently pregnant while lactating, so have higher costs of breeding than otariids that do not lactate and gestate simultaneously (Lima & Páez 1995). Otariids are also central place foragers, and must alternate between foraging at sea and suckling pups ashore. Hence, the distance and duration of successful foraging trips are limited by the fasting ability of offspring (Villegas-Amtmann et al. 2017). As a result of these changing demands, females may alter their diet and habitat use during offspring development (Krebs & Davies 1997; Berger 1991, Rachlow & Bowyer 1998).

Changes in maternal foraging ecology during gestation and lactation could also differ among individual mothers (Rea et al. 2015). This is because body size, age and experience can affect diet preference, search efficiency and prey handling ability (Estes et al. 2003; Villegas-Amtmann et al. 2008; Jeglinski et al. 2012; Baylis et al. 2016). Individuals may therefore consistently use only a subset of resources available to all individuals within the population (Zango et al. 2019). Individual specialisation by mothers can reduce competitive interactions within a population and so enhance offspring growth, survival and ultimately maternal fitness (Laidre et al. 2008; Bowman et al. 2010; Urquía & Páez-Rosas 2019). During lactation, individual offspring may also allocate the energy they obtain from ingesting milk differently into their own development, as a result of their sex, condition and body size (e.g. McDonald et al. 2012a; McDonald et al. 2012b). For example, female Antarctic fur seal pups, *Arctocephalus gazella*, and Australian fur seal pups, *Arctocephalus pusillus doriferus,* may allocate more energy into accumulating fat stores and males into growing lean body tissues (Arnould et al. 1996; Arnould & Hindell 2002). Hence, quantifying individual specialization and accounting for how offspring allocate energy, enables a more complete understanding of maternal resource use.

Offspring are usually easier to capture and handle than adults and stable isotopes in young animals have been used as proxies for maternal foraging behaviour in sharks (Olin et al. 2011), cetaceans (Meissner et al. 2012), and pinnipeds (Wolf et al. 2008; Drago et al. 2010; Lowther & Goldsworthy 2011; Hindell et al. 2012). Stable isotopes reflect the ratio of heavy to light isotopes used by an organism, plus an added trophic discrimination factor from processes involved in assimilating into growing tissues (Ben-David & Flaherty 2012). Nitrogen isotope ratios ($^{15}N/^{14}N$ expressed as $\delta^{15}N$) generally indicate trophic position, as they increase with trophic level since ^{15}N is preferentially retained in the body and ^{14}N excreted in urine and faeces (Minagawa & Wada 1984; Fry 1988; DeNiro & Epstein 1976; Post 2002). In marine systems, carbon isotope ratios ($^{13}C/^{12}C$ expressed as $\delta^{13}C$) indicate geographic source of prey, as $\delta^{13}C$ values in primary producers generally decline with increasing latitude and are typically higher in benthic and inshore regions than pelagic and offshore regions (Hobson et al. 1994; France 1995; Kelly 2000; McCutchan et al. 2003).

In addition to considering ecological processes, interpreting isotope values relies on an understanding of the influence of physiological processes, such as growth, pregnancy and nutritional stress (McHuron et al. 2019). Foetal development likely requires a constant and reliable supply of energy, in which remobilised endogenous maternal proteins are primarily used for foetal protein synthesis, as revealed by amino acid analyses along southern elephant seal, *Mirounga leonina*, pup whiskers (Lübcker et al. 2020). Indeed this mechanism can cause a gradual enrichment in $\delta^{13}C$ along pup whiskers during gestation (Lübcker et al. 2020). Furthermore, trophic level enrichment in ^{15}N often occurs from mother to offspring during lactation in mammals (Jenkins et al. 2001; Aurioles et al. 2006). Fasting also leads to increased $\delta^{15}N$ values in tissues of several marine species including northern elephant seals, *Mirounga angustirostris* (Spurlin et al. 2019), king penguins, *Aptenodytes patagonicus* (Cherel et al. 2005) and polar bears, *Ursus maritimus* (Polischuk et al. 2001). Since ecological and physiological processes vary among species, isotope profiles in offspring are species- and tissue-specific (Jenkins et al. 2001).

Whiskers from South American fur seal pups, *Arctocephalus australis australis*, provide an ideal case study of maternal resource use during an extended period of pup development. Pup whiskers are composed of keratin, they are inert (in terms of isotope ratios) at formation, continuously grow, and reach over 8 cm in length toward the end of lactation. Stable isotopes can therefore be analysed over a fine temporal scale throughout offspring development, from in-utero growth to lactation, by sampling segments along the length of pup whiskers. Adult female South American fur seals give birth on pupping beaches around mid-December (Franco-Trecu 2005), then alternate between suckling their pups on land, and foraging at sea over a period of ~10 months. Beginning in March–April, adult females must provide energy to their nursing pup as well as their growing foetus (Lima & Páez 1995). They are effectively central-place foragers year-round, only free from breeding constraints for about two months between weaning their pup in October and giving birth in December. Changes in δ^{13}C values along whiskers therefore more likely reflect inshore/benthic foraging vs offshore/pelagic foraging, as opposed to foraging over a large latitudinal gradient (e.g. Cherel et al. 2009). Mothers may take longer foraging trips toward the end of lactation, as they have higher energetic demands of supporting a large pup and developing foetus, and their pups can withstand longer fasts for up to several weeks (Thompson et al. 2003, Baylis et al. 2018a). Since fur seals target oceanographic features that enhance biological productivity and aggregate prey (Baylis et al. 2008), they may also feed on different prey according to seasonal changes in oceanography and prey availability (Laptikhovsky 2009). Trends in δ^{15}N values along whiskers can reflect these dietary changes, but physiological processes (i.e. pregnancy, lactation and fasting) should also be accounted for.

Studying maternal foraging ecology in South American fur seals is valuable, given marine megafauna are often regarded as playing important roles in ecosystem structure and function (Estes et al. 2016), and compared to other otariid species, South American fur seals are poorly studied. Indeed, in the Falklands, which hosts the largest population in the world, research has been limited to only a limited number of studies (Thompson et al. 2003; Laptikhovsky 2009; Baylis et al. 2014; Baylis et al. 2018a; Baylis et al. 2018b; Baylis et al. 2019). We aimed to determine how stable isotope values of South American fur seal pup whiskers from the Falklands, change throughout pup development from *in utero* growth to mid-end of lactation and how these differ among individuals. We interpret trends in $\delta^{13}C$ and $\delta^{15}N$ values by considering habitat use, diet, and physiological processes.

5.3. Materials and Methods

5.3.1. Ethics Statement

The procedures in this study were reviewed and approved by the Falkland Islands Government (permit R19/2018). Every effort was made to minimise disturbance, and no pups were injured during handling procedures.

5.3.2. Sample Collection and Preparation

Fieldwork was conducted at Bird Island, Falkland Islands (52.1678° S, 60.9260° W), from 12th – 18th August 2018. Only 10 pups were sampled as a result of funding and time constraints. Five male and five female pups of approximately 8 months of age (assuming peak births occurred in mid-December; Franco-Trecu 2005) were selected at the edge of the colony to reduce disturbance. Each pup was caught in a net, measured (total body length, girth, fore flipper length, fore flipper width, fore flipper end i.e. length between the first and fifth digits, hind flipper length and ankle) and the longest whisker was cut from the right side of the face as close to the skin as possible. Since pups were caught away from breeding females, body measurements were considered more reliable indicators of pup size than mass, as mass fluctuates substantially according to milk consumption (e.g. Jones et al. 2020a).

Whiskers were cleaned with a sponge and Ecover washing-up liquid, placed in an ultrasonic water bath for five minutes, inspected under a microscope (any dirt was removed with a scalpel blade), then rinsed with 100% ethanol. Sample segments weighing a target mass of 0.7 mg (which weighed 0.66 mg on average), were cut every 5 mm along the length of each whisker (from base to tip), then weighed into 3 x 5 mm tin capsules. Samples (n = 173) were loaded into an Elementar (Hanau, Germany) Pyrocube Elemental Analyser (Scottish Universities Environmental Research Centre, UK), which converted carbon and nitrogen in the samples to CO_2 and N_2 gases. Stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) of evolved gases were measured on a Thermo-Fisher-Scientific (Bremen, Germany) Delta XP Plus Isotope Ratio Mass Spectrometer (IRMS). Ratios were corrected for instrument drift and linearity using interspersed samples of reference materials with known stable isotope values (mean ± SD): GEL (gelatin solution, $\delta^{13}C$ = -20.09 ± 0.19 ‰, $\delta^{15}N$ = 5.59 ± 0.12 ‰), ALAGEL (alanine-gelatine solution spiked with ^{13}C-alanine, $\delta^{13}C$ = -8.69 ± 0.17, $\delta^{15}N$ = 2.22 ± 0.08 ‰), and GLYGEL (glycine-gelatine solution spiked with ^{15}N-alanine, $\delta^{13}C$ = -38.35 ± 0.13 ‰, $\delta^{15}N$ = 23.19 ± 0.22 ‰), each dried for two hours at 70°C. Four USGS 40 glutamic acid standards (Qi et al. 2003; Coplen et al. 2006) were also used as independent checks of accuracy. Stable isotope ratios were expressed in parts per thousand (‰) deviation from the international standards (Vienna Pee Dee Belemnite for carbon and AIR, N_2 for nitrogen) according to the equation:

$$\delta X = [(Rsample/Rstandard) - 1]$$

where X is ^{15}N or ^{13}C and R is the corresponding ratio ($^{15}N/^{14}N$) or ($^{13}C/^{12}C$).

5.3.3. Data Analysis

All data analyses were conducted in R version 3.6.0. (R Core Team 2019). To indicate whether male pups invested more energy into whisker growth than female pups, as found in adults of closely related otariid species (e.g. Kernaléguen et al. 2015; Jones et al. 2020b), we conducted a Welch's t-test on whisker lengths (as data were normally distributed and had unequal variances). We also tested whether body morphology significantly differed between four male pups (as girth was not obtained for male P7 and we considered girth an important indicator of body size) and five female pups by running a Principal Components Analysis (PCA) on body measurements and testing the output from Principal Component 1 (PC1) and Principal Component 2 (PC2) in Welch's t-tests.

For each pup whisker, the convex hull area was calculated as a measure of isotopic niche width using the SIBER package (Jackson et al. 2011). Locally weighted scatterplot smoothers (LOESS) were then fitted to $\delta^{15}N$ values along the length of each whisker, revealing distinct troughs in values where the minimum $\delta^{15}N$ value presumably occurred close to timing of pup birth, as reported in whiskers of Steller sea lion, *Eumetopias jubatus*, pups (Rea et al. 2015). This trough was used to estimate growth rate of each whisker (per month) by dividing whisker length from the facial end to the minimum $\delta^{15}N$ value by pup age at capture (~8 months). Whisker growth rates were then used to estimate pup age at every 5 mm interval along the length of each whisker (including *in utero*).

To determine how stable isotope values changed on a continuous scale throughout pup development, δ^{13}C and δ^{15}N values were used as separate response variables in generalised additive mixed models (GAMMs) using the mgcv package in R (Wood 2017). Predictor variables in candidate models included pup age, sex and their interactions. Pup ID was specified as a random intercept and smooth effect to account for variability in δ^{13}C and δ^{15}N values among individuals and a corARMA structure (p = 2, q = 0) was applied to account for temporal autocorrelation in residuals. Models were ranked by Akaike Information Criterion (AIC) and the best fit model for each analysis was selected according to the lowest AIC (the simplest model was selected if models differed by less than 2 AIC units). Residual plots were checked for normality and homoscedasticity. To give a broad indication of how pup isotope values compared with those of adult females, mean δ^{13}C and δ^{15}N values in whiskers of 14 adult females (Baylis et al. unpublished data) in segments that were grown approximately over the same time period as pup whiskers were included in figures (these females were not the pups' mothers).

Individual specialisation indices in pup δ^{13}C and δ^{15}N values were also quantified to determine the average similarity among individuals and the sample population (Araújo et al. 2011). The variance components were partitioned from each best-fit model and the within individual component (WIC) was divided by the total niche width (TNW i.e. the sum of the variance components). An individual specialisation value of 0 indicates individuals are complete specialists, whereas a value of 1 indicates individuals occupied the whole range of the sample population's (isotopic) niche (Roughgarden 1972; Bolnick et al. 2002).

To broadly determine whether isotope values differed between the sexes and between different stages of pup growth, as well as quantify variance in isotopes values between these stages, δ^{13}C and δ^{15}N values were used as separate response variables in linear mixed effects models using the nlme package (Pinheiro et al. 2019). Predictor variables in candidate models included stage of pup growth based on the known life cycle (pup growing *in utero* while mother suckles an older pup; pup growing *in utero* while mother is free from nursing constraints; pup suckling from the mother), sex and their interactions. Pup ID was also specified as a random intercept to account for variability in δ^{13}C and δ^{15}N values among individuals. Levene's tests were conducted to determine whether variance in δ^{13}C and δ^{15}N values differed between stages of pup growth. To indicate the statistical power of the linear mixed effects models, repeatability indices of δ^{13}C and δ^{15}N values were estimated (while accounting for individual and stage of pup growth) using the R package rptR (Stofell et al. 2019). Repeatability indices show the proportion of variation that is reproducible by comparing the original data with simulated response data from the fitted model using parametric bootstrapping (Nakagawa & Schielzeth 2010). All results were reported as means ± standard deviation unless otherwise stated.

5.4. Results

5.4.1. Pup Morphology

Pup whisker length averaged 9.28 ± 0.38 cm and did not significantly differ between the sexes (Welch's t-test: t = 0.35, *P* = 0.74; Table 5.1). Pup whisker growth rates averaged 0.67 ± 0.14 cm per month and also did not differ significantly between the sexes (Welch's t-test: t = 1.33, *P* = 0.84; Table 5.1). Males were slightly larger in body size than females, as indicated by PCA. Specifically, loadings for PC1 were highest for fore flipper end (0.44), followed by fore flipper width (0.42), hind flipper length (0.40), body length (0.36), ankle (0.36), fore flipper length (0.33) and girth (0.30), while loadings for PC2 were highest for girth (0.62), followed by fore flipper length (-0.59), body length (0.39), ankle (-0.31), hind flipper length (-0.11) fore flipper end (0.03) and fore flipper width (0.03). PC1 and PC2 explained 72.5 % and 15.5 % of the variability in pup morphology measurements respectively. The mean scores between males and females differed by 2.84 for PC1 (Welch's t-test: t = -38, *P* = 0.05) and 0.18 for PC2 (Welch's t-test: t = -0.22, *P* = 0.84) (Fig. 5.1).

Table 5.1. Range in δ^{13}C and δ^{15}N values and total isotopic area for each South American fur seal pup whisker.

Pup ID	Sex	Body length (cm)	Whisker length (cm)	Whisker growth rate (cm/month)	δ^{13}C range (‰)	δ^{15}N range (‰)	Convex Hull Area
P1	F	78	8.7	0.75	-16.15 – -14.43	15.57 – 17.21	2.02
P2	F	81	10	0.75	-16.76 – -14.85	13.52 – 16.52	1.11
P8	F	93	10	0.81	-16.08 – -14.19	15.38 – 17.75	2.34
P9	F	78	7.5	0.56	-17.11 – -15.13	13.90 – 17.13	3.57
P10	F	88	9.5	0.69	-15.81 – -14.15	15.25 – 18.53	2.86
P3	M	93	10	0.81	-16.46 – -14.75	14.92 – 17.68	2.95
P4	M	87	7.1	0.38	-15.71 – -14.56	15.64 – 17.04	0.95
P5	M	95	10.5	0.56	-15.87 – -14.89	15.37 – 17.06	0.69
P6	M	83	10.5	0.56	-16.29 – -15.09	15.11 – 17.42	1.87
P7	M	84	9	0.69	-16.73 – -14.62	15.06 – 17.77	2.68

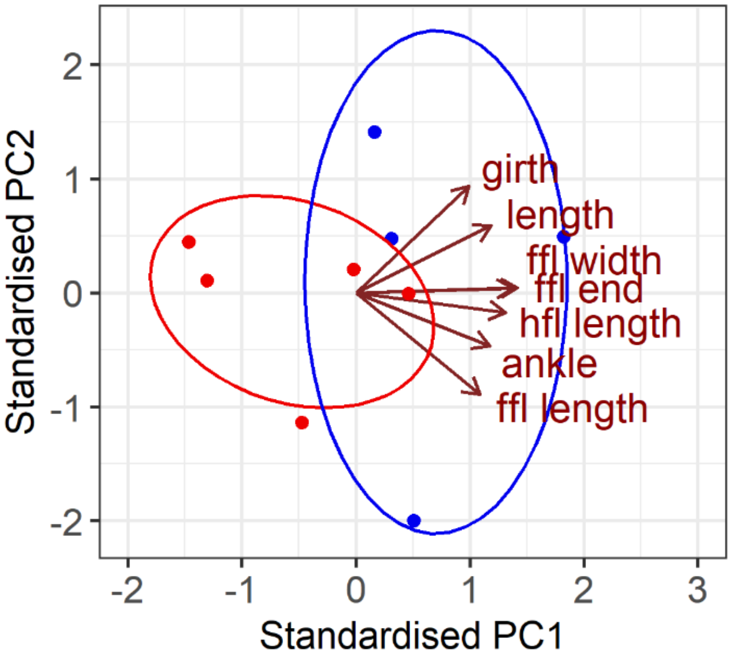

Figure 5.1. Relationship between Principal Component 1 (explaining 72.5% of variability) and Principal Component 2 (explaining 15.5% of variability) using morphology measurements from five female (red) and four male (blue) of eight month-old South American fur seal pups (ffl: fore flipper; hfl: hind flipper).

5.4.2. Trends in Isotope Values along Whiskers

The δ^{15}N values along the length of pup whiskers did not differ significantly between sexes and were best explained by age: a trough in δ^{15}N values occurred during the transition from gestation to lactation, then δ^{15}N values increased throughout lactation (GAMM; s(Age) $P < 0.0001$, R-squared = 0.54; Fig. 5.2a; Table 5.2). The individual specialisation index was 0.48, indicating that individuals used almost half of the sample population's isotopic niche.

The δ^{13}C values along the length of whiskers did not differ significantly between sexes and were best explained by age: a trough in δ^{13}C values also occurred during the transition from gestation to lactation, but this was less prominent along individual pup whiskers than the trough in δ^{15}N values (GAMM; s(Age) $P < 0.0001$, R-squared = 0.27; Fig. 5.2b; Table 5.3). The individual specialisation index was 0.34 – individuals therefore used a lower proportion of the isotopic niche along the δ^{13}C axis than δ^{15}N axis. Two female pups (P2 and P10) had noticeably lower mean δ^{13}C values and δ^{15}N values than other pups.

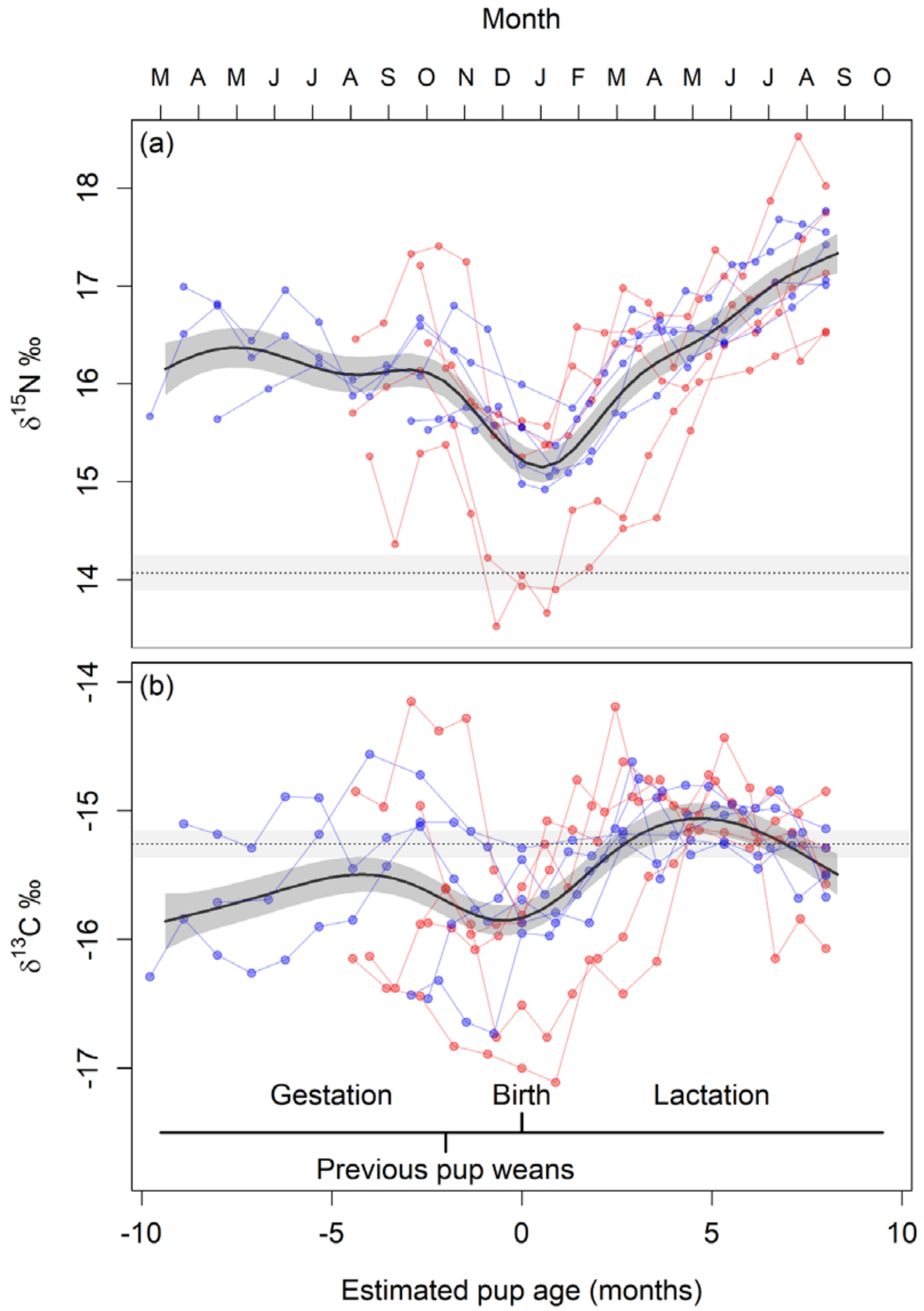

Figure 5.2. (a) δ^{13}C values and (b) δ^{15}N values along the length of South American fur seal whiskers. Black lines indicate fitted values from Generalised Additive Mixed Models (R-squared = 0.54 for δ^{15}N values and 0.27 for δ^{13}C values), grey shading represents standard error of fitted values, and coloured lines show raw data values along each pup whisker (red = females (n = 5) and blue = males (n = 5)). Dotted lines with grey shading show mean isotope value with standard error of distal segments of adult female South American fur seal whiskers grown over the same time period (n = 14).

Table 5.2. Generalised Additive Mixed Model selection with δ^{13}C and δ^{15}N values modelled as separate response variables and individual seal modelled as a random effect. The values for each candidate model (where ‘s’ indicates a smooth function) include degrees of freedom (d.f.), log-likelihood, AIC value and difference in AIC value (ΔAIC) between the candidate model and best fit model.

Model terms	**d.f.**	**Log-likelihood**	**AIC**	**ΔAIC**
δ^{15}N response				
s(Age)	9	-126.2	270.3	0
s(Age) + Sex	10	-125.8	271.6	1.3
s(Age + Sex)	11	-132.6	287.3	17
s(Age + Sex) + Sex	12	-132.2	288.4	18.1
Sex	8	-208.3	432.5	162.2
δ^{13}C response				
s(Age)	9	-108.4	234.9	0
s(Age) + Sex	10	-108.3	236.5	1.6
s(Age + Sex)	11	-114.6	251.2	16.3
s(Age + Sex) + Sex	12	-114.5	253.1	18.2
Sex	8	-133.2	282.3	47.4

5.4.3. Shifts in Isotope Values during Pup Growth

Pup isotope values shifted between stages of pup growth and there were no significant differences in δ^{13}C or δ^{15}N values between the sexes (Fig. 5.3; Table 5.2). The mean δ^{13}C value changed from -15.84 ± 0.12 ‰ when the pup was *in utero* while the mother suckled another pup to -15.28 ± 0.12 when the pup was *in utero* and its sibling had weaned, to -15.59 ± 0.10 when the pup suckled from the mother (Linear mixed effects model: $P < 0.001$, conditional R-squared = 0.31, marginal R-squared = 0.09). The mean δ^{15}N value changed from 15.57 ± 0.18 ‰ when the pup was *in utero* while the mother suckled another pup to 16.32 ± 0.18 ‰ when the pup was *in utero*, to 16.17 ± 0.15 ‰ when the pup sucked from the mother (Linear mixed effects model: $P < 0.001$, conditional R-squared = 0.36, marginal R-squared = 0.13) (Table 5.2). The variance in δ^{13}C values significantly differed between stages of pup growth, as variance was greater when mothers were not suckling (due to large differences between individuals) than during other time periods (Levene’s test: F = 5.8, $P = 0.004$). However, the variance in δ^{15}N values did not differ significantly between stages of pup growth (Levene’s test: F = 2.4, $P = 0.09$). Our sample size provided sufficient power for these results, as the repeatability indices of isotope values were significant at 0.11 ± 0.05 (CI: 0.03 – 0.23, *P* < 0.001) for δ^{13}C and 0.22 ± 0.12 (CI: 0.06 – 0.50, *P* < 0.001) for δ^{15}N.

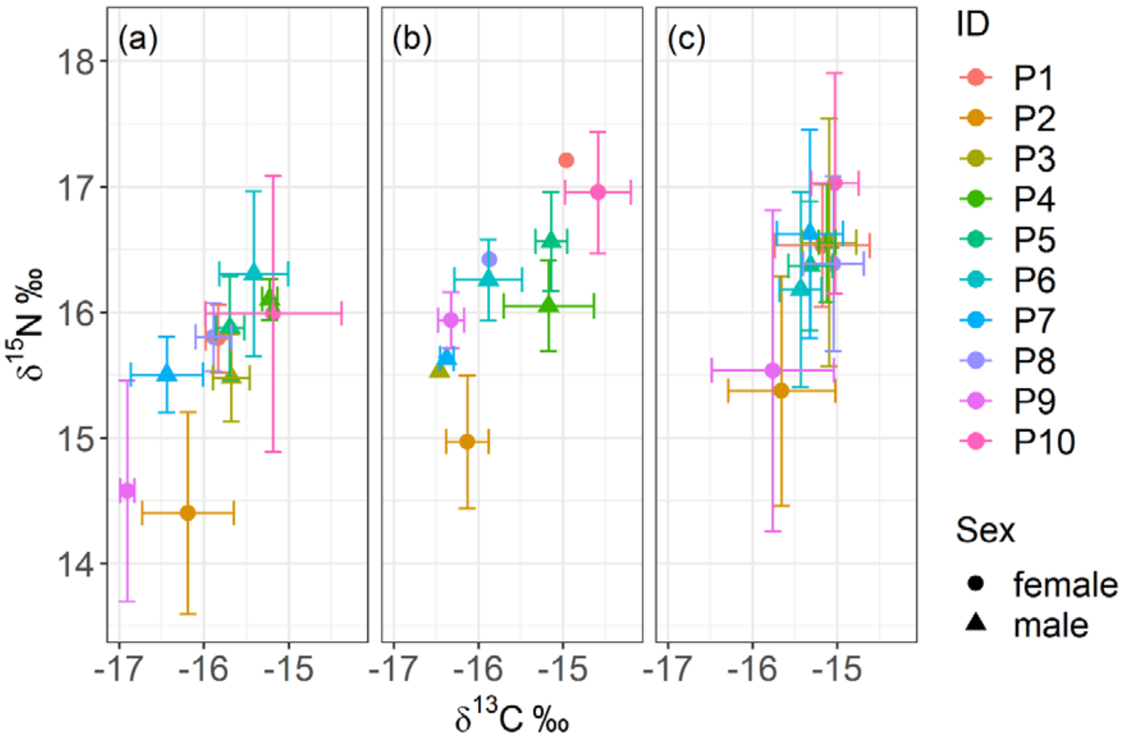

Figure 5.3. Means (points) and standard deviations (lines) of South American fur seal pup whisker stable isotopes when: (a) pup growing *in utero* while mother suckles an older sibling; (b) pup growing *in utero* after sibling has weaned; (c) pup suckling from mother.

Table 5.3. Linear Mixed Model selection with $\delta^{13}C$ and $\delta^{15}N$ values modelled as separate response variables and individual seal modelled as a random effect. The values for each candidate model include degrees of freedom (d.f.), log-likelihood, AIC value and difference in AIC value (ΔAIC) between the candidate model and best fit model.

Model terms	**d.f.**	**Log-likelihood**	**AIC**	**ΔAIC**
$\delta^{15}N$ response				
Stage	6	-196.0	404.6	0
Sex + Stage	7	-195.6	405.8	1.2
Sex + Stage + Sex*Stage	9	-194.7	408.4	3.8
Sex	5	-208.3	426.9	22.3
$\delta^{13}C$ response				
Stage	6	-113.9	240.2	0
Sex + Stage	7	-113.7	242.1	1.9
Sex + Stage + Sex*Stage	9	-112.6	244.2	4.0
Sex	5	-133.2	276.7	36.5

5.5. Discussion

This is the first study to quantify trends in stable isotope values along the length of South American fur seal pup whiskers, providing insights into maternal resource use during pup development. We found a characteristic trough in both $\delta^{15}N$ and $\delta^{13}C$ values, which likely occurred around the timing of pup birth, and that $\delta^{15}N$ values gradually increased during the lactation period. Isotope values also indicated individual specialisation in resource use by the mothers, particularly along the $\delta^{13}C$ axis. We explore the underlying drivers of these findings by addressing maternal resource use, as well as physiological processes occurring in mothers and pups, during gestation and lactation.

5.5.1. Gestation

Trophic enrichment of ^{15}N was apparent in pup whiskers *in utero*, as $\delta^{15}N$ values were higher than the mean $\delta^{15}N$ value in whiskers of adult females breeding at Bird Island (Fig. 5.2a). Isotopic fractionation in $\delta^{15}N$ between mother and offspring during gestation has been found in several marine mammal species including northern elephant seals and harbour porpoises, *Phocoena phocoena* (Habran et al. 2010; Fontaine 2002). Small isotope fractionations may occur from placental uptake and excretion between mother and offspring *in utero* (Fuller et al. 2004).

However, the degree of fractionation may change according to maternal foraging success and body condition during pregnancy (Lübcker et al. 2020).

A characteristic trough in δ^{15}N values occurred along pup whiskers (Fig, 5.2a), which presumably corresponded to timing around pup birth as documented in Steller sea lion pup whiskers (Rea et al. 2015). This pattern may occur in additional otariid species, but is often missed as fewer samples are cut from each pup whisker (e.g. Urquía & Páez-Rosas 2019; Baylis et al. 2016). The decline in δ^{15}N values prior to birth may result from maternal changes in prey selection or physiological processes when the pup is still *in utero*. In some marine mammals, such as bottlenose dolphins, *Tursiops truncatus*, pregnancy poses an energetic cost by increasing drag forces during swimming (Noren et al. 2011). Pregnancy could also limit dive capacity, for example dive duration in northern elephant seals declines during the last weeks of pregnancy, potentially because of increased foetal O_2 demand (Hückstädt et al. 2018). Females may therefore consume lower trophic level prey that is easier to capture or in higher abundance to meet their physiological abilities and energetic requirements. A change in maternal foraging behaviour is also supported by the corresponding decline in δ^{13}C values prior to pup birth. Adult females are freed from central place foraging constraints at this time, so have the option of foraging further offshore where baseline δ^{13}C values and δ^{15}N values tend to be lower. Indeed, tracking data suggests that some individuals move further offshore on extended foraging trips (Thompson 2003, Baylis et al 2018a).

Alternatively, physiological mechanisms may have driven the decline in δ^{15}N values prior to pup birth. During pregnancy nitrogen stress could activate a complex physiological process, whereby urea synthesis and excretion decrease while nitrogen is retained and returned to the maternal metabolic pool (Forrester et al. 1994; McClelland et al. 1997; King 2000; Fuller et al. 2004). This may cause a decline in δ^{15}N values in maternal tissues and offspring tissues, which is observed in the fingernails of human mothers and their newborn children (Fuller et al. 2006). The decline in δ^{15}N values may result from more direct routing of amino acids from the diet towards tissues synthesis and/or increased urea salvage in the colon (whereby δ^{15}N values in the diet and urine are lower than the consumer's tissues) (Fuller et al. 2004). This process may occur in otariids, including toward the end of South American fur seal gestation, when pup growth and maintenance place greater demands on the mother. Given that the trend in δ^{15}N values is apparent in humans, Steller sea lion pups and South American fur pups, nitrogen retention may be a common mechanism acting in income breeders prior to giving birth. However, since nitrogen retention alone does not explain the decline in δ^{13}C values, we postulate that both nitrogen retention and changes in maternal foraging ecology may explain the decline in stable isotope values prior to pup birth.

5.5.2. Lactation

During the lactation period adult female otariids are limited in the duration and distance of their foraging trips, so they likely exploit a lower variety of habitats than when they are not suckling a pup (Páez-Rosas and Aurioles-Gamboa 2010; Urquía & Páez-Rosas 2019). Indeed, adult female South American fur seals tracked from Bird Island in 1999 made shorter trips during lactation than when they were freed from central place foraging constraints in spring (Oct – Dec) (Thompson et al. 2003). δ^{13}C values along pup whiskers were therefore more consistent when mothers were suckling pups, as mothers were obliged to forage closer to the colony since time constraints prevented them from accessing habitats further afield. This pattern has also been documented in Galapagos sea lion pup whiskers, *Zalophus wollebaeki* (Urquía & Páez-Rosas 2019) and may be present in other otariid species.

Variation in adult female habitat use, as indicated by the near-cyclic pattern in δ^{13}C values, likely reflects seasonal changes in maternal foraging behaviour, according to the availability and distribution of preferred prey and changing pup needs. In early lactation (mid Dec – Feb), pups are small and could benefit from regular meals (Thompson et al. 2003). Lactating females therefore concentrate their foraging efforts near to Bird Island (Thompson et al. 2003), which is reflected by an increase in δ^{13}C values after pup birth. At this time, adult females potentially feed on lobster krill, *Munida sp.* (a near-shore species), which is a common prey species in the diet of South American fur seals (Strange 1992; Thompson & Moss 2001), that aggregates in dense shoals in January – March (Baylis et al. 2014). In April – May, the peak in δ^{13}C values and similarity in δ^{13}C values among individuals may indicate an influx of prey, driving females to forage in particular regions with higher baseline isotope signatures. For example, Patagonian squid, *Doryteuthis gahi*, is one of the more frequently occurring prey species in South American fur seal diet (with that of Falkland herring, *Sprattus fuegensis*; Baylis et al. 2014), and was particularly abundant in April 2018 (Falkland Islands Government 2019). As the lactation period progresses (mid-May – August), pups can withstand longer fasts and the decline in δ^{13}C values indicates that mothers forage further offshore, where they may maximise energy intake. Determining more precise foraging locations from isotopes is difficult, due to complex physical structures and oceanography in this region, such as shelf breaks (where baseline δ^{13}C values could be lower than offshore areas from upwelled δ^{13}C-depleted dissolved inorganic carbon (e.g. Troina et al. 2020)), coupled with incursions of the Falklands current. However, our results indicate that maternal foraging ecology changes throughout reproduction, enabling sufficient allocation of resources to pup growth and development.

The δ^{15}N values along every pup whisker increased as pups aged from 0 – 8 months. This pattern also occurred along Steller sea lion pup whiskers (although δ^{15}N values levelled off around mid-lactation) (Rea et al. 2015) and along fingernails of children (Fuller et al. 2006). It is unlikely that mothers consumed higher trophic level prey, as there was no concurrent increase in δ^{15}N values along adult female whiskers (Baylis et al. unpublished data). Physiological processes in pups had likely overridden the maternal δ^{15}N signatures. During lactation, mothers catabolise their own tissues to synthesise milk and pups start digesting and incorporating nutrients from milk, therefore feeding at a higher trophic level than their mothers (Newsome et al. 2010). Indeed, the tissues of suckling northern fur seal pups, *Callorhinus ursinus,* and California sea lion pups, *Zalophus californianus*, were ^{15}N-enriched by ~3‰ relative to their mothers (Newsome et al. 2006). Changes in diet are not instantaneously reflected by isotope values, as a result of tissue turnover and the use of amino acids from dietary components as well as endogenous protein reserves (Ayliffe et al. 2004).

Pup fasting cycles likely also contributed to the increasing δ^{15}N values along whiskers. As the lactation period progressed, pups can withstand longer fasts as their mothers undertake longer foraging trips (female trip duration lasts ~100 hrs, ~170 hrs and 190 hrs for those breeding at Bird Island, North Fur Island and

Volunteer Rocks respectively; Thompson et al. 2003; Baylis et al. 2018a). During the austral winter in 2018, adult females breeding at Bird Island had exceptionally long foraging trips and spent up to three weeks at sea when pups were approximately 8 months old (Baylis et al. unpublished data). During this time pups fasted ashore and mainly relied on their own energy stores. When animals are under nutritional or physiological stress they effectively 'feed on themselves' (Cherel et al. 2005). If nitrogen from lean tissues (which is ^{15}N enriched relative to diet) is used for protein synthesis then δ^{15}N is preferentially returned to the nitrogen pool and recycled again, resulting in tissues enriched in ^{15}N (Kurle & Worthy 2001; Fuller et al. 2005; Habran et al. 2010; Newsome et al. 2010). Indeed, this catabolism occurs in Steller sea lion pups after only 2.5 days of fasting (Rea et al. 2000). We therefore propose that South American fur seal pups were in a catabolic-anabolic state during lactation, as their sources of nutrition alternated between milk and their own endogenous stores.

5.5.3. Individual Specialisation

Individual offspring may allocate resources differently because of their sex, size, and condition (Arnould et al. 1996; McDonald et al. 2012a; McDonald et al. 2012b). Male South American fur seal pups were slightly larger in body size than females, potentially reflecting the importance of a large body size to future male reproductive success in otariids (Cappozzo et al. 1991). However, whisker length, whisker growth rate and stable isotope values along whiskers did not significantly differ between male and female pups, indicating that similar resources were allocated into growing these vital sensory organs at this early life stage. For three male pups a greater proportion of whisker was present representing in-utero growth, presumably because less abrasion of whisker tips occurred as a result of pup behaviour or more resilient whiskers. Whisker lengths and whisker growth rates may also differ among individual pups as a result of individual differences in maternal investment (Rea et al. 2015).

Stable isotopes in offspring tissues can provide insights into maternal individual specialisation (e.g. Lowther & Goldsworthy 2011). The δ^{13}C values along South American fur seal pup whiskers indicated that mothers used less than half the proportion (34 %) of the population's niche along the δ^{13}C axis. For example, pups P2 and P9 had notably lower δ^{13}C and δ^{15}N values than other pups, suggesting their mothers foraged further offshore and consumed lower trophic level prey than other mothers, representing an alternative foraging strategy. Both $\delta^{13}C$ and $\delta^{15}N$ values were more variable among individuals during early lactation when central place foraging constraints were greater, than during mid-late lactation when these constraints were more relaxed (Fig. 5.2.). During early lactation, mothers' foraging distributions may overlap spatially and competition may force them to specialise (e.g. on benthic vs pelagic prey or different trophic level prey) to enhance their foraging success. Other marine species, such as Gentoo penguins, *Pygoscelis papua*, also show higher individual specialisation when foraging effort and competition increase (e.g. Ratcliffe et al. 2018). Individual specialisation in South American fur seals potentially developed from intense competition, as a result of their colonial breeding and central place foraging, as well as their prolonged lactation period (e.g. Urquía & Páez-Rosas 2019).

5.5.4. Conclusion

Stable isotopes in offspring tissues can improve understanding of maternal foraging ecology and physiology. We found that sampling offspring is a valuable method as offspring can usually be handled more easily than adults and stable isotopes in their tissues can reveal distinct trends during reproduction (e.g. during birth and lactation) and over a relatively long time scale (i.e. over a year). Stable isotope values along otariid pup whiskers provide broad-scale information on their mother's habitat use, whether foraging habitat or prey changes over time, and whether individual specialisation is present. South American fur seal mothers changed their foraging strategies throughout offspring development, as a result of their changing energetic needs, changes in the pup's ability to fast, and seasonal changes in prey. Individual specialisation was present in foraging distribution, which may enable mothers to forage successfully to enhance pup growth and survival, as well as their own survival. Since both ecological and physiological processes influence isotope values (e.g. with trophic enrichment and pup fasting cycles during lactation complicating the overall picture), interpreting isotope values requires additional knowledge of the species' diet, ecology and physiology.

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Chapter 6. Conclusion

6.1. Summary

Sexual segregation has been well-studied in the adult life stages of a wide range of taxa in the animal kingdom. Common hypotheses for its existence include sexual size dimorphism (Main et al. 1996; Ruckstuhl 2007), sex differences in predation risk (Ruckstuhl & Neuhaus 2002; Croft et al. 2006), and sex differences in social roles (Conradt 1998; Pellegrini 2004). However, few studies have investigated the development of sexual segregation as animals grow and age. We aimed to address this research gap to gain valuable insights into the underlying drivers and ecological consequences of sexual segregation.

