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An interannual study of foraging behaviour in sympatrically breeding macaroni *Eudyptes chrysolophus* and chinstrap penguins *Pygoscelis antarcticus* at Bouvetøya

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Audun Narvestad
BIO-3950 Master's thesis in Biology
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Cover photo by Audun Narvestad

Chinstrap penguin *Pygoscelis antarcticus* chicks

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Abstract

Species are likely to segregate their ecological niches to minimize competition for resources, but for centrally foraging predators that breed on sub-Antarctic islands in the Southern Ocean the possibility of niche segregation may be minimal. This study is the first to examine the spatial and trophic aspects of the foraging niche of sympatrically breeding macaroni and chinstrap penguins at the poorly-studied sub-Antarctic island Bouvetøya over multiple years. To measure at-sea movements and dive behavior, 90 breeding macaroni *Eudyptes chrysolophus* and 49 breeding chinstrap penguins *Pygoscelis antarcticus* were deployed with satellite transmitters and time-depth recorders over two austral summer breeding seasons, 2015 and 2018. In addition, tracked birds were sampled for blood for biogeochemical dietary analysis. Chinstrap penguins displayed large interannual variation in foraging behavior between the two years, and dove deeper, utilized larger foraging areas during late breeding stages and showed enriched values of $\delta^{15}N$ in the first- compared to the second- year. Conversely, macaroni penguins dove to similar depths and displayed similar values of $\delta^{15}N$ in both years. Our results suggest that potentially low krill abundances in the waters around Bouvetøya in 2015 forced the chinstrap penguins to search for alternative prey, like myctophid fishes, which resulted in increased overlap in the two species' foraging niche. Consequently, the chinstrap penguins may have faced increased interspecific competition for prey or catabolism from food shortage. Irrespective, our findings may partly explain the decreasing number of breeding chinstrap penguins at the world's most remote island, Bouvetøya.

KEY WORDS: ecological niche, niche segregation, competition, central place foraging, Southern Ocean, low krill events, stable isotope analysis, radio telemetry

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Introduction

The set of all abiotic and biotic variables essential for a species survival makes up a multidimensional hypervolume, referred to as the species ecological niche (Hutchinson, 1957; Schoener, 1974; Alley, 1982). Two species, or more, with substantial overlap in their realized niche cannot coexist in a system with limited and mutually exploited resources (Hutchinson, 1957; Schoener, 1974). If they are to co-exist, they must come to occupy different ecological niches through segregation (Hardin, 1960; Mori & Boyd, 2004). The competitive exclusion principle further predicts that species with similar ecological niche, and without the ability to diverge, will suffer severe competition that finally results in the exclusion of inferior competitors (Gause *et al*., 1934; Hutchinson, 1957; Hardin, 1960; Schoener, 1974). Niche segregation may occur along all axes of the multidimensional hypervolume (i.e. temporal, spatial or trophic) (Schoener, 1974; Adams & Brown, 1989; Hull 1999; Hindell *et al*., 1995 Mori & Boyd, 2004, Whitehead *et al*., 2017), and co-existing species are expected to differ in at least one dimension to avoid being excluded from the system (Hutchinson, 1957). However, some species must return to a central place in between foraging trips in order to provision dependent offspring (Charnov, 1976; Waluda *et al*., 2010; Clewlow *et al*., 2019). Consequently, the offspring's energy demands regulates the parent's abilities for dispersal during foraging and therefore potentially limit the capacity for niche segregation (Barlow *et al*., 2002) (Meyer *et al*., 1997; Ichii *et al*., 2007; Thiebot *et al*., 2011).

In the Southern Ocean, all centrally foraging species are air-breathing marine predators (such as otariid seals and seabirds) that utilizes remote sub-Antarctic islands as terrestrial breeding grounds (Barlow *et al*., 2002; Lowther *et al*., 2014; Petry *et al*., 2018). Upwelling of organic matter and influx of minerals from land causes high productivity in the waters close to the islands (known as "The Island Mass effect"), and makes them relatively resource-rich oases surrounded by a marine desert (Doty & Oguri, 1956; Boden, 1988; Blain *et al*., 2001). Thus, sub-Antarctic islands support large multispecies guilds due to the predictable nature of foraging areas for marine predators (Trivelpiece *et al*., 1987; Adams & Brown, 1989; Reid & Croxall, 2001; Petry *et al*., 2018). Following, high predation pressure potentially gives rise to localized depletion of these resources (Ashmole's halo) and increases competition for food between centrally foraging species as the breeding season progresses (Dann & Norman, 2006; Elliot *et al*., 2009). Sub-Antