Sexual segregation in a highly pagophilic and sexually dimorphic marine predator

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Abstract : Sexual segregation is common in many species and has been attributed to intra-specific competition, sex-specific differences in foraging efficiency or in activity budgets and habitat choice. However, very few studies have simultaneously quantified sex-specific foraging strategies, at sea distribution, habitat use, and trophic ecology. Moreover, these studies come from low latitude areas reflecting a lack of evidence for polar species. We investigated sexual segregation in snow petrels *Pagodroma nivea* and combined movement, foraging trip efficiency, stable isotope and oceanographic data to test whether sexual segregation results from sex-specific habitat use. Breeding birds foraging in the Dumont dðUrville sea, Antarctica, were tracked during incubation. Some similarities between males and females foraging characteristics did not support the sexual segregation hypothesis. Indeed, s~~S~~pace-use sharing and utilization distribution, $\delta^{13}C$ values and foraging trip performances (trip duration, length, speed and directions, mass gain, proportion mass gain) were similar between males and females ~~indicating no spatial segregation~~. ~~Males and females foraged more in waters ≈400 m deep and less in waters deeper than ≈1000 m. There was no difference in $\delta^{13}C$ values between males and females~~. However, there was support for sexual segregation in foraging characteristics linked to foraging habitats. Females foraged less than males in areas with higher sea ice concentration (SIC >70%) and had lower $\delta^{15}N$ values in plasma, blood cells and feathers. ~~Male and female foraging trip performances (trip duration, length, speed and directions, mass gain, proportion mass gain) were similar, but f~~ Foraging efficiency (proportionate daily mass gain while foraging), was greater for females than for males, and was greater for larger females with deeper bills. Females were more efficient than males during short (<2 days) foraging trips, and~~.~~ ~~F~~for females, but not for males, mass gain, proportion mass gain and body condition at return from a foraging trip were positively correlated to SIC of the foraging areas. Together, these results suggest an absence of sexual segregation at large spatial scales~~indicate that sexual segregation~~ in snow petrels during

incubation, but strongly support ~~is mainly driven by~~ habitat segregation between high (>70%) more profitable SIC (males) and low SIC areas (females), probably driven by intra-specific competition. Therefore, male and female snow petrels segregate at small spatial scales mainly determined by habitat (SIC) characteristics.

Keywords : bio-logging, competition, foraging, isotopic niche, *Pagodroma nivea*, sea ice concentration, snow petrel

1 Introduction

Sexual segregation occurs in a many living animals including invertebrates (Hochkirch et al. 2007, Romey & Wallace 2007) and vertebrates (Ruckstuhl & Neuhaus 2005, Wearmouth & Sims 2008) but also in plants (Harder et al. 2000). Investigating sexual segregation is of particular relevance from a fundamental point of view to understand how and why the sexes differentially distribute themselves and the consequences on population processes and dynamics. It is also relevant from a management and conservation point of view since sex specific distribution influences overlap with spatial distribution of human activities and/or contamination gradient (Carravieri et al. 2014). Two main concepts have been proposed to describe sexual segregation: social segregation, where males and females tend to form single-sex groups within the same or homogeneous habitat; and habitat segregation, where males and females use different habitats within a home range and with habitats differing in their amount or quality of forage distributed heterogeneously or patchily (Conradt 2005, Ruckstuhl 2007). Both social segregation~~aggregation~~ and habitat segregation can or cannot lead to spatial or temporal segregation, which have been~~can~~ be considered as auxiliary concepts (Conradt 2005, Ruckstuhl 2007). However, the distinction between habitat segregation and spatial segregation is scale-dependent: spatial segregation is a mechanism to avoid competing for the

same habitat by choosing different locations, while habitat segregation is a mechanism to avoid competing for resources at the same location. These concepts can also be understood in the framework of equalizing and stabilizing mechanisms applied to movement ecology (Chesson 2000, Jeltsch et al. 2013).

Several hypotheses have been proposed to explain social ~~segregation~~ and habitat segregations (Conradt 2005, Ruckstuhl 2007, Wearmouth & Sims 2008). In solitary animals, social segregation is unlikely to occur since by definition a single animal is not social (Conradt 1998, Neuhaus & Ruckstuhl 2004), except perhaps in rare cases (Martin & Da Silva 2004). Four main hypotheses explain habitat segregation in solitary species (Ruckstuhl 2007, Wearmouth & Sims 2008). ~~The predation-risk hypothesis proposes sexual differences in risk of predation and in reproductive strategies. According to this hypothesis males select high-risk, high-energy-gain habitats, whereas females trade off food quality of the habitat in favor of safety to them and their offspring (Main et al. 1996).~~ The forage-selection hypothesis, which incorporates the scramble competition hypothesis, suggests sex differences in nutritional requirements linked to sex-specific differences in body size (Gross 1998). The larger sex individuals select habitats where intake rates are high whereas the smaller sex individuals are constrained to sites where they can obtain a high-quality food (Beier 1987, Barboza & Bowyer 2000). Alternatively, one sex may forage more efficiently, thus outcompeting and excluding the other (scramble-competition hypothesis or intersexual competition hypothesis) (Clutton Brock et al. 1987). The activity-budget hypothesis, initially developed for group-living species, was extended to solitary species and to species with unequal reproductive investment (Wearmouth & Sims 2008). This hypothesis proposes that sex differences in activity budgets will increase with divergence in the body size of the sexes. Therefore, the sex-specific energy requirements will result in sex-specific habitat used due to allometric relationships between body size and metabolic rate. Finally, t~~T~~he predation-risk

hypothesis proposes sexual differences in risk of predation and in reproductive strategies~~.~~ ~~According to this hypothesis males select high-risk, high-energy gain habitats, whereas females trade-off food quality of the habitat in favor of safety to them and their offspring~~ (Main et al. 1996), and~~,~~ the thermal niche-fecundity hypothesis assumes ~~that fecundity is temperature dependent and~~ that sex differences occur in the temperature at which fecundity is maximized~~. This last hypothesis is restricted to ectotherms~~ (Sims 2005).

Sexual segregation has been widely studied among terrestrial animals, particularly mammals, but only relatively recently in marine organisms (Wearmouth & Sims 2008). Yet, despite an ongoing interest in sexual segregation in marine animals such as seabirds and marine mammals (Lewis et al. 2002, Elliott et al. 2010, Phillips et al. 2011, Mancini et al. 2013, Baylis et al. 2016, Kernaléguen et al. 2016), the underlying causes and the mechanisms driving habitat segregation remain poorly understood. In addition, very few studies focused on between-sex differences in habitat segregation in relation to dynamic oceanographic features (Pinet et al. 2012, Cleasby et al. 2015, Paiva et al. 2017), thereby limiting our ability to distinguish between the concurrent sexual segregation hypotheses. Moreover, these studies come from temperate or tropical areas reflecting a lack of evidence for polar species. However, foraging strategies may differ between polar, temperate and tropical oceanographic environments, at least in seabirds (Baduini & Hyrenbach 2003, Weimerskirch 2007). Furthermore, for practical, technical and ethical reasons most studies that have investigated sexual segregation on marine animals have focused on large species (Phillips et al. 2011), complicating the possibility to discriminate between the various hypotheses proposed to explain sexual segregation.

In this study we aimed to quantify sexual differences in the foraging strategies, at sea distribution, habitat use, and trophic ecology of a sexually dimorphic polar seabird, the snow petrel, *Pagodroma nivea*, during the incubation period. Snow petrels are endothermic animals,

126 therefore excluding the thermal niche-fecundity hypothesis as an explanatory hypothesis.
127 Since predation on this species is occasional and no sex-specific predation is known to occur
128 (Barbraud 1999), the predation-risk hypothesis can be discounted. Therefore, both the forage-
129 selection hypothesis and the activity budget hypothesis can be highlighted as possible
130 mechanisms for segregation in this species. There is considerable overlap between the forage-
131 selection hypothesis and the activity-budget hypothesis, complicating our ability to make
132 clear predictions to distinguish between the two, and to estimate the relative support of each
133 hypothesis (Wearmouth & Sims 2008). Nevertheless, using GPS tracking data, isotopic data
134 and environmental data we addressed the following main questions: (1) do female snow
135 petrels differ from males in their foraging tactics, distribution and habitat use?; (2) how are
136 body reserves regulated during incubation in the two sexes?; and (3) do sex-specific
137 morphological characteristics influence foraging efficiency? Based on results from
138 comparative studies suggesting that dimorphic seabird species from polar/temperate regions
139 are more prone to show trophic or spatial segregation than dimorphic species from the tropics
140 (Mancini et al. 2013), and on a relationship between sexual segregation in diet and sexual size
141 dimorphism in seabirds (Phillips et al. 2011), we predicted sexual segregation in diet and/or
142 spatial segregation in the snow petrel, which is one of the most sexually dimorphic seabird
143 species (Croxall 1982, Fairbairn & Shine 1993).
144

145 2 Material and methods

146 2.1 Study species

147 The snow petrel is endemic to Antarctica and the Southern Ocean, with a circumpolar
148 breeding distribution (Croxall et al. 1995). It is a specialist forager and ship-based
149 observations indicate that this is the most pagophilic species amongst flying seabirds,
150 occurring only where there is some degree of sea ice cover (Griffiths 1983, Ainley et al. 1984,

1986), generally within the marginal ice zone and areas of heavy ice concentrations ((Ainley et al. 1992, 1993). Snow petrels forage by flying rapidly along the edges of ice floes, ice shelves and icebergs in search of its prey (Ainley et al. 1984). The species feeds primarily on fish, including the myctophid *Electrona antarctica* in oceanic waters and the pelagic notothenid *Pleuragramma antarctica* (Antarctic silverfish) in neritic waters; they prey also upon swarming crustaceans, the Antarctic (*Euphausia superba*) and ice (*E. crystallorophias*) krill, and the hyperiid amphipod *Themisto gaudichaudii* (Ainley et al. 1984, 1991, Ridoux & Offredo 1989, Van Franeker & Williams 1992, Ferretti et al. 2001). At Pointe Géologie (Adélie Land), undetermined fish dominated the chick diet in 1982 (Ridoux & Offredo 1989) and fish items identified in 1994 were all Antarctic silverfish (authorsô unpublished data). Prey are caught by dipping and surface-seizing (Harper et al. 1985) generally on the wing but also by ambush feeding (Ainley et al. 1984).

Snow petrels breed in crevices and under boulders. Adult birds arrive at the colonies in late October to copulate before departing at sea for a two to three week pre-laying exodus, and females lay a single egg in early December (Mougin 1968, Isenmann 1970). Incubation lasts ≈44 days on average during which males and females alternately incubate their egg until hatching (Brown 1966, Barbraud et al. 1999). After hatching the chick is guarded by parents alternating short spells until it attains homeothermy. Then the chick is left unattended and regularly fed by both parents until fledging, which occurs on average ≈47 days after hatching. Adults leave the colony during the first two weeks of March before dispersing at sea where they remain in the sea ice zone during the non-breeding period (Delord et al. 2016).

2.2 Fieldwork

Fieldwork was carried out at Ile des Pétrels (66°40ôS, 140°01ôE), Pointe Géologie archipelago, Adélie Land, East Antarctica, between 7 December 2015 and 17 January 2016.

This corresponds to the incubation period. On average 550 pairs of snow petrels breed on Ile des Pétrels in dense colonies or in loosely aggregated nests (CEBC-CNRS unpublished data). By daily visits at 36 nests, we studied laying dates and the duration of the foraging trips and incubation shifts of 36 males and 36 females until hatching. Incubating birds were identified using their metal ring number. Sixty five snow petrels (n = 36 females and n = 29 males) were tracked with GPS loggers (nanoFix-Geo; PathTrack Limited, UK) during the incubation period. We tracked only one foraging trip per bird to minimize disturbance and to ensure independence between trips. The devices weighed 2.2 g, which represented between 0.5% and 0.8% of the birdsô mass, thus well below the 3% threshold advised by Phillips et al.(2003). Birds were manually captured at the nest and weighted (± 5 g) in a bag with a Pesola spring balance before being equipped with a GPS. The birds were initially sexed by vocalization when approached on the nest and handled (male calls have a lower pitch and a lower rhythm than those of females (Guillotin & Jouventin 1980, Barbraud et al. 2000). GPS units were deployed on birds about to leave for a foraging trip (i.e. when both partners were at the nest) and were attached to the two central tail feathers using Tesa® tape. The GPS recorded locations at 15, 30, 40 or 60 min intervals. Several intervals (15 min, n = 15; 30 min, n = 4; 40 min, n = 43; 60 min, n = 3) were tested to estimate the minimum interval frequency that allowed the GPS battery to last for a complete foraging trip. Birds were recaptured on the day they returned to the nest following their foraging trip, weighed, measured (wing length ± 1 mm with a ruler, tarsus length, bill length, and bill depth ± 0.1 mm with calipers) and the loggers were recovered. All birds were recaptured but three birds lost their GPS during the foraging trip. Data from all other GPS (n = 62) were retrieved successfully.

2.3 Tissue sampling, molecular sexing and stable isotopes

Adults equipped with GPS and 24 additional individuals (11 females and 13 males) were sampled during incubation for stable isotope and molecular sexing analyses. A blood sample from the alar vein was taken immediately after capture of the bird upon return from a foraging trip using a 1-mL heparinized syringe and a 25-gauge needle and maintained at 4°C until being processed. Collected blood volumes ranged from 0.50 to 0.80 mL. Blood samples were separated into plasma and blood cells by centrifugation at 12,000 rpm for 5 min, within 2-3 hours of sampling and stored frozen at -20°C until analyses at the laboratory. For each individual, 6 whole body feathers were pulled out from the upper chest and stored dry in sealed individual plastic bags for stable isotope analysis.

From a subsample of blood cells, the sex was determined by polymerase chain reaction amplification of part of two highly conserved genes present on the sex chromosomes as detailed in Weimerskirch et al. (2005).

Stable carbon (ŭ^{13}C) and nitrogen (ŭ^{15}N) isotope ratios in the blood cells, plasma and body feathers of snow petrels were determined to investigate the trophic choices of each sex and consistency ~~over time~~ of their foraging niche over time. The isotopic method was validated in the Southern Ocean for several seabird species: δ^{15}N values mainly define the trophic position, with values increasing with trophic level (Cherel et al. 2010), and δ^{13}C values indicate the latitude of the foraging habitat (Cherel & Hobson 2007, Jaeger et al. 2010). Plasma has a half-life of about 3 days (Hobson & Clark 1993), a shorter period than the average ~~duration of foraging~~ trip duration during incubation (≈7 days, Barbraud et al. 1999), and represents prey ingestion and trophic ecology during the last trip before sampling (Cherel et al. 2005a). Blood cells have a half-life of about 30 days (Hobson & Clark 1993) and represent dietary information integrated over a few months. Feathers contain dietary information at the time they were grown, because keratin is inert after synthesis (Hobson & Clark 1992, 1993, Bearhop et al. 2002). In snow petrels body moult is a gradual process

225 extending over at least 4 months in summer and autumn. It begins during incubation, but most
226 body feathers grow in the weeks following completion of breeding, i.e. from February to
227 April (Maher 1962, Beck 1969). Therefore, isotopic values of body feathers contain
228 information about diet near the end of the previous breeding season and the beginning of the
229 previous non-breeding season.

230 Feathers (one single feather per bird) were cleaned to remove surface contaminants using
231 a 2:1 chloroform:methanol solution followed by two methanol rinses. They were then oven
232 dried for 48 h at 50°C and cut into small pieces using stainless steel scissors. Blood cells and
233 plasma samples were freeze-dried and powdered. Since avian plasma, unlike blood cells,
234 contains a high and variable lipid content that affect its ŭ^{13}C values, lipids were removed from
235 plasma samples using chloroform/methanol (Cherel et al. 2005a, Cherel et al. 2005b). Then,
236 tissue sub-samples were weighed with a microbalance (aliquots mass: ≈ 0.3 mg dw), packed
237 in tin containers, and nitrogen and carbon isotope ratios were subsequently determined at the
238 laboratory LIENSs by a continuous flow mass spectrometer (Thermo Scientific Delta V
239 Advantage) coupled to an elemental analyser (Thermo Scientific Flash EA 1112). Results are
240 presented in the usual δ notation relative to Vienna PeeDee Belemnite and atmospheric N_2 for
241 ŭ^{13}C and ŭ^{15}N, respectively. Replicate measurements of internal laboratory standards
242 (acetanilide and peptone) indicate measurement errors <0.15 ă for both δ^{13}C and δ^{15}N
243 values.
244

245 **2.4 Foraging analysis and spatial usage**

246 Spatial and statistical analyses were performed using R 3.2.1 using the ñstatsò package (R
247 Development Core Team 2015) and ñ*adehabitatLT*ò package (Calenge 2006, Calenge et al.
248 2009). From the GPS recorded data, foraging trips were reconstructed and data were
249 rediscretized to have one location each 40 min. Some of the trips were largely incomplete

(return journey not initiated; n = 15 corresponding to the 15 min intervals) because of battery limitations and were removed from the analysis. For each complete (n = 40) and incomplete (return journey initiated; n = 7) foraging trip, we computed the following foraging indices: maximum distance to the colony (*Dmax*, km), average movement speed (*MS*, km h^{-1}) and daily distance covered (*Dday*, km d^{-1}). For each complete trip, we calculated the additional following metrics: total distance travelled (*Dtotal*, km) and trip duration (*T*, h). Spatial distribution of snow petrels was investigated by producing utilization distributions (UDs 25%, 50%, 75% and 95%; Worton 1989) for each individual, using kernel analysis with a cell size of 0.1° × 0.1° and a smoothing parameter (h) that was estimated using the ad hoc method href. Grid cell size was based on the mean accuracy of the devices (≈ 10 m), the mean maximum speed of flying snow petrels (see Results) and on the time interval between two GPS locations (40 min). To investigate whether space use differed between sexes, we calculated observed overlaps in each UD representing the high core (25%), core (50%), middle (75%) and general (90%) use areas using utilization distribution overlap index (UDOI), which is the most appropriate measure of quantifying similarity among UD estimates (Fieberg & Kochanny 2005). The extent of overlap between male and female home ranges was estimated using Bhattacharyyaôs affinity (BA), which ranges from 0 (no overlap) to 1 (complete overlap). Using these metrics we performed a randomization procedure to test the null hypothesis that there was no difference in the spatial distribution of males and females at the population level (Breed et al. 2006). The sex of each bird was randomly assigned using the observed sex ratio in our data set and the overlap metric between males and females was calculated for 25%, 50%, 75% and 95% kernels. We performed 1000 randomizations of our dataset from which the probability of accepting the null hypothesis was calculated as the proportion of random overlaps that were smaller than the observed overlap. Since we were testing only if the observed overlap was smaller than random overlap, we considered this as a one-tailed test.

Second, we tested the null hypothesis that there was no difference in the extent of overlap in spatial distribution of males and females at the individual level.

For each foraging trip we also calculated the following metrics from the phenotypic data: the body mass change (Δm, in g) between departure and arrival of a foraging trip, the daily mass gain (Mday, in $g.day^{-1}$) calculated as the ratio between Δm and the trip duration, the proportion mass gain calculated as the ratio between Δm and mass at departure for a foraging trip, and the proportion daily mass gain calculated as the ratio between Daym and mass at departure for a foraging trip. A body condition index before departure and after return from a foraging trip was also calculated. To estimate the body condition we used the body measurements to calculate the scale mass index (SMI) as recommended by Peig and Green (2009, 2010). The SMI adjusts the mass of all individuals to that expected if they had the same body size. We used the score of the first axis of a principal component analysis (PC1) combining wing, bill, tarsus lengths and bill depth to characterize body size. PC1 accounts for 70.9% of the total variance and all measurements are highly correlated with PC1 (Pearsonôs r > 0.80; P < 0.001). The SMI was calculated for each individual *i* according to the formula:

$$SMI_i = M_i * \left(\frac{L_0}{L_i}\right)^b$$

where M_i and L_i are, respectively, the body mass and the PC1 score of the individual *i*, L_0, is the value of PC1 for the whole studied population and *b* the slope estimate of the RMA (Reduced Major Axis) regression of log-transformed body mass on log-transformed PC1.

2.5 Foraging habitat covariates

To investigate the foraging habitats used by males and females, the tracking locations were categorized as occurring during commuting (outward and inward) or foraging (middle) stage of foraging trips, as commonly used for central-place foragers. Among Procellariformes the distinction between these stages varies greatly between species and breeding stages

299 (Weimerskirch et al. 1997, Phillips et al. 2009). Moreover, at the individual level defining
300 objectively the transition between such behaviors may prove to be difficult (Phillips et al.
301 2009, Wakefield et al. 2009). To avoid this pitfall, we applied the method used by Wakefield
302 et al. (2009) and Phillips et al. (2009) to determine the stage of the trips at which the
303 transitions occurred at the population level. For each location within a foraging trip the ratio
304 d_{col}/D_{max} was calculated, where d_{col} is the distance from the colony and D_{max} is the maximum
305 distance from the colony reached during that trip. The ratio t/T was also calculated, where t is
306 the time elapsed since the beginning of the trip and T is the total trip time. Then, the total
307 variance in d_{col}/D_{max} for all locations occurring before t/T was plotted against t/T. The point of
308 inflexion of this curve was determined as well as the value of t/T at this point. Tracking
309 locations recorded before this point were classified as those corresponding to the outward trip.
310 Similarly, the total variance in d_{col}/D_{max} occurring after t/T was plotted against t/T and the t/T
311 value from which a monotonic decrease of the variance began was recorded. Tracking
312 locations recorded after this point were classified as those corresponding to the return trip, and
313 locations between both points were considered as foraging locations.
314 Previous studies have shown that the snow petrel is a sea ice obligate species and remains
315 highly associated with sea ice year round (Griffiths 1983, Ainley et al. 1984, 1986, 1992,
316 1993, Delord et al. 2016). We therefore used sea ice concentration (SIC) to describe the
317 foraging habitat of snow petrels. Although sea surface temperature is commonly used to
318 describe foraging habitats in seabirds, there are very few sea surface temperature observations
319 in regions covered by sea ice, especially in the Southern Ocean (Rayner et al. 2003).
320 Therefore this covariate could not be used. We used passive-microwave estimates of daily sea
321 ice concentration from the Special Sensor Microwave Imager (SSMI/I) brightness
322 temperatures (12.5 × 12.5 km resolution) from the Institut Français de Recherche pour
323 lŒExploitation de la Mer (Ifremer, ftp://ftp.ifremer.fr/ifremer/cersat/products/gridded/psi-

concentration/data/antarctic). We also used bathymetry data (ocean depth at one-minute horizontal spatial resolution) obtained from NOAAôs ETOPO (https://sos.noaa.gov/datasets/etopo1-topography-and-bathymetry/) as an additional habitat variable. Daily sea ice concentration and depth values were extracted for each foraging location (therefore excluding the commuting part of the trips at sea) on each track using bilinear interpolation from the native ice and depth grids using ñ*raster*ò package in R (Hijmans 2018). Since snow petrels are highly associated with the sea ice region (as defined by the region within >15% sea ice concentration isocline, Cavalieri et al. 1991), the SIC data were filtered to retain SIC values >15%.

2.6 Statistical analysis

Isotopic niche of the two sexes was established using the metric SIBER (Stable Isotope Bayesian Ellipses), which is based on a Bayesian framework that confers a robust comparison to be made among data sets concerning different sample sizes (Jackson et al. 2011). The area of the standard ellipse (SEA_C, an ellipse having a 40% probability of containing a subsequently sampled datum) was used to compare female and male isotopic values and their overlap in relation to the total niche width (i.e. both sexes combined), and a Bayesian estimate of the standard ellipse and its area (SEA_B) was used to test whether femalesô isotopic niche is narrower than malesô isotopic niche (Jackson et al. 2011). The *standard.ellipse* and *convexhull* functions were used to calculate these metrics from SIBER implemented in the package ó*SIAR*ô (Parnell et al. 2010) under R.

Consistency in foraging niche was estimated following Votier et al. (2010) and Ceia et al. (2012), by regressing stable isotope ratios in plasma on those of blood cells to obtain an index of consistency in carbon source (habitat) and trophic level. Since $\delta^{13}C$ has a trophic component, we used the studentized residuals of the relationship with $\delta^{15}N$ in the same tissue

(male plasma: $F_{1,25}$=1.438 , P=0.242, r=0.233; male blood cells: : $F_{1,36}$=0.838, P=0.366, r=0.151; female plasma: $F_{1,33}$=1.470 , P=0.234, r=0.206; female blood cells: $F_{1,45}$=6.507, P=0.014, r=0.355) to determine the degree of short-term repeatability in $\delta^{13}C$ independently of trophic effects. Longer-term foraging consistency was estimated by regressing stable isotope values of blood cells (actual breeding period) with those of feathers (most likely the end of the previous breeding period and subsequent fall at sea). We also used the residuals to correct the trophic component associate with $\delta^{13}C$ by regressing these values upon $\delta^{15}N$ signatures in feathers (male: $F_{1,36}$=1.945, P=0.172, r=0.226; female: $F_{1,45}$=5.863, P=0.020, r=0.340).

Foraging probability was modelled using a binomial generalized additive mixed model (GAMM) in the ó*gamm4***ô** package in R (Wood et al. 2017). This allowed for the possibility of nonlinear responses to environmental covariates, which we expected. The response variable was the tracking location, which was coded as 1 for a foraging location and as 0 for a commuting location, and explanatory variables were sea ice concentration and bathymetry. Because interactions between the variable sex and environmental covariates would be difficult to interpret in complex nonlinear models, separate models were developed for male and female birds. Models included sea ice concentration and bathymetry as fixed factors, and bird identity as a random term to account for pseudoreplication issues. The smoothing parameter was chosen automatically using generalized cross-validation. To model spatial auto-correlation an isotropic thin plate spline was included, set up as a two dimensional smoother based on both x and y coordinates (Cleasby et al. 2015). To ascertain whether collinearity between covariates may have occurred we examined the correlations between environmental variables using a Spearman correlation coefficient since covariates were not normally distributed. We assumed that a correlation of greater than r_s 0.4 was problematic, but the correlation was below this threshold (r_s = 0.14).

Foraging intensity was modelled using GAM in the ó*gam***ô** package in R (Hastie & Tibshirani 1990). Foraging intensity was defined based on the frequency distribution of the tracking locations classified as foraging only. The environmental covariates were divided into K classes. Then, within each class the number of foraging locations was extracted and the count was used as the response variable. A GAM with a quasi-Poisson distribution was then fitted to the data. Separate models were developed for male and female birds. Models included sea ice concentration and bathymetry as fixed factors. The smoothing parameter was chosen automatically using generalized cross-validation. For SIC we used K=1% SIC classes and for bathymetry we used K=50 m classes.

Differences between sexes in body measurements, sea ice characteristics used, and foraging trip metrics were tested using Studentôs t-tests and differences in stable isotope date using Studentôs t-tests and Wilcoxon rank tests. Since we performed a large number of tests when comparing male and female body size measurements, isotopic values and foraging trip characteristics, we used the Benjamini-Hochberg procedure (Benjamini & Hochberg 1995) to control for false discovery rate. We chose a false discovery rate (q*) of 0.10 when applying the Benjamini-Hochberg procedure. This choice was motivated by the fact that this study was conducted on a single year and was exploratory. In such cases setting a FDR to an extremely low value results in decreasing the statistical power for detecting genuine effects and several authors recommend setting FDR to a relatively large value (Yoccoz 1991, Field et al. 2004, Roback and Askins 2005).

3 Results

Male snow petrels were ~~structurally~~ larger than females, particularly for bill length and bill depth, and were 10% heavier than females (Table 1). Bill length, bill depth and body mass were the most sexually dimorphic phenotypic traits.

399

400 **3.1 Spatial distribution of males and females and habitat differences**

401 Males and females foraged in offshore waters to the east and to the west of the colony in
402 equal proportions (χ^2=0.03, p=0.86, Figure 1). Space-use sharing was similar between males
403 and females as the UDOI was not significantly lower than the null expectation for 25%, 50%,
404 75% or 95% UDs (Table 2). The 95% UDOI was > 1, indicating a higher than normal overlap
405 between male and female UDs relative to uniform space use, i.e. male and female UDs were
406 non-uniformly distributed and had a high degree of overlap. By contrast, the 25% UDOI was
407 relatively close to 0 indicating less overlap between male and female UDs relative to uniform
408 space use. Males and females UDs were also similar whatever the UDs considered since BA
409 were not significantly lower than the null expectation for 25%, 50%, 75% or 95% UDs (Table
410 2).

411 In average males foraged in areas with higher SIC than females (Table 3). Fitted models
412 on foraging probability contained sex-specific smoothers for bathymetry and SIC (Table 4).
413 For females, the GAMM model explained 10% of the deviance of foraging probability. All
414 smoothers for SIC and bathymetry were significant (Table 4). Foraging probability increased
415 sharply with increasing SIC up to 30% and more smoothly for high SIC (Figure 2). Foraging
416 probability showed a first peak at depth of ≈600 m and a second and high peak at depth of
417 ≈1600 m. Foraging probability sharply increased at depths >2500 m but sample size was
418 small and there was high uncertainty. Both the random intercept for bird identity and the
419 spatial smoother were significant.

420 For males, the model explained 4.6% of the deviance of foraging probability. All
421 smoothers for SIC and bathymetry, the random intercept for bird identity and the spatial
422 smoother were significant (Table 4). Male foraging probability varied non-linearly with SIC
423 and bathymetry. It increased smoothly with increasing SIC, and was higher when SIC was

424 higher than ≈90% (Figure 2). Foraging probability also increased with bathymetry up to ≈600
425 m and remained relatively stable until ≈2000 m from which its increased.

426 Female foraging intensity was non-linearly related to SIC and bathymetry (Table 5).
427 Foraging intensity increased with SIC up to a maximum for SIC ≈40% and then decreased for
428 higher SIC (Figure 3). Lowest foraging intensity was observed for SIC >80%. Foraging
429 intensity showed a rather bimodal distribution as a function of bathymetry. It was maximal in
430 waters ≈400 m deep, then decreased to reach a minimum at ≈1400 m, and increased again for
431 water depths between ≈2000-2700 m. Male foraging intensity was non-linearly related to SIC
432 and bathymetry (Table 5). It showed a bimodal distribution as a function of SIC, with a
433 maximum for SIC ≈36% and a second peak for SIC ≈85% (Figure 3). As for females, male
434 foraging intensity was bimodal as a function of bathymetry. It was maximal in waters ≈400 m
435 deep, then decreased to reach a minimum at ≈1500 m, and increased up to a second peak in
436 waters ≈2400 m deep.
437
438 **3.2 Stable isotope ratios**
439 Male plasma, blood cells and feathers had significantly 0.6-0.8‰ higher $\delta^{15}N$ values than
440 those of females (Table 6). There was no difference in $\delta^{13}C$ values between males and
441 females, except for plasma for which males had higher values. Males and females had similar
442 SEA_B for all tissues (Figure 4). Overlap between SEA_B areas for males and females was
443 0.462, 0.586 and 0.599 for blood cells, plasma and feathers, respectively.

444 Strong significant positive relationships were found in $\delta^{15}N$ between blood cells and
445 plasma (males: $F_{1,25}$=18.846, P<0.001, r=0.656; females: $F_{1,33}$=31.679, P<0.001, r=0.700;
446 Figure 5), but not between feathers and blood cells (males: $F_{1,36}$=0.036, P=0.850, r=0.032;
447 females: $F_{1,45}$=0.062, P=0.805, r=0.037). No significant positive relationship was found in
448 residual $\delta^{13}C$ between blood cells, plasma and feathers (all p̂s>0.243).

There was no significant relationship between isotopic values and body measurements or body condition (all p's>0.08).

3.3 Foraging trip performance and foraging efficiency

Foraging trip duration, length, speed and directions (Table 7), as well as mass gain and proportion mass gain (Table 8) did not differ between males and females. Foraging efficiency, measured as the proportionate daily mass gain while foraging, was significantly greater for females than for males (Table 8), and was greater for larger females with deeper bills (PC1: $F_{1,20}$=5.279, P=0.033, r=0.457; bill depth: $F_{1,20}$=8.630, P=0.008, r=0.549). In females, but not in males, foraging efficiency decreased with the duration of the foraging trip (Figure 6). Females were more efficient than males during short (<2 days) foraging trips, but for trips longer than 2 days, foraging efficiency was similar in males and in females (daily mass gain: t_{39}=0.397, P = 0.693; proportion daily mass gain : t_{39}=0.862, P = 0.394).

3.4 Regulation of the foraging trips

To investigate how birds regulate foraging trips according to the depletion of their body reserves, we correlated the body condition at departure with the duration of the foraging trips and the mass gain metrics while foraging. Foraging trip duration was not correlated to body condition at departure (Pearson correlation coefficient: p = 0.417 for females, p = 0.576 for males~~all p's>0.417~~), but mass gain and proportionate mass gain were negatively related to body condition at departure for both sexes (all ~~p~~P's<0.005; Figure 6). In addition, in males, but not in females, daily mass gain and proportionate daily mass gain were negatively correlated to body condition at departure (males: all ~~p~~P's<0.010; females: all ~~p~~P's>0.429). Male (but not female) body condition at return from a foraging trip was positively correlated to the time spent at sea (Pearson correlation coefficient: p = 0.05).

3.5 Factors affecting mass gain at sea

For females, but not for males, mass gain, proportion mass gain and body condition at return from a foraging trip were positively correlated to mean and maximum sea ice concentration of the foraging trip locations (females: all $P_{p\hat{o}s}$<0.049; males: all $P_{p\hat{o}s}$>0.232; Figure 7). For males and females, there was no relationship between bathymetry and mass gain, proportion mass gain, and body condition at return (all $P_{p\hat{o}s}$>0.100).

4 Discussion

This study provides clear evidence of sexual segregation and foraging tactics in snow petrels. In accordance with our prediction, we found evidence for sexual segregation in diet, with males feeding on average on higher trophic level prey when compared to females, but no evidence for spatial segregation as indicated by spatial data and $\delta^{13}C$ isotopic data. Males and females differed in their usage of sea ice, providing evidence for sex-specific habitat segregation.

4.1 Differences in habitat use

During incubation males and females foraged predominantly in pack-ice areas over the deep Antarctic continental shelf and adjacent continental margin (500-900 m, due to the isostatic effect of the ice sheet), and to a lesser extent in oceanic waters. These results are consistent with previous observational work at sea showing that high densities of breeding snow petrels in the Ross Sea were found within the pack ice along the continental slope (Ainley et al. 1984). The low tissue $\delta^{13}C$ values of snow petrels is a consistent characteristic of consumers foraging in high-Antarctic waters (Cherel 2008, Cherel et al. 2011). Blood cell, plasma and feather $\delta^{13}C$ values were similar in males and females, which indicates that both sexes foraged

offshore in pelagic waters without an~~that present no~~ obvious neritic-oceanic $\delta^{13}C$ gradient in high-Antarctica (Cherel et al. 2011). Blood cell and plasma $\delta^{13}C$ values of birds from Adélie Land were similar to values obtained from snow petrel muscle tissue in the Weddell Sea (Rau et al. 1992) between 64°S and 66°S, but were slightly lower than those measured in whole blood of birds from Hop Island (Hodum & Hobson 2000). However, the shape of the relationships between foraging intensity and SIC suggested that males and females used different sea ice habitats. Female foraging intensity was highest for SIC between ≈20% and ≈40%, and then decreased non-linearly for higher SIC, with a sharp decrease for SIC higher than ≈70%. By contrast male foraging intensity remained high for high SIC. Therefore, although foraging intensity decreased with increasing SIC for both sexes, males foraged more intensively in high sea ice concentration areas (> 70%) than females. Males and females made greater use of pack-ice areas over the continental shelf and continental margin than of oceanic pack-ice areas, but males were more likely to forage and foraged more intensively on the continental margin (-550 to -950 m) than females.

Few studies have simultaneously quantified between-sex differences in habitat use and foraging behavior in marine species in relation to dynamic oceanographic features such as sea ice. In the northern gannet (*Morus bassanus*), sexual segregation was driven largely by spatial and habitat segregation with males, smaller than females, mainly foraging in coastal mixed waters where net primary production was high, and females mainly foraging in offshore stratified waters (Cleasby et al. 2015). Similarly, the sex-specific habitat use reported in the monomorphic Barauôs petrel (*Pterodroma baraui)* during the prelaying exodus (males used more frequently marine areas with high productivity) can be partly explained by spatial segregation between sexes (Pinet et al. 2012). During the incubation and chick rearing period, they did not found evidence for habitat segregation and foraging areas largely overlapped. In the Adélie penguin (*Pygoscelis adeliae*) at Pointe Géologie, females foraged more intensively

524 in areas of higher sea ice concentration than males during the guard stage, and there was
525 spatial segregation between sexes with females foraging further from the colony than males
526 (Widmann et al. 2015). Using a multiyear comprehensive dataset, Paiva et al. (2017) found
527 that sexual segregation in foraging areas and foraging habitats of Coryôs shearwaters
528 (*Calonectris borealis*) varied between years, with greater sexual (habitat and spatial)
529 segregation during years when sea surface temperatures were higher and chlorophyll *a*
530 concentrations were lower, presumably corresponding to lower food availability. In favorable
531 years no spatial segregation was observed and habitat segregation was low. The hatching
532 success of snow petrels during the 2015/2016 breeding season was 46.9%, i.e. lower than the
533 long-term average of 63.3% (Chastel et al. 1993), suggesting that environmental conditions
534 were relatively poor. However, we did not observed spatial segregation between sexes but
535 foraging habitat use differed, with males foraging more frequently in high sea ice
536 concentration areas than females. Such a pattern was found in the wandering albatross
537 (*Diomedea exulans*) at South Georgia in which, despite no clear sexual segregation at large
538 scales, sex-specific microhabitat selection was found during the chick-rearing period,
539 resulting in sexual segregation in core foraging areas (Pereira et al. 2018). Multiple years of
540 tracking are needed to shed light into the effects of environmental stochasticity (sea ice
541 variability) on habitat segregation and spatial segregation.
542 As opposed to other highly sexually size-dimorphic seabirds (wandering albatross:
543 Weimerskirch et al. 1993, giant petrels *Macronectes spp.*: Gonzá~~a~~les-Solí~~i~~s et al. 2000,
544 boobies *Sula spp.*: Weimerskirch et al. 2009, frigatebirds *Fregata spp.*: Hennicke et al. 2015)
545 snow petrels did not show spatial segregation in their foraging habitat during incubation.
546 Spatial segregation in snow petrels may occur during other periods of the year such as during
547 the chick-rearing period when which food requirements are particularly high for provisioning
548 the chick. Alternatively, this lack of spatial segregation may be constrained by the specific

549 foraging habitat requirements of snow petrels. These seabirds forage exclusively in a sea ice
550 environment, which is limited during the breeding season around breeding colonies and may
551 thus constraint males and females to spatially overlap at a broad spatial scale.
552
553 **4.2 Influence of sex on diet and foraging tactics**
554 The snow petrel diet is relatively well known during the chick-rearing period and isotopic
555 data together with prey biometric data suggest that snow petrels mainly feed on postlarvae
556 and juvenile Antarctic silverfish (*Pleuragramma antarcticum*) (Ridoux & Offredo 1989,
557 Hodum & Hobson 2000, Pinkerton et al. 2013). Although, snow petrel diet during incubation
558 remains poorly known, $\delta^{15}N$ values obtained in our study are similar or slightly higher than
559 those found in other studies during the chick rearing period (Hodum & Hobson 2000, Delord
560 et al. 2016), suggesting a similar diet. Nevertheless, and despite large overlap in their core
561 isotopic niches as indicated by the standard ellipse areas, female snow petrels had lower $\delta^{15}N$
562 values than males for all tissues sampled, which suggests they were feeding on lower trophic
563 level prey than males. Similar results were found by Tartu et al. (2014) for blood cells during
564 the pre-laying period. We speculate that there might be at least two reasons for this. First,
565 compared to males, females may feed more frequently on other prey than Antarctic silverfish,
566 such as crustaceans which~~ith~~ are situated at a lower trophic level than Antarctic silverfish.
567 Indeed, diet studies indicate that snow petrels also feed on crustaceans such as *Euphausia*
568 *superba*, *E. crystallorophias*, *Themisto gaudichaudii*, and other amphipods (Ainley et al.
569 1984, Ridoux & Offredo 1989) which have lower $\delta^{15}N$ values than Antarctic silverfish
570 (Pinkerton et al. 2013). Second, females may feed on Antarctic silverfish in similar
571 proportions than males but on smaller sized individuals (i.e. younger). It is known that $\delta^{15}N$
572 values increase with body length (and age) in Antarctic silverfish from ≈7-8ă in larvae (10-
573 20 mm standard length) to ≈10-11ă in juvenile and adult fish (Giraldo et al. 2011, Pinkerton

et al. 2013). It is currently unknown whether sea ice concentration and characteristics differentially affect the spatial distribution of Antarctic silverfish age-classes. However, it is likely that females fed more on crustaceans than on young silverfish since crustaceans have much lower $\delta^{15}N$ values than young silverfish (Cherel 2008). Thus, our results suggest that males ate more silverfish in areas with higher sea ice concentration.

The strong positive relationship between plasma $\delta^{15}N$ and blood $\delta^{15}N$ indicates short term (over weeks) consistency in trophic level between successive foraging trips during incubation. Values of $\delta^{15}N$ in plasma and feathers did not differ in both sexes (Appendix 1), but blood $\delta^{15}N$ were smaller than feather and plasma $\delta^{15}N$ in both sexes, suggesting that males and females fed on lower trophic level prey prior to incubation than during the breeding season. Short and long term consistency in foraging water masses was also low as indicated by the lack of relationship between plasma and blood $\delta^{13}C$, and between feather and blood $\delta^{13}C$, respectively. Indeed tracking data indicated that birds foraged on the continental shelf, continental margin, and to a lesser extent in oceanic waters. Values of $\delta^{13}C$ in feathers were higher than those in blood and plasma for both sexes (Appendix 1), suggesting that during the latter part of the breeding season and the beginning of the non-breeding season snow petrels foraged in more oceanic waters (snow petrels start molting during the chick rearing period and until early May (Beck 1969, 1970, Delord et al. 2016). This period coincides with the sea ice growth and its northward extension.

The negative relationship between mass gain (and proportion daily mass gain) during a foraging trip and body condition at departure for a foraging trip (i.e. at the end of fasting while incubating the egg), indicated that males and females were able to regulate their body reserves as found in other Procellariiformes species (Chaurand & Weimerskirch 1994, Gonzáles-Solís et al. 2000). Although both sexes regulated body condition, this ability seemed greater for females than for males. Indeed, body condition at departure for a foraging

trip was lower in females than in males, but similar for both sexes at return from a foraging trip despite similar trip durations. This is further supported by the fact that females had higher daily mass gains and proportion daily mass gains than males. However, this greater ability in females may be partly explained by the fact that females undertook short foraging trips during which mass gain was particularly high (Figure 1). Although some males also made short foraging trips, mass gain was still lower than female mass gain during these trips. ~~In fact, when considering foraging trips longer than 2 days, daily mass gain and proportion daily mass gain were similar for males and females (daily mass gain: t_{39}=0.397, P = 0.693; proportion daily mass gain: t_{39}=0.862, P = 0.394).~~ Therefore, these results suggest that female foraging efficiency was similar in males and females, except during short (<2 days) foraging trips during which females appeared more efficient. We suspect that some females undertook short foraging trips during their incubation shift in order to restore their body condition to avoid abandoning the egg while their partner was foraging at sea. This could result from the lower fasting capacities of females compared to males due to their smaller body size (Barbraud & Chastel 1999).

Interestingly, the ability of females (but not of males) to restore their body condition during a foraging trip was affected by sea ice concentration. Indeed, female body condition at return from a foraging trip was positively related to sea ice concentration in the foraging area, contrary to males. This suggests that areas with heavy sea ice concentration were more profitable. This is further supported by the positive relationship between male (but not female) body condition at return from a foraging trip and time spent at sea ~~(Pearson correlation coefficient: p = 0.05)~~, and given that males foraged more frequently in high sea ice concentration areas. Thus, foraging on highly nutritional preys such as silverfish in high sea ice concentration areas might be more efficient to restore body condition that feeding in more open water areas.

Body condition at the start of a foraging trip was not related to the time spent at sea ~~(Pearson correlation coefficient: p = 0.417 for females, p = 0.576 for males)~~, suggesting that the time spent at sea was not only dependent on the restoration of body condition. Although only a few birds returned to undertake the next incubation shift after losing mass (n = 3, 6.3%) or without gaining mass (n = 3, 6.3%), this suggests that mass gain alone does not explain the decision to return to the colony. Perhaps birds took into account the increased probability of partners deserting the egg with the increasing duration of the foraging trip (Tveraa et al. 1997).

Thus, incubating female snow petrels seemed more efficient at restoring their body condition during a foraging trip despite similar trip duration, length or speed, while foraging areas were identical to those of males at a broad spatial scale. However, this higher efficiency mainly concerned short (<2 days) foraging trips. In addition, our results show that females foraging in high sea ice concentration areas foraged more efficiently (this relationship holds when excluding foraging trip <2 days), and female fed on lower trophic level preys that males. Together, these results suggest that areas with high sea ice concentration may be more profitable for resource acquisition, perhaps due to higher abundance, availability or quality of prey such as the Antarctic silverfish.

4.3 Factors underlying sexual segregation

Sex differences in foraging behavior could result from the influence of sexual size dimorphism on foraging efficiency and intra-specific competition (forage-selection hypothesis and scrambled competition hypothesis). The positive relationship between female bill depth and proportion daily mass gain suggests that foraging efficiency is size dependent in females, which are smaller than males. Our results also suggest that the most favorable areas were areas of high sea ice concentration (females body condition at return increased with increase

649 sea ice concentration, male body condition at return increased with foraging trip length),
650 which were used less frequently by females. Therefore, it is possible that females were
651 excluded from high sea ice concentration areas via direct competition. This could possibly
652 indicate that male and female snow petrels try to avoid competition and thus diverged in
653 habitat preference in more profitable areas, where intra-specific competition might be more
654 intense. Such a mechanism was also proposed to explain sex-specific differences in broad
655 scale foraging areas in highly sexually size dimorphic species (wandering albatross:
656 Weimerskirch et al. 1993, Shaffer et al. 2001; giant petrels: Gonzáales-Solís et al. 2000), but
657 also in foraging habitat at a microhabitat scale (Pereira et al. 2018). A major assumption of
658 the intersexual competition hypothesis is that prey capture should be a function of bill size
659 (Selander 1966, Shine 1989). Although we do not have the data in hand to test this prediction
660 explicitly, we note that $\delta^{15}N$ values suggested that females consumed lower sized prey than
661 males (crustaceans vs fish). Females with thicker bills were also more efficient during their
662 foraging trip, suggesting they were feeding on more profitable prey, and bill size was among
663 the most sexually dimorphic phenotypic trait in this species.
664 Sex-specific niche divergence and habitat segregation can also arise from a difference
665 between sexes in parental roles and investment (the activity budget hypothesis, Clarke et al.
666 1998, Thaxter et al. 2009, Weimerskirch et al. 2009, Pinet et al. 2012). Although males
667 undertake a greater investment in chick provisioning though higher feeding frequencies
668 (Barbraud et al. 1999), there is little differentiation in the reproductive role of male and
669 female snow petrels during incubation. Males make slightly shorter foraging trips than
670 females during incubation (Isenmann 1970, Barbraud et al. 1999), but in average the total
671 time spent foraging during the incubation period is very similar for both sexes (males: average
672 19.8 days, females: average 21.0 days, Barbraud 1999), indicating that the roles of male and
673 female snow petrels do not appear to differ substantially during incubation. Therefore, it

674 seems unlikely that such limited constraints related to reproductive role specialization could
675 explain why female snow petrels foraged less intensively in high sea ice concentration areas;
676 this hypothesis can probably, therefore, be discounted. Sex-specificity in flight performance
677 may also be responsible for sexual segregation (Shaffer et al. 2001, Phillips et al. 2004).
678 Indeed, sexual dimorphism in wing area and wing loading in several albatross species may
679 partially explain large-scale sexual segregation in foraging areas in these species: sex-specific
680 foraging locations were likely influenced by activity budgets since smaller birds are more
681 efficient flyers. Therefore, other aspects of the morphology not measured here, such as wing
682 loading and agility, may be important. Female snow petrels appear to have a lower aspect
683 ratio and lower wing loading than males (Spear & Ainley 1998), suggesting they might be
684 less flight efficient but more maneuverable than males. However, since there was no spatial
685 segregation between sexes at large-spatial scales, environmental conditions potentially
686 affecting flight efficiency (wind speed) were identical for males and females. Thus, these
687 aspects are also unlikely to be of importance in snow petrels to explain sex-specific foraging
688 habitat use during incubation.

689 Overall, our study demonstrates sex-specific foraging tactics in a highly sexually size
690 dimorphic species during the incubation period, probably driven by intra-specific competition.
691 Results indicate an absence of sexual segregation at a broad-spatial scale, but suggest that
692 sexual segregation in snow petrels is mediated by habitat segregation at a microhabitat scale.
693 Males foraged more intensively than females in high sea ice concentration areas, which
694 seemed to be more profitable in terms of resource acquisition as results suggest that males ate
695 more fish in these areas. Studying sex-specific foraging tactics during the entire breeding
696 period, thus including the pre-laying exodus and the chick-rearing period, is however
697 necessary to better understand the underlying drivers of sexual segregation in snow petrels
698 and in marine predators in general (Pinet et al. 2012). Sexual segregation in foraging behavior

may also vary between years as a function of environmental conditions (Cleasby et al. 2015, Paiva et al. 2017), highlighting the need for multi-year tracking studies.

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References

Ainley D, Fraser W, Smith W, Hopkins T, Torres J (1991) The structure of upper level pelagic food webs in the Antarctic: effect of phytoplankton distribution. J Marine Systems 2:111ï 122

Ainley D, Fraser W, Sullivan C, Torres J, Hopkins T, Smith W (1986) Antarctic mesopelagic micronekton¡ evidence from seabirds that pack ice affects community structure. Science 232:847ï 849

Ainley DG, OôConnor EF, Boekelheide RJ (1984) The marine ecology of birds in the Ross Sea, Antarctica. Ornithological Monographs 32:1ï 97

Ainley DG, Ribic CA, Fraser WR (1992) Does prey preference affect habitat choice in Antarctic seabirds¿ Mar Ecol Prog Ser 90:207ï 221

726 Ainley DG, Ribic CA, Spear LB (1993) Species-habitat relationships among antarctic
727 seabirds: a function of physical or biological factors? The Condor 95:806ï 816

728 Baduini CL, Hyrenbach KD (2003) Biogeography of procellariiform foraging strategies: does
729 ocean productivity influence provisioning. Mar Ornithol 31:101ï 112

730 Barboza PS, Bowyer RT (2000) Sexual segregation in dimorphic deer: a new gastrocentric
731 hypothesis. Journal of Mammalogy 81:473ï 489

732 Barbraud C (1999a) Subspecies-selective predation of snow petrels by skuas. Oikos:275ï 282

733 Barbraud C (1999b) Aspects écologiques et évolutifs de la variation de la taille corporelle
734 chez le pétrel des neiges, *Pagodroma nivea*. Unpublished PhD Thesis, Université de
735 Tours, France.

736 Barbraud C, Chastel O (1999) Early body condition and hatching success in the snow petrel
737 *Pagodroma nivea*. Polar Biol 21:1ï 4

738 Barbraud C, Mariani A, Jouventin P (2000) Variation in call properties of the snow petrel,
739 *Pagodroma nivea*, in relation to sex and body size. Australian Journal of Zoology
740 48:421ï 430

741 Barbraud C, Weimerskirch H, Robertson GG, Jouventin P (1999) Size related life history
742 traits: insights from a study of snow petrels (*Pagodroma nivea*). Journal of Animal
743 Ecology 68:1179ï 1192

744 Baylis A, Orben R, Costa D, Arnould J, Staniland I (2016) Sexual segregation in habitat use is
745 smaller than expected in a highly dimorphic marine predator, the southern sea lion.
746 Marine Ecology Progress Series 554:201ï 211

747 Bearhop S, Waldron S, Votier SC, Furness RW (2002) Factors that influence assimilation
748 rates and fractionation of nitrogen and carbon stable isotopes in avian blood and
749 feathers. Physiological and Biochemical Zoology 75:451ï 458

750 Beck J (1969) Breeding seasons and moult in some smaller Antarctic petrels. In: Antarctic
751 Ecology, London.p 542ï 550

752 Beck J (1970) Breeding seasons and moult in some smaller Antarctic petrels. Antarctic
753 ecology 1:542ï 550

754 Beier P (1987) Sex differences in quality of white-tailed deer diets. Journal of Mammalogy
755 68:323ï 329

756 Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and
757 powerful approach to multiple testing. Journal of the Royal Statistical Society B
758 57:289-300

759 Breed GA, Bowen W, McMillan J, Leonard ML (2006) Sexual segregation of seasonal
760 foraging habitats in a non-migratory marine mammal. Proceedings of the Royal
761 Society of London B: Biological Sciences 273:2319ï 2326

762 Brown D (1966) Breeding biology of the Snow petrel *Pagodroma nivea* (Forster). Anare
763 Scientific Reports 89:1ï 63

764 Calenge C, Dray S, Royer-Carenzi M (2009) The concept of animalsôtrajectories from a data
765 analysis perspective. 4:34ï 41

766 Carravieri A, Cherel Y, Blévin P, Brault-Favrou M, Chastel O, Bustamante P (2014) Mercury
767 exposure in a large subantarctic avian community. Environmental Pollution 190:51ï 57

768 Cavalieri D, Crawford J, Drinkwater M, Eppler D, Farmer L, Jentz R, Wackerman C (1991)
769 Aircraft active and passive microwave validation of sea ice concentration from the
770 Defense Meteorological Satellite Program Special Sensor Microwave Imager. Journal
771 of Geophysical Research: Oceans 96:21989ï 22008

772 Ceia FR, Phillips RA, Ramos JA, Cherel Y, Vieira RP, Richard P, Xavier JC (2012) Short-
773 and long-term consistency in the foraging niche of wandering albatrosses. Marine
774 biology 159:1581ï 1591

775 Chastel O, Weimerskirch H, Jouventin P (1993) High annual variability in reproductive
776 success and survival of an antarctic seabird, the snow petrel *Pagodroma nivea*.
777 Oecologia 94:278ï 285

778 Chaurand T, Weimerskirch H (1994) Incubation routine, body mass regulation and egg
779 neglect in the blue petrel *Halobaena caerulea*. Ibis 136:285ï 290

780 Cherel Y (2008) Isotopic niches of emperor and Adélie penguins in Adélie Land, Antarctica.
781 Marine Biology 154:813ï 821

782 Cherel Y, Fontaine C, Richard P, Labat JP (2010) Isotopic niches and trophic levels of
783 myctophid fishes and their predators in the Southern Ocean. Limnology and
784 Oceanography 55:324ï 332

785 Cherel Y, Hobson KA (2007) Geographical variation in carbon stable isotope signatures of
786 marine predators: a tool to investigate their foraging areas in the Southern Ocean. Mar
787 Ecol Prog Ser 329:281ï 287

788 Cherel Y, Hobson KA, Bailleul F, Groscolas R (2005) Nutrition, physiology, and stable
789 isotopes: new information from fasting and molting penguins. Ecology 86:2881ï 2888

790 Cherel Y, Hobson K, Weimerskirch H (2005) Using stable isotopes to study resource
791 acquisition and allocation in procellariiform seabirds. Oecologia 145:533ï 540

792 Cherel Y, Koubbi P, Giraldo C, Penot F, Tavernier E, Moteki M, Ozouf-Costaz C, Causse R,
793 Chartier A, Hosie G (2011) Isotopic niches of fishes in coastal, neritic and oceanic
794 waters off Adélie Land, Antarctica. Polar science 5:286ï 297+

795 Chesson P (2000) Mechanisms of maintenance of species diversity. Annual Review of
796 Ecology and Ecosystems 31:343-366

797 Clarke J, Manly B, Kerry KR, Gardner H, Franchi E, Corsolini S, Focardi S (1998) Sex
798 differences in Adélie penguin foraging strategies. Polar biology 20:248ï 258

Cleasby IR, Wakefield ED, Bodey TW, Davies RD, Patrick SC, Newton J, Votier SC, Bearhop S, Hamer KC (2015) Sexual segregation in a wide-ranging marine predator is a consequence of habitat selection. Mar Ecol Prog Ser 518:1ï 12

Clutton Brock T, Iason G, Guinness F (1987) Sexual segregation and density related changes in habitat use in male and female Red deer (*Cervus elaphus*). Journal of Zoology 211:275ï 289

Conradt L (1998) Could asynchrony in activity between the sexes cause intersexual social segregation in ruminants? Proceedings of the Royal Society of London B: Biological Sciences 265:1359ï 1368

Conradt L (2005) Definitions, hypotheses, models and measures in the study of animal segregation. Sexual segregation in vertebrates: ecology of the two sexes (KE Ruckstuhl and P Neuhaus, eds) Cambridge University Press, Cambridge, United Kingdom:11ï 34

Croxall J (1982) Sexual dimorphism in Snow petrels *Pagodroma nivea*. Notornis 29:171ï 180

Croxall JP, Steele WK, McInnes SJ, Prince PA (1995) Breeding distribution of the snow petrel *Pagodroma nivea*. Marine Ornithology 23:69ï 99

Delord K, Pinet P, Pinaud D, Barbraud C, Grissac S de, Lewden A, Cherel Y, Weimerskirch H (2016) Species-specific foraging strategies and segregation mechanisms of sympatric Antarctic fulmarine petrels throughout the annual cycle. Ibis 158:569ï 586

Elliott KH, Gaston AJ, Crump D (2010) Sex-specific behavior by a monomorphic seabird represents risk partitioning. Behavioral Ecology 21:1024ï 1032

Fairbairn J, Shine R (1993) Patterns of sexual size dimorphism in seabirds of the southern hemisphere. Oikos 68:139ï 145

Ferretti V, Soave GE, Casaux R, Coria NR (2001) Diet of the Snow Petrel *Pagodroma nivea* at Laurie Island, Antarctica, during the 1997/98 breeding season. Marine Ornithology 29:71ï 73

Fieberg J, Kochanny CO (2005) Quantifying home-range overlap: the importance of the utilization distribution. Journal of wildlife management 69:1346ï 1359

Field SA, Tyre AJ, Jonzen N, Rhodes JR, Possingham HP (2004) Minimizing the cost of environmental management decisions by optimizing statistical thresholds. Ecology Letters 7:669-675

Giraldo C, Cherel Y, Vallet C, Mayzaud P, Tavernier E, Moteki M, Hosie G, Koubbi P (2011) Ontogenic changes in the feeding ecology of the early life stages of the Antarctic silverfish (*Pleuragramma antarcticum*) documented by stable isotopes and diet analysis in the Dumont dõUrville Sea (East Antarctica). Polar Science 5:252ï 263

Gonzáales-Solíis J, Croxall J, Wood A (2000) Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels *Macronectes halli* during incubation. Oikos 90:390ï 398

837 Griffiths A (1983) Factors affecting the distribution of the Snow Petrel (*Pagodroma nivea*)
838 and the Antarctic Petrel (*Thalassoica antarctica*). Ardea 71:145ï 150

839 Gross JE (1998) Sexual segregation in ungulates: a comment. Journal of Mammalogy
840 79:1404ï 1409

841 Guillotin M, Jouventin P (1980) Le Pétrel des Neiges à Pointe Géologie. Gerfaut 70:51ï 72

842 Harder LD, Barrett SC, Cole WW (2000) The mating consequences of sexual segregation
843 within inflorescences of flowering plants. Proceedings of the Royal Society of London
844 B: Biological Sciences 267:315ï 320

845 Harper PC, Croxall JP, Cooper J (1985) A guide to foraging methods used by marine birds in
846 antarctic and subantarctic seas. Biomass Handbook 24:1ï 22

847 Hastie TJ, Tibshirani RJ (1990) Generalized additive models, volume 43 of Monographs on
848 Statistics and Applied Probability.

849 Hennicke JC, James DJ, Weimerskirch H (2015) Sex-specific habitat utilization and
850 differential breeding investments in Christmas Island frigatebirds throughout the
851 breeding cycle. PloS one 10:e0129437

852 Hijmans R (2018) raster: Geographic Data Analysis and Modeling. R package version 2.6-7.

853 Hobson KA, Clark RG (1992) Assessing avian diets using stable isotopes I: turnover of ^{13}C in
854 tissues. The Condor 94:181ï 188

855 Hobson KA, Clark RG (1993) Turnover of ^{13}C in cellular and plasma fractions of blood:
856 implications for non destructive sampling in avian dietary studies. The Auk 110:638ï
857 641

858 Hochkirch A, Gröning J, Krause S (2007) Intersexual niche segregation in Ceperoôs Ground-
859 hopper, *Tetrix ceperoi*. Evolutionary Ecology 21:727ï 738

860 Hodum PJ, Hobson KA (2000) Trophic relationships among Antarctic fulmarine petrels:
861 insights into dietary overlap and chick provisioning strategies inferred from stable-
862 isotope (delta N-15 and delta C-13) analyses. Mar Ecol Prog Ser 198:273ï 281

863 Isenmann P (1970) Contribution à la biologie de reproduction du pétrel des neiges
864 (*Pagodroma nivea* Forster). Le problème de la petite et de la grande forme.

865 Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among
866 and within communities: SIBERï Stable Isotope Bayesian Ellipses in R. Journal of
867 Animal Ecology 80:595ï 602

868 Jaeger A, Connan M, Richard P, Cherel Y (2010) Use of stable isotopes to quantify seasonal
869 changes of trophic niche and levels of population and individual specialisation in
870 seabirds. Mar Ecol Prog Ser 401:269ï 277

871 Jeltsch F, Bonte D, Pe'er G, Reineking B, Leimgruber P, Balkenhol N, Schröder B, Buchman
872 CM, Mueller T, Blaum N, Zurell D, Böhning-Gaese K, Wiegand T, Eccard JA, Hofer
873 H, Reeg J, Eggers U, Bauer S (2013) Integrating movement ecology with biodiversity

874 research - exploring new avenues to address spatiotemporal biodiversity dynamics.
875 Movement Ecology 1:6

876 Kernaléguen L, Arnould J, Guinet C, Cazelles B, Richard P, Cherel Y (2016) Early-life sexual
877 segregation: ontogeny of isotopic niche differentiation in the Antarctic fur seal.
878 Scientific reports 6:33211

879 Lewis S, Benvenuti S, Dallï Antonia L, Griffiths R, Money L, Sherratt T, Wanless S, Hamer
880 K (2002) Sex-specific foraging behaviour in a monomorphic seabird. Proceedings of
881 the Royal Society of London B: Biological Sciences 269:1687ï 1693

882 Maher WJ (1962) Breeding biology of the snow petrel near Cape Hallett, Antarctica. The
883 Condor 64:488ï 499

884 Main MB, Weckerly FW, Bleich VC (1996) Sexual segregation in ungulates: new directions
885 for research. Journal of Mammalogy 77:449ï 461

886 Mancini P, Bond A, Hobson K, Duarte L, Bugoni L (2013) Does sexual size dimorphism
887 facilitate trophic segregation? Testing the intersexual competition hypothesis with
888 tropical and polar seabirds. Journal of Experimental Marine Biology and Ecology
889 449:186ï 193

890 Martin A, Da Silva V (2004) River dolphins and flooded forest: seasonal habitat use and
891 sexual segregation of botos (*Inia geoffrensis*) in an extreme cetacean environment.
892 Journal of zoology 263:295ï 305

893 Mougin J (1968) Etude écologique de quatre espèces de pétrels antarctiques. LõOiseau et R F
894 O 38:1ï 52

895 Neuhaus P, Ruckstuhl KE (2004) A Critique: Can the Activity Budget Hypothesis Explain
896 Sexual Segregation in Desert Bighorn Sheep? Behaviour:513ï 520

897 Paiva VH, Pereira J, Ceia FR, Ramos JA (2017) Environmentally driven sexual segregation in
898 a marine top predator. Scientific reports 7:2590

899 Parnell AC, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable isotopes:
900 coping with too much variation. PloS one 5:e9672

901 Peig J, Green AJ (2009) New perspectives for estimating body condition from mass/length
902 data: the scaled mass index as an alternative method. Oikos 118:1883ï 1891

903 Peig J, Green AJ (2010) The paradigm of body condition: a critical reappraisal of current
904 methods based on mass and length: The paradigm of body condition. Functional
905 Ecology 24:1323ï 1332

906 Pereira JM, Paiva VH, Phillips RA, Xavier JC (2018) The devil is in the detail: small-scale
907 sexual segregation despite large-scale spatial overlap in the wandering albatross.
908 Marine Biology 165:55

909 Phillips RA, Mcgill RAR, Dawson DA, Bearhop S (2011) Sexual segregation in distribution,
910 diet and trophic level of seabirds: insights from stable isotope analysis. Marine
911 Biology 158:2199ï 2208

912 Phillips RA, Silk JRD, Phalan B, Catry P, Croxall JP (2004) Seasonal sexual segregation in
913 two *Thalassarche* albatross species: competitive exclusion, reproductive role
914 specialization or foraging niche divergence? Proceedings of the Royal Society of
915 London Series B: Biological Sciences 271:1283ï 1291

916 Phillips RA, Wakefield ED, Croxall JP, Fukuda A, Higuchi H (2009) Albatross foraging
917 behaviour: no evidence for dual foraging, and limited support for anticipatory
918 regulation of provisioning at South Georgia. Marine Ecology Progress Series
919 391:279ï 292

920 Phillips RA, Xavier JC, Croxall JP, Burger AE (2003) Effects of satellite transmitters on
921 albatrosses and petrels. The Auk 120:1082ï 1090

922 Pinet P, Jaquemet S, Phillips RA, Le Corre M (2012) Sex-specific foraging strategies
923 throughout the breeding season in a tropical, sexually monomorphic small petrel.
924 Animal Behaviour 83:979ï 989

925 Pinkerton M, Forman J, Bury S, Brown J, Horn P, OôDriscoll R (2013) Diet and trophic niche
926 of Antarctic silverfish *Pleuragramma antarcticum* in the Ross Sea, Antarctica. Journal
927 of fish biology 82:141ï 164

928 R Development Core Team 2015. R: A language and environment for statistical computing.
929 Vienna: R Foundation for statistical computing, https://www.R-project.org

930 Rau GH, Ainley DG, Bengtson JL, Torres JJ, Hopkins TL (1992) 15 N/14 N and 13 C/12 C in
931 Weddell Sea birds, seals, and fish: implications for diet and trophic structure. Marine
932 Ecology Progress Series:1ï 8

933 Rayner N, Parker DE, Horton E, Folland C, Alexander L, Rowell D, Kent E, Kaplan A (2003)
934 Global analyses of sea surface temperature, sea ice, and night marine air temperature
935 since the late nineteenth century. Journal of Geophysical Research: Atmospheres 108

936 Ridoux V, Offredo C (1989) The diets of five summer breeding seabirds in Adélie Land,
937 Antarctica. Polar biology 9:137ï 145

938 Roback PJ, Askins RA (2005) Judicious use of multiple hypothesis tests. Conservation
939 Biology 19:261-267

940 Romey WL, Wallace AC (2007) Sex and the selfish herd: sexual segregation within
941 nonmating whirligig groups. Behavioral Ecology 18:910ï 915

942 Ruckstuhl K (2007) Sexual segregation in vertebrates: proximate and ultimate causes.
943 Integrative and Comparative Biology 47:245ï 257

944 Ruckstuhl K, Neuhaus P (2005) Sexual segregation in vertebrates: ecology of the two sexes.
945 1st edn. Cambridge: Cambridge University Press

946 Selander RK (1966) Sexual dimorphism and differential niche utilization in birds. The Condor
947 68:113ï 151

948 Shaffer SA, Costa D, Weimerskirch H (2001) Behavioural factors affecting foraging effort of
949 breeding wandering albatrosses. Journal of animal ecology 70:864ï 874

950 Shine R (1989) Ecological causes for the evolution of sexual dimorphism: a review of the
951 evidence. The Quarterly Review of Biology 64:419ï 461

952 Sims DW (2005) Differences in habitat selection and reproductive strategies of male and
953 female sharks. Sexual segregation in vertebrates: Ecology of the two sexes 8:127ï 147

954 Spear LB, Ainley DG (1998) Morphological differences relative to ecological segregation in
955 petrels (Family: Procellariidae) of the Southern Ocean and tropical Pacific. The
956 Auk:1017ï 1033

957 Tartu S, Bustamante P, Goutte A, Cherel Y, Weimerskirch H, Bustnes JO, Chastel O (2014)
958 Age-Related Mercury Contamination and Relationship with Luteinizing Hormone in a
959 Long-Lived Antarctic Bird. Plos One 9

960 Thaxter CB, Daunt F, Hamer KC, Watanuki Y, Harris MP, Grémillet D, Peters G, Wanless S
961 (2009) Sex specific food provisioning in a monomorphic seabird, the common
962 guillemot *Uria aalge*: nest defence, foraging efficiency or parental effort? Journal of
963 Avian Biology 40:75ï 84

964 Tveraa T, Lorensten S-H, Sæther B-E (1997) Regulation of foraging trips and costs of
965 incubation shifts in the Antarctic petrel (*Thalassoica antarctica*). Behavioral Ecology
966 8:465ï 469

967 Van Franeker J, Williams R (1992) Diet of fulmarine petrels in the Windmill Islands, Wilkes
968 Land, Antarctica. Preliminary results.

969 Votier SC, Bearhop S, Witt MJ, Inger R, Thompson DR, Newton J (2010) Individual
970 responses of seabirds to commercial fisheries revealed using GPS tracking, stable
971 isotopes and vessel monitoring systems. Journal of applied ecology 47:487ï 497

972 Wakefield ED, Phillips RA, Matthiopoulos J, Fukuda A, Higuchi H, Marshall GJ, Trathan PN
973 (2009) Wind field and sex constrain the flight speeds of central-place foraging
974 albatrosses. Ecological Monographs 79:663ï 679

975 Wearmouth VJ, Sims DW (2008) Sexual segregation in marine fish, reptiles, birds and
976 mammals: behaviour patterns, mechanisms and conservation implications. Advances
977 in marine biology 54:107ï 170

978 Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? Deep Sea
979 Research Part II: Topical Studies in Oceanography 54:211ï 223

980 Weimerskirch H, Lallemand J, Martin J (2005) Population sex ratio variation in a
981 monogamous long lived bird, the wandering albatross. Journal of Animal Ecology
982 74:285ï 291

983 Weimerskirch H, Mougey T, Hindermayer X (1997) Foraging and provisioning strategies of
984 black-browed albatrosses in relation to the requirements of the chick: natural variation
985 and experimental study. Behavioral ecology 8:635ï 643

986 Weimerskirch H, Salamolard M, Sarrazin F, Jouventin P (1993) Foraging strategy of
987 wandering albatrosses through the breeding season: a study using satellite telemetry.
988 The Auk 110:325ï 342

Weimerskirch H, Shaffer SA, Tremblay Y, Costa DP, Gadenne H, Kato A, Ropert-Coudert Y, Sato K, Aurioles D (2009) Species-and sex-specific differences in foraging behaviour and foraging zones in blue-footed and brown boobies in the Gulf of California. Marine Ecology Progress Series 391:267ï 278

Widmann M, Kato A, Raymond B, Angelier F, Arthur B, Chastel O, Pellé M, Raclot T, Ropert-Coudert Y (2015) Habitat use and sex-specific foraging behaviour of Adélie penguins throughout the breeding season in Adélie Land, East Antarctica. Movement ecology 3:30

Wood S, Scheipl F, Wood MS (2017) Package ógamm4.ô Am Stat 45:339

Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164ï 168

Yoccoz NG (1991) Overuse, and misuse of significance tests in evolutionary biology and ecology. Bulletin of the Ecological Society of America 72:106-111

Table 1. Body measurements of male and female snow petrels and percentage of difference between sexes for each measurement. For t-tests homogeneity of variances we checked using a Brown and Forsythe tests (Brown and Forsythe 1974), and corrected p values are reported (uncorrected in brackets). Significant differences with a false detection rate of 0.10 are shown in bold. Δ is the difference in %. The sample size is 47 individuals.

	Sex	Mean (SD)	Range	Δ	t-test
Wing length (mm)	Male	298.3 (6.8)	287.0-311.0	2.3	**t_{45}=4.215**
	Female	290.0 (6.7)	280.0-302.0		**p<0.001** (<0.001)
Tarsus length (mm)	Male	40.2 (1.2)	38.0-42.7	4.5	**t_{45}=4.846**
	Female	38.4 (1.2)	35.9-41.0		**p<0.001** (<0.001)
Bill length (mm)	Male	24.4 (1.0)	22.1-26.6	9.0	**t_{45}=8.488**
	Female	22.2 (0.8)	20.9-23.7		**p<0.001** (<0.001)
Bill depth (mm)	Male	10.8 (0.5)	9.6-11.8	8.3	**t_{45}=6.408**
	Female	9.9 (0.4)	8.9-10.9		**p<0.001** (<0.001)
Body mass[1] (g)	Male	389.0 (30.4)	331.5-464.0	10.3	**t_{45}=6.014**
	Female	340.5 (24.0)	300.0-385.0		**p<0.001** (<0.001)
Body mass[2] (g)	Male	431.4 (34.0)	365.0-495.0	10.3	**t_{45}=4.467**
	Female	387.0 (33.9)	320.0-460.0		**p<0.001** (<0.001)

[1]before a foraging trip; [2]on return from a foraging trip.

Table 2. Estimated overlap in utilization distributions (UD) between male and female snow petrels from Ile des Pétrels, Adélie Land, East Antarctica. UDOI: Utilization distribution overlap index. BA: Bhattacharyyaôs affinity

UD (%)	Observed UDOI	Randomized UDOI	p	Observed BA	Randomized BA	p
25	0.062	0.064	0.417	0.127	0.123	0.452
50	0.226	0.243	0.262	0.379	0.398	0.273
75	0.502	0.545	0.227	0.634	0.662	0.212
95	1.215	1.229	0.439	0.858	0.863	0.359

Table 3. Mean, maximum and variance in sea ice concentration, mean, minimum and maximum bathymetry for foraging localities of male and female snow petrels from Ile des Pétrels, Adélie Land, East Antarctica. For t-tests homogeneity of variances we checked using a Brown and Forsythe tests (Brown and Forsythe 1974), corrected p values are reported (uncorrected in brackets). Significant differences with a false detection rate of 0.10 are shown in bold.

	Sex	Mean (SD)	Range	t-test
Mean SIC (%)	Male	54.8 (14.6)	30.4-77.9	**t_{44}=2.600**
	Female	44.0 (13.4)	16.8-72.5	**p=0.063~~13~~** (0.013)
Maximum SIC (%)	Male	83.8 (16.8)	43.9-99.9	t_{44}=1.867
	Female	72.6 (23.8)	19.8-100.0	p=0.171~~069~~ (0.069)
Variance in SIC	Male	375.7 (224.2)	69.5-840.2	t_{44}=1.772
	Female	264.0 (198.3)	3.9-749.9	p=0.139 (0.083)
Mean bathymetry (m)	Male	503.8 (248.7)	285-1490	t_{45}=0.911
	Female	582.4 (341.2)	259-1706	p=0.367 (0.367)
Maximum bathymetry (m)	Male	1354.1 (632.1)	809-2973	t_{45}=1.285
	Female	1617.4 (771.4)	613-3223	p=0.257 (0.205)

Table 4. Generalized Additive Mixed Model (GAMM) results for foraging probability of male and female snow petrels as a function of sea ice concentration (SIC), bathymetry (BAT) and spatial autocorrelation (s(x,y)). edf indicates the estimated degrees of freedom.

Variable	Sex	Smoother edf (p value)	Estimate (SE)	σ^2 (SE)
Intercept	Male		3.543 (1.101)	
	Female		3.087 (1.365)	
SIC	Male	**7.97 (<0.001)**		
	Female	**1.00 (0.003)**		
BAT	Male	**3.89 (<0.001)**		
	Female	**1.00 (0.044)**		
s(x,y)	Male	**22.96 (<0.001)**		
	Female	**24.52 (<0.001)**		
Random intercept for bird ID	Male			10.250 (3.201)
	Female			1.174 (0.343)

Table 5. Generalized Additive Model (GAM) results for foraging intensity of male and female snow petrels as a function of sea ice concentration (SIC) and bathymetry (BAT). edf indicates the estimated degrees of freedom.

Variable	Sex	Smoother edf (p value)	Scale	Adjusted R^2
SIC	Male	**4.99 (<0.001)**	2.50	0.223
	Female	**4.11 (<0.001)**	2.25	0.663
BAT	Male	**6.47 (<0.001)**	16.01	0.779
	Female	**6.82 (<0.001)**	9.28	0.863

Table 6. Stable isotope values in blood cells, plasma and feathers of male and female snow petrels sampled Ile des Pétrels, Adélie Land, East Antarctica. Values are mean ± SD. SEA_B are Bayesian approximation of the standard ellipse area. Values in brackets indicate n and range for $\delta^{13}C$ and $\delta^{15}N$, and 95% credible interval for SEA_B. p indicates the probability that SEA_B of males and females differ. Sample sizes are 47 individuals for blood cells and feathers, and 46 individuals for plasma. For t-tests homogeneity of variances we checked using a Brown and Forsythe tests (Brown and Forsythe 1974), corrected p values are reported (uncorrected in brackets). Significant differences with a false detection rate of 0.10 are shown in bold.

Tissue	$\delta^{13}C$(ă)			$\delta^{15}N$(ă)			SEA_B		p
	Male	Female		Male	Female		Male	Female	
Plasma	-25.46 ± 0.35 (-26.01;-24.56)	-25.66 ± 0.22 (-26.06;-25.26)	**t_{83}=2.105 p=0.057** (0.039)	12.11 ± 0.74 (10.70;13.38)	11.49 ± 0.97 (9.04;12.83)	**t_{83}=3.418 p=0.002** (0.001)	0.69 (0.45;0.99)	0.79 (0.55;1.09)	0.311
Blood cells	-25.79 ± 0.21 (-26.13;-25.35)	-25.72 ± 0.27 (-26.13;-25.19)	t_{83}=1.491 p=0.168 (0.140)	10.65 ± 0.68 (9.37;12.17)	9.96 ± 0.65 (8.36;11.46)	**t_{83}=5.568 p<0.001** (<0.001)	0.41 (0.29;0.55)	0.39 (0.29;0.52)	0.586
Feather	-23.68 ± 0.71 (-25.05;-22.06)	-23.50 ± 0.67 (-25.00;-22.49)	t_{83}=0.335 p=0.738 (0.738)	12.11 ± 1.35 (8.75;14.03)	11.34 ± 1.35 (8.61;14.10)	**t_{83}=4.289 p<0.001** (<0.001)	2.41 (1.72;3.28)	2.65 (1.94;3.49)	0.331

Table 7. Summary of foraging trip metrics for snow petrels from Ile des Pétrels, Adélie Land, East Antarctica. For t-tests homogeneity of variances we checked using a Brown and Forsythe tests (Brown and Forsythe 1974), corrected p values are reported (uncorrected in brackets). Significant differences with a false detection rate of 0.10 are shown in bold.

	Sex	Mean (SD)	Range	t-test
Trip duration (d)	Male	5.2 (1.8)	1.1-8.0	t_{45}=0.979
	Female	4.8 (1.9)	0.7-8.0	p=1.160 (0.333)
Trip length (km)	Male	851.6 (352.1)	302.0-1957.5	t_{45}=0.292
	Female	856.4 (389.0)	173.8-1803.8	p=0.772 (0.772)
Trip mean speed ($km \cdot h^{-1}$)	Male	2.0 (0.6)	1.2-3.5	t_{45}=0.762
	Female	2.1 (0.4)	1.7-3.2	p=0.788 (0.450)
Trip maximum speed ($km \cdot h^{-1}$)	Male	13.5 (2.6)	9.2-21.4	t_{45}=0.670
	Female	13.3 (2.5)	9.5-18.9	p=0.709 (0.506)
Trip start direction (°)	Male	161.5 (114.0)	0.8-355.2	t_{45}=1.066
	Female	204.6 (143.2)	2.6-348.6	p=2.045 (0.292)
Trip mean direction (°)	Male	190.9 (110.4)	70.1-307.9	t_{45}=0.336
	Female	209.2 (117.6)	68.8-342.7	p=0.862 (0.739)
Trip end direction (°)	Male	167.5 (114.0)	46.9-282.8	t_{45}=0.773
	Female	184.8 (68.6)	102.9-291.6	p=1.035 (0.444)

Table 8. Summary of metrics of foraging trip efficiency for snow petrels from Ile des Pétrels, Adélie Land, East Antarctica. For t-tests homogeneity of variances we checked using a Brown and Forsythe tests (Brown and Forsythe 1974), corrected p values are reported (uncorrected in brackets). Significant differences with a false detection rate of 0.10 are shown in bold.

	Sex	Mean (SD)	Range	t-test
Mass at departure (g)	Male	389.0 (30.4)	331.5-464.0	**t_{45}=6.014**
	Female	340.5 (24.0)	300.0-385.0	**p<0.001** (<0.001)
Mass at return (g)	Male	431.4 (34.0)	365.0-495.0	**t_{45}=4.467**
	Female	387.0 (33.9)	320.0-460.0	**p<0.001** (<0.001)
BCI[1] at departure	Male	377.1 (25.2)	336.2-437.7	**t_{45}=2.633**
	Female	358.1 (24.0)	321.3-414.1	**p=0.031** (0.012)
BCI at return	Male	419.5 (31.2)	372.5-479.3	t_{45}=1.636
	Female	405.0 (29.3)	361.0-458.4	p=0.145 (0.109)
Δmass (g)	Male	42.4 (38.1)	-20-110	t_{45}=0.392
	Female	46.6 (34.6)	-10-95	p=0.697 (0.697)
Daily mass gain (g·day^{-1})	Male	9.2 (8.2)	-4.2-28.0	t_{45}=1.707
	Female	14.6 (13.2)	-2.0-45.0	p=0.152 (0.095)
Proportion mass gain (%)	Male	0.11 (0.10)	-0.05-0.29	t_{45}=0.886
	Female	0.14 (0.11)	-0.03-0.31	p=0.435 (0.381)
Proportion daily mass gain (%)	Male	0.02 (0.02)	-0.01-0.07	**t_{45}=2.064**
	Female	0.04 (0.04)	-0.01-0.12	**p=0.089** (0.045)

[1] Body Condition Index

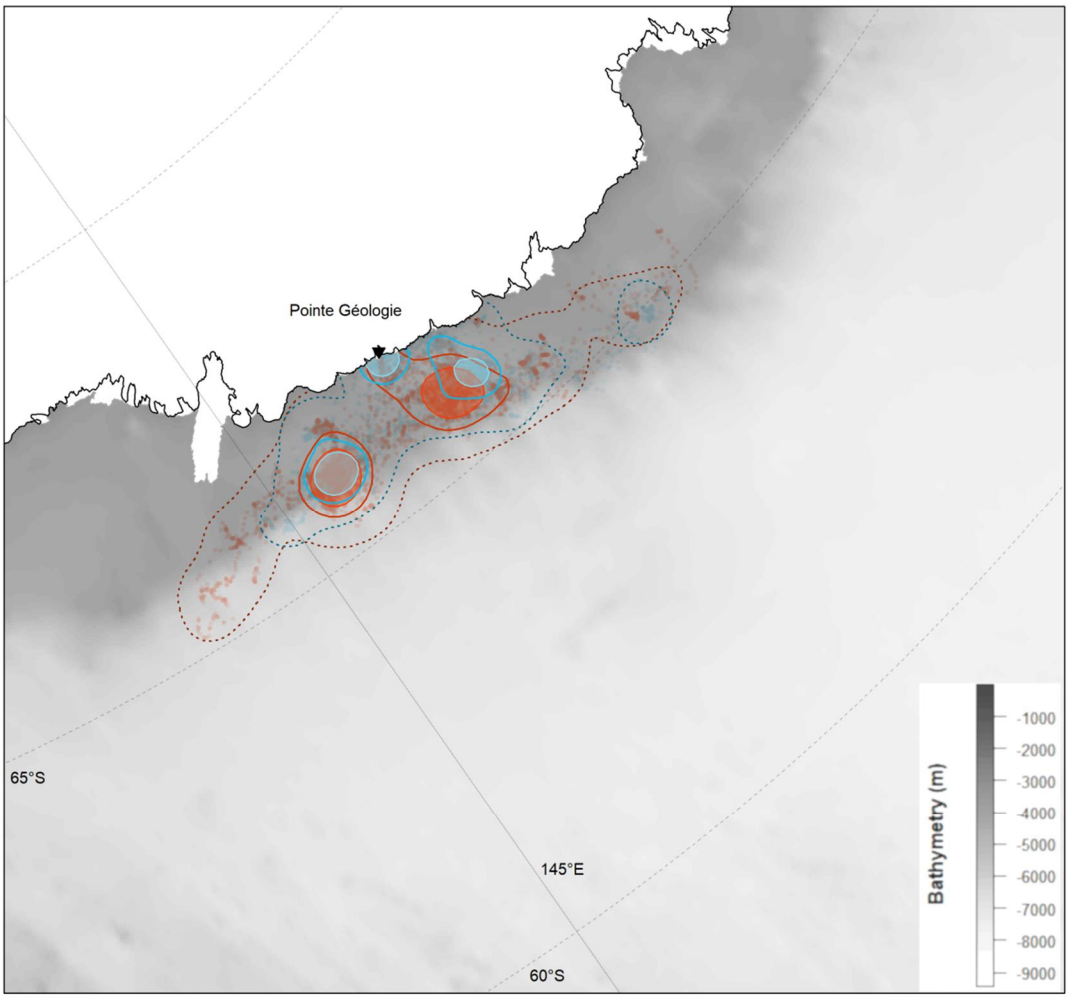


Figure 1. Foraging ranges of male (blue) and female (red) snow petrels during incubation sampled at Ile des Pétrels, Adélie Land, East Antarctica. Dots show raw location data. Kernel density based utilization distributions at 95% (dotted lines), 50% (solid lines) and 25% (filled areas). Bathymetry shown in grey and land in white. Ile des Pétrels is shown as a black triangle.

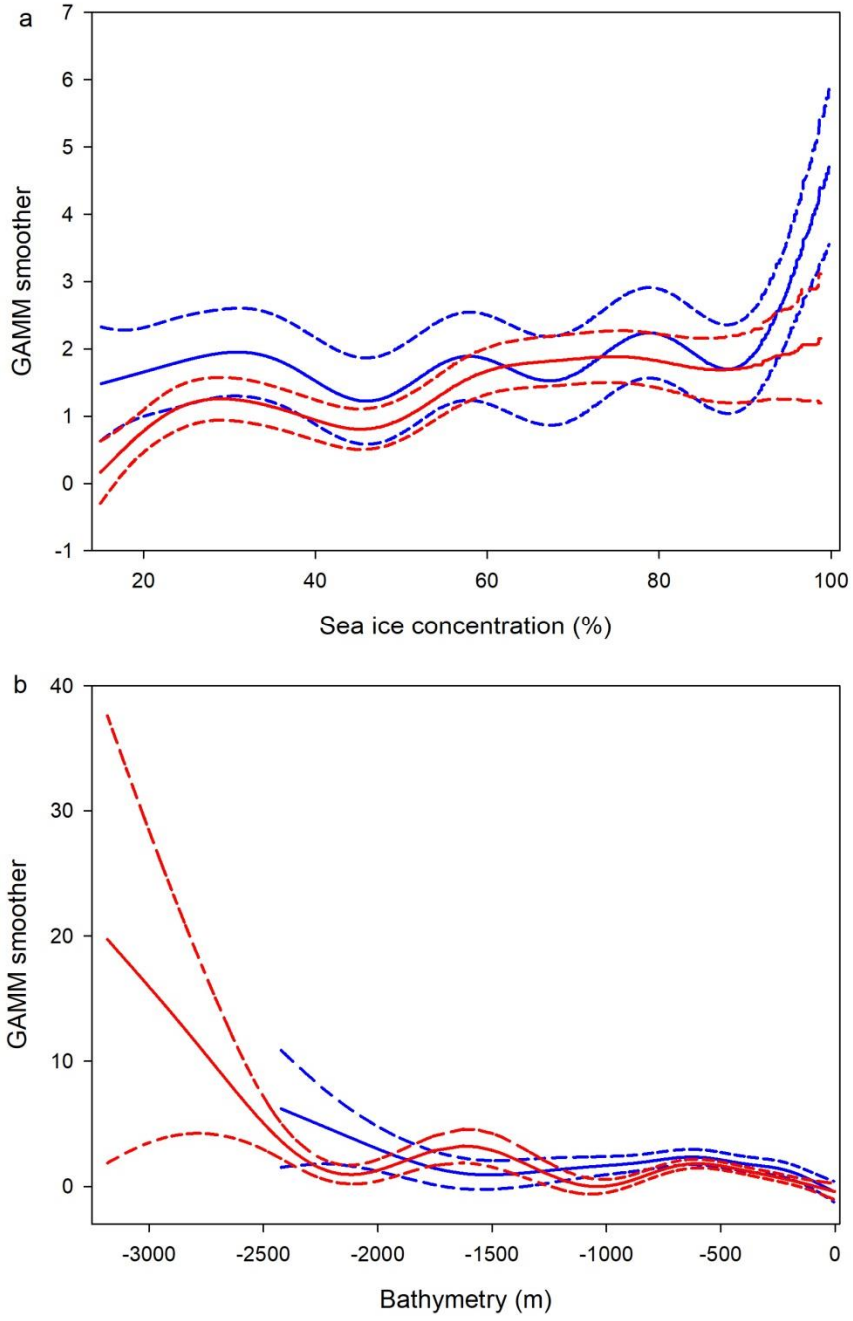


Figure 2. Foraging probability habitat selection functions for (a) sea ice concentration and (b) bathymetry). Plots show the predicted curve from the model (solid line) and 95% confidence intervals (dashed lines) for male (blue) and female (red) snow petrels sampled at Ile des Pétrels, Adélie Land, East Antarctica. GAMM: generalized additive mixed model.

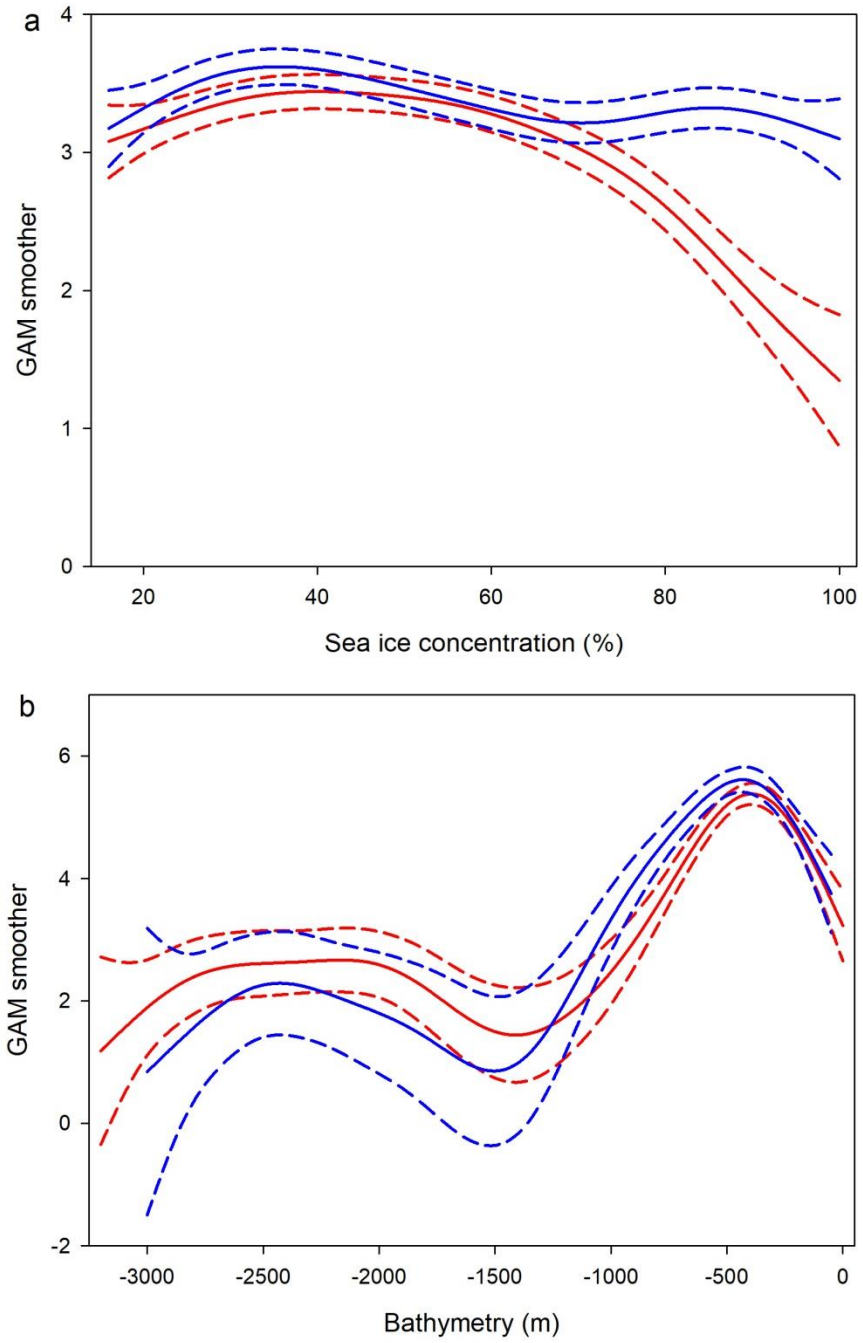
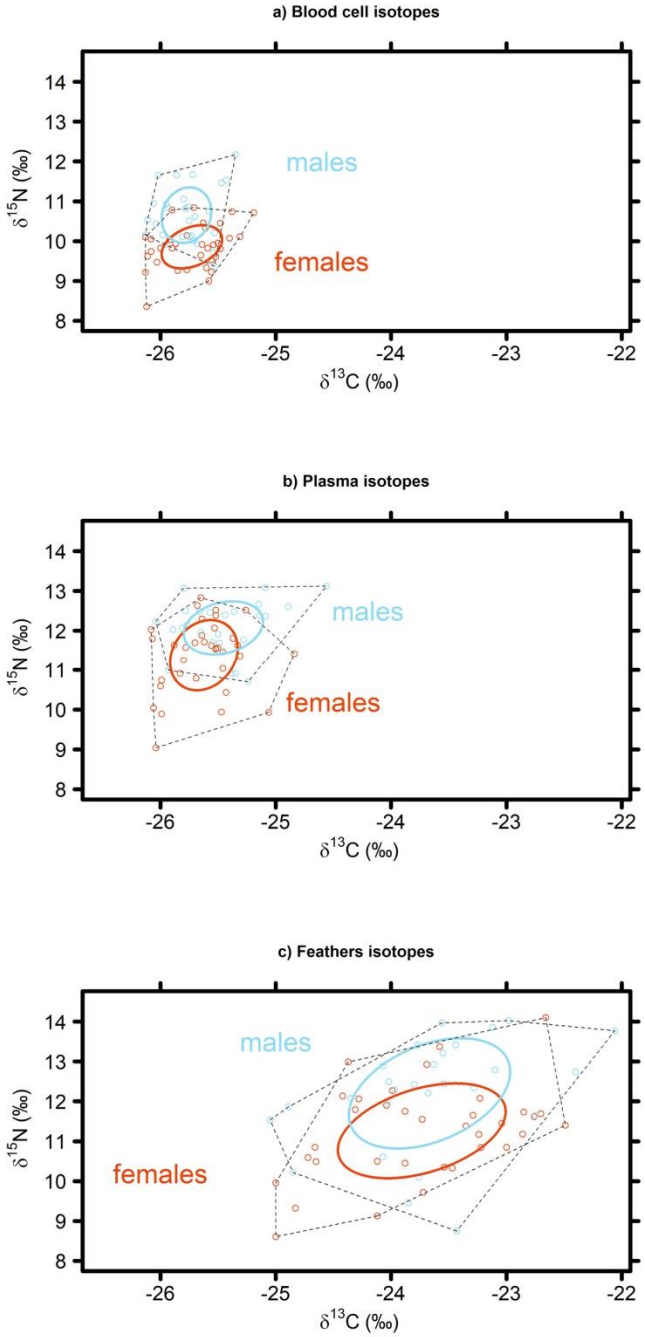


Figure 3. Foraging intensity habitat selection functions for (a) sea ice concentration and (b) bathymetry). Plots show the predicted curve from the model (solid line) and 95% confidence intervals (dashed lines) for male (blue) and female (red) snow petrels sampled at Ile des Pétrels, Adélie Land, East Antarctica. GAM: generalized additive model.



1186

1187 Figure 4. Isotopic niche area based on stable isotope values ($\delta^{15}N$ and $\delta^{13}C$) in blood cells

1188 (top), plasma (middle) and body feathers (bottom) of male (blue) and female (red) snow

1189 petrels breeding at Ile des Pétrels, Pointe Géologie, Antarctica during the incubation period.

1190 The areas of the standard ellipses are represented by the solid lines, and the layman metric of

1191 convex hull area by black dotted lines.

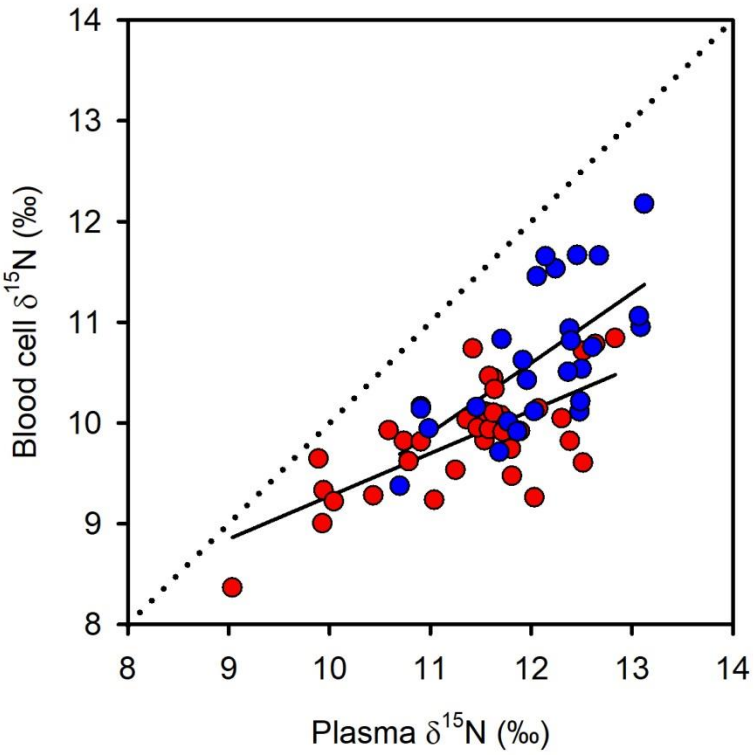


Figure 5. Relationships between blood cells and plasma $\delta^{15}N$ values for male (n = 27, blue) and female (n = 35, red) snow petrels sampled at Ile des Pétrels, Adélie Land, East Antarctica. Males: $F_{1,22}=15.203$, $P<0.001$, $R^2 = 0.409$; females: $F_{1,20}=24.300$, $P<0.001$, $R^2 = 0.549$.

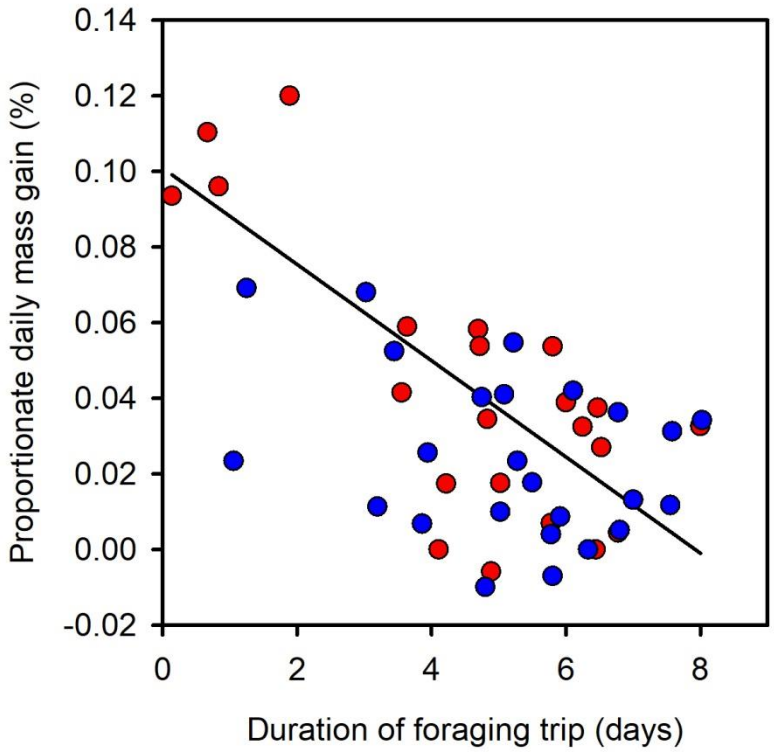


Figure 6. Foraging efficiency (proportionate daily mass gain while foraging) as a function of the total duration of the foraging trip for male (blue) and female (red and solid line) snow petrels sampled at Ile des Pétrels, Adélie Land, East Antarctica. For females: $F_{1,20}$=25.349, P<0.001, R^2 = 0.559.

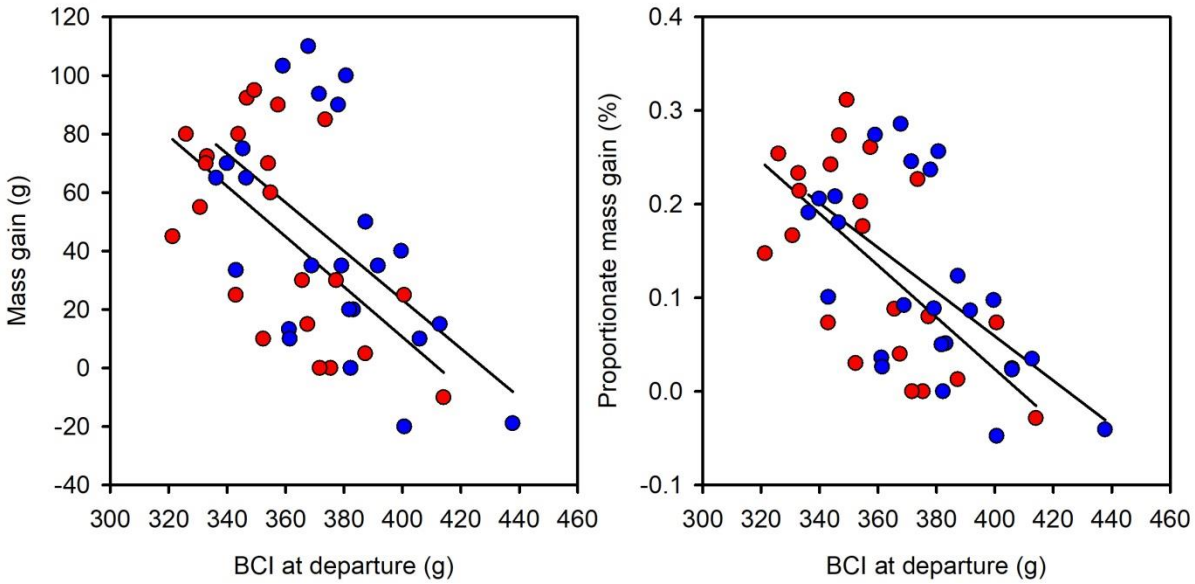


Figure 7. Mass gain and proportionate mass gain as a function of body condition before a foraging trip for male (blue) and female (red) snow petrels sampled at Ile des Pétrels, Adélie Land, East Antarctica. Male mass gain: $F_{1,23}$=10.010, P=0.004, r^2=0.303; female mass gain: $F_{1,20}$=11.071, P=0.003, r^2=0.356; male proportionate mass gain: $F_{1,23}$=12.361, P=0.002, r^2=0.350; female proportionate mass gain: $F_{1,20}$=13.258, P=0.002, r^2=0.399.

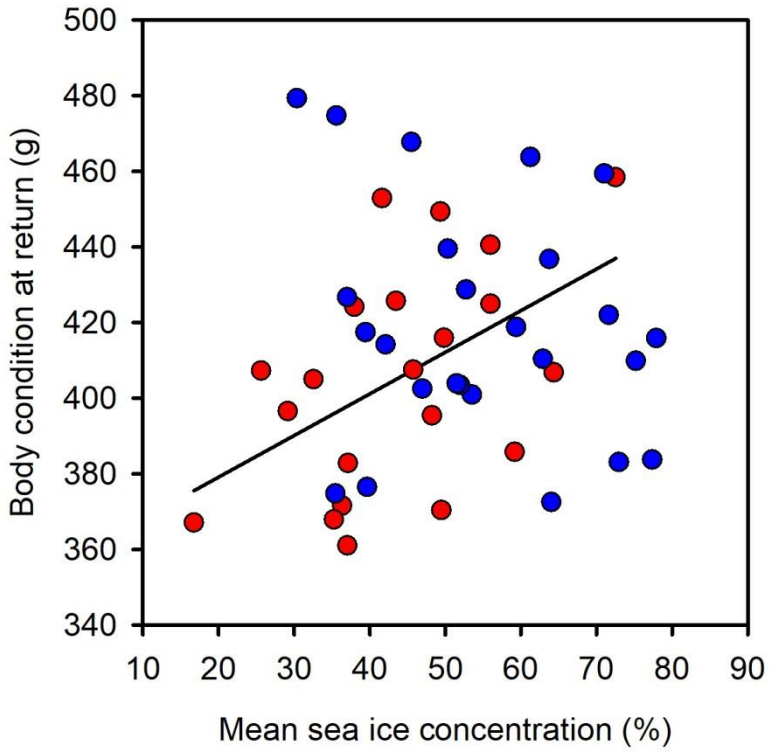


Figure 8. Body condition at return from a foraging trip as a function of the mean sea ice concentration of the foraging trip locations for male (blue) and female (red and solid line) snow petrels sampled at Ile des Pétrels, Adélie Land, East Antarctica. For females: $F_{1,19}$=6.106, P=0.023, R^2 = 0.243.

1225 Appendix I. Testing for differences in $\delta^{15}N$ (ă) and $\delta^{13}C$ (ă) values between tissues for
1226 male and female snow petrels sampled Ile des Pétrels, Adélie Land, East Antarctica. t
1227 indicates Studentôs t-tests with df, Z indicates Wilcoxon rank test. ** indicates P < 0.01,- ***
1228 indicates P < 0.001 after applying the Benjamini-Hochberg procedure with a false discovery
1229 rate of 0.10. Values above diagonal are for $\delta^{15}N$ (ă), values below diagonal are for $\delta^{13}C$(ă).
1230 $\delta^{15}N$ (ă) and $\delta^{13}C$ (ă) values in feathers were corrected following Cherel et al. (2014a)
1231 before comparison with blood cells. $\delta^{13}C$ (ă) values for plasma were normalized following
1232 Post et al. (2007) and Cherel et al. (2014b).

	Plasma	Blood	Feather
Male			
Plasma	-	t_{47}=7.206***	t_{47}=0.008
Blood cells	Z=2.743**	-	t_{47}=3.060**
Feather	t_{47}=17.166***	t_{47}=29.033***	-
Female			
Plasma	-	t_{42}=0.039	t_{42}=0.435
Blood cells	t_{42}=0.039	-	t_{42}=2.967**
Feather	t_{42}=23.219***	Z=4.107***	-

1233