6.1.1. Sexual Segregation in Antarctic Fur Seals

Antarctic fur seals were considered ideal candidates to study the ontogeny of sexual segregation as they display pronounced sexual size dimorphism, which develops early in life. It was speculated that sexual segregation initially develops in dependent pups, but this conjecture had not been confirmed. Warren et al. (2006) found that male weaners travelled further from the pupping site than females during the first year of life, but additional knowledge of juvenile foraging distributions was lacking. In adults, sexual segregation had been documented during the mating season, whereby males dived deeper, closer to breeding beaches, and foraged more frequently during the day than females (Staniland & Robinson 2008). During the non-breeding season, several studies indicated that tracked adult females dispersed after weaning their pups (Boyd et al. 2002; Staniland et al. 2012; Arthur et al. 2015) whereas males were observed further south near the Antarctic Peninsula (Waluda et al. 2010), but the extent of this sexual segregation had not yet been quantified. We aimed to fill these knowledge gaps by quantifying the ontogeny of sexual segregation in Antarctic fur seals.

6.1.1.1. Pups

We confirmed that sexual segregation in Antarctic fur seals can initially develop in early life stages. By analysing Antarctic fur seal pup GPS-tracking data and long-term monitoring data, we found that sex differences can occur in pup habitat use and trip metrics during the lactation period (Chapter 2). Males had a slightly higher association with riskier habitats (beaches and water) than females, as these habitats likely provide better opportunities for social interaction such as play-fighting. Males must develop fighting skills early in life to improve chances of gaining access to mates in future, as large competitive males have better chances of reproducing. Female pups had a slightly higher association with safer tussock grass habitats than males, as they are smaller in body size and more vulnerable to predation and injury. Females also have more certain reproductive outputs (Darwin 1871), so using safer habitats can improve their chances of surviving to reproductive age. Toward the end of lactation male pups travelled further at sea than females, likely because of their greater swimming abilities (due to their larger body size and higher lean body composition; Arnould et al. 1996), risk-prone exploration strategy and/or greater behavioural drive to discover foraging areas. Our findings indicate that the initial development of sexual segregation in Antarctic fur seals is driven by sex differences in body size, predation risk and social roles related to reproductive selection.

6.1.1.2. Juveniles

We found that sexual segregation in Antarctic fur seals becomes more pronounced as seals develop from dependent pups to independent juveniles. By analysing juvenile Antarctic fur seal GLS-tracking data (from seals aged 1 – 3 years), we found distinct sexual segregation in foraging distribution with males generally foraging further south near the Antarctic Peninsula and females foraging closer to South Georgia (Chapter 3). The co-occurring development of more extreme sexual segregation with greater sexual size dimorphism (from pups to weaners to juveniles) indicates that sexual size dimorphism contributes to sexual segregation in Antarctic fur seals. Males must maximise foraging intake and body growth by discovering the most productive areas at the expensive of increased risk (e.g. Carter et al. 2019), such as predation and thermoregulation costs, to increase their future reproductive potential. They likely forage more successfully in maritime Antarctica where prey may be more abundant or competition less intense. In contrast, female juveniles must prioritise survival and may gain sufficient resources to sustain themselves in waters around South Georgia and the Polar Front. Female juveniles may begin forming divergent foraging strategies, whereby some individuals forage north of the Polar Front and some to the south of it to reduce competition with an abundance of marine predators in the region (indicated by an Area of Ecological Significance (AES);

Hindell et al. 2020). These findings provide further support that reproductive selection pressures can operate even when there are no immediate breeding constraints, leading to sexual size dimorphism, sex differences in risk, and sex-specific social roles, which drive sexual segregation.

6.1.1.3. Adults

By analysing stable isotopes along adult Antarctic fur seal whiskers, we found that sexual segregation becomes more pronounced as seals develop to adulthood (Chapter 4). Trends in carbon isotope values implied that males spent more time foraging in maritime Antarctica as they grew and aged, potentially because they developed the necessary experience and physiology (e.g. aerobic limits and thermoregulation abilities; Staniland & Robinson 2008) to forage for longer in cooler Antarctic waters. Carbon and nitrogen isotope values also indicated that females had two main foraging strategies that remained consistent over many years, whereby 30 % of females mainly foraged north of the Polar Front and consumed different prey to 70 % of females that mainly foraged south of the Polar Front. The females that mainly foraged north of the Polar Front were larger in body size, potentially indicative of greater prey availability in the region. Overall, the carbon isotope values along male and female whiskers revealed distinct sexual segregation in foraging distribution, whereby males generally spent more time foraging south in maritime Antarctica during each annual cycle than females. This sexual segregation may be driven by the same mechanisms proposed for juveniles, in addition to the breeding constraints imposed during adulthood. Specifically, during adulthood, females are constrained in their foraging movements for four months each year while provisioning their pups, while males are free from breeding constraints after mating so can forage further afield. These findings support our postulations that non-mutually exclusive hypotheses, including sexual size dimorphism, sex differences in risk, and sex-specific social roles, drive sexual segregation in Antarctic fur seals as a result of reproductive selection pressures.

6.1.2. Sex Differences in South American Fur Seals

Sex differences were apparent in South American fur seal pups in the Falkland Islands. Indeed, sexual size dimorphism was present in ~ 8 month old pups, reflecting reproductive selection pressures operating in early life (Chapter 5). We expect that the drivers for the ontogeny of sexual segregation in Antarctic fur seals also apply to South American fur seals. However, sexual segregation in South American fur seals likely manifests differently because of their environment, diet, and ~ 10 month lactation period. Since adult female South American fur seals are only free from breeding constraints for ~ 2 months each year, they generally have smaller foraging distributions than Antarctic fur seals, supported by a narrower range in carbon isotope values along their whiskers. Carbon isotope values along pup whiskers also revealed that adult female South American fur seals demonstrate individual specialisation in foraging distributions, which may reduce competition and enhance foraging success. Knowledge on male foraging distribution and individual specialisation in the Falklands is limited to five tracked individuals (Thompson et al. 2003; Baylis et al. 2018), so understanding of sexual segregation is still developing. However, during the austral winter in July – August 2018 at Bird Island, Falklands, adult male South American fur seals were observed congregating on the opposite side of the island as adult females (pers obv.), indicating that sexual segregation is present to some degree. Further research will be vital to quantify the ontogeny of sexual segregation in South American fur seals in the Falkland Islands.

6.1.3 The Ultimate Driver of Sexual Segregation

We propose that sexual segregation in otariids is ultimately driven by intense reproductive selection pressures, whereby reproductive success is more varied in males than females (Darwin 1871). These reproductive selection pressures lead to sex differences in body size, predation risk and social behaviour, which are inter-linked. Males must prioritise body growth (by foraging in the most productive areas) and gain fighting skills (by socially interacting) at the expense of increased risks, to increase their chances of gaining territory and access to mates. Females must prioritise survival to increase probability of reaching breeding age by using safer habitats or by foraging in less risky areas, as they have more predictable reproductive outputs. The sexes therefore have different resource requirements, which drives sexual segregation in habitat use and foraging distribution.

Our findings indicate that the nature of sexual segregation in a species may predominantly rely on its reproductive strategy. The reproductive strategy hypothesis was proposed by Main & Du Toit (2005) to explain sexual segregation in ungulates, but has received relatively little attention. This ultimate over-arching hypothesis contends that sexual segregation is driven by selection pressures operating differently on each sex, leading to sex differences in reproductive objectives. It encompasses non-mutually exclusive hypotheses (such as sex differences in body size, predation risk and social behaviour) as a result of reproductive selection. Given that males and females are inherently different because of their different sex organs and hormones, and the drive to reproduce is fundamental to species existence, the reproductive strategy hypothesis could explain sexual segregation in many species throughout the animal kingdom and should be considered in future studies on sexual segregation.

6.2. Implications

The ontogeny of sexual segregation has important ecological implications. The distinct niche partitioning in Antarctic fur seals between and within sexes reduces intra-specific and inter-specific competition, which likely contributed to the high population carrying capacity at South Georgia and may have enabled the population to recover from near extinction. The individual specialisation in adult female South American fur seals can also reduce competition and enhance mother and pup survival. Niche partitioning between and within sexes can therefore benefit populations and species as a whole.

Niche partitioning between and within sexes could also expose conspecifics to different environmental and anthropogenic stressors (Leung et al. 2012). By spending more time in higher risk habitats, male Antarctic fur seal pups are more frequently exposed to threats of predation and injury, as well as harsh weather conditions. However, small female pups are more vulnerable to these risks and the importance of shelter to their behaviour and survival highlights the need to monitor and conserve tussock grass habitats. Since juvenile and adult males generally foraged further south in maritime Antarctica than females, they may be more likely to compete with the krill fishery that operates around the Antarctic Peninsula in winter. In contrast, juvenile and adult females that migrate north of the Polar Front will more likely interact with the abundance of squid jiggers, longliners and benthic trawlers that operate in the South Atlantic. They will also more likely compete with other otariid species, namely South American fur seals and Southern sea lions. The need to consider female Antarctic fur seal movements north of the Polar Front is particularly important for species conservation efforts, as female survival is critical to population dynamics and the Convention for the Conservation of Antarctic Seals (1972) only protects Antarctic fur seals south of 60° south (BAS 2020).

Two of the main threats to fur seals are fishing and climate change. Fishing pressure is expected to intensify (Nicol et al. 2012; Chown & Brooks 2019), the sub-Antarctic AES is projected to move southwards (Hindell et al. 2020) and krill density near the Western Antarctic Peninsula is projected to decline (Hückstädt et al. 2020). Both male and female Antarctic fur seals and South American fur seals may need to adapt to changes in prey distribution. However, the sexes may respond differently. For example, male Antarctic fur seals may forage further south to maximise energy intake at the expense of increased thermoregulatory costs, whereas more females may seek other foraging strategies (e.g. by a greater proportion of individuals exploiting regions north of the Polar Front). The impacts of these stressors have the potential to lead to sex-biased mortalities and population declines. With new knowledge on Antarctic fur seal foraging ecology, the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) should consider the potential cumulative impacts of climate change and fishing pressure on specific sex and age groups according to their foraging distributions to effectively manage fisheries and protect the species.

6.3. Study Limitations

Our study had several limitations. Firstly, Antarctic fur seal pups were GPS-tracked during one breeding season only (Chapter 2). During this year, prey availability was poor and sexual size dimorphism less pronounced than average. Tracking pups in additional breeding seasons would be advantageous to assess whether sexual segregation in pup habitat use and trip metrics is more pronounced with greater sexual size dimorphism. Secondly, the exact ages of GLS-tracked juveniles were unknown and juveniles were tracked in different years, so we could not determine how juvenile foraging distributions changed with increasing age (Chapter 3). Deploying a large number of weaned pups (e.g. 40 individuals) with GLS-loggers in the same year would be invaluable to determine how males and females change their foraging distributions as they age over several years. Thirdly, whiskers were cut from 20 dead adult males and 20 live adult females (Chapter 4). Sampling whiskers from live healthy adult males may provide better representation of male resource use (but is practically difficult due to unpredictable responses of males to anaesthesia). Cutting whiskers from seals whose exact ages are known (e.g. from individuals tagged as pups) would be advantageous to better determine how sexual segregation changes along a continuous scale in time as seals age. Sampling whiskers from more individuals could also reveal additional foraging strategies (e.g. more than two main foraging strategies in females).

Disentangling hypotheses for sexual segregation was practically difficult as factors such as sexual size dimorphism, social roles and predation risk are all interlinked. Quantifying the influence of each hypothesis for sexual segregation may not be feasible in wild populations of fur seals. To quantify the influence of each hypothesis may require controlled captive studies whereby one factor is artificially changed at a time while others factors are controlled. Even with these unfeasible captive studies, it may not be possible to control for sexual size dimorphism as males have different body compositions and grow faster than females. We therefore believe that hypotheses for sexual segregation in fur seals cannot be disentangled, but that sexual segregation is ultimately driven by reproductive selection.

Sampling whiskers from South American fur seal pups was a useful method to gain insights into maternal foraging ecology over long time periods (i.e. over a year) (Chapter 5). However, trophic enrichment during lactation, in additional to pup fasting in between feeding bouts, complicated interpretations of nitrogen isotope values during the lactation period. Investigating maternal foraging ecology through pup whiskers is therefore not the most reliable solution to study maternal foraging ecology, but offers a practical and relatively cheap method that is useful when physiology and ecology are both considered. Sampling whiskers from a large number of pups (e.g. > 30 individuals) would be valuable to determine the proportions of adult females demonstrating different foraging strategies. Sampling pup whiskers from additional colonies in the Falklands would also be interesting to ascertain whether patterns in stable isotope values (and hence maternal foraging behaviour and pup fasting behaviour) are similar to those at Bird Island.

6.4. Recommendations for Further Research

Future research will be essential to advance knowledge on Antarctic fur seal foraging ecology and quantify the impacts of sex- and age-specific foraging on marine ecosystems. Fine-scale information on adult male year-round foraging distributions is still limited, and future studies should aim to develop effective methods to track a large number of individuals (i.e. using GPS loggers, satellite tags and light-level geolocators). Further research should also aim to improve Antarctic fur seal population estimates (e.g. using drone camera footage) and quantify the proportion that each sex and age group contributes to the population. This information would be invaluable to apply bio-energetics models to determine current estimates of krill consumption by each sex and age group. This further research would be critical to inform effective management and conservation in one of the world's most extraordinary and rapidly changing marine ecosystems.

Studying the ontogeny of sexual segregation in additional species, including South American fur seals, is vital to investigate the underlying drivers of sexual segregation that may be species-specific, primarily as a result of the animal's reproductive strategy and natural environment. This research could determine the extent that different sex and age groups compete for resources, how they respond differently to environmental or anthropogenic change, and what the implications are on population dynamics. Since the requirements for survival may differ substantially within a species, it is critical that the needs of all sex and age groups are thoroughly considered in species conservation.

6.5. References

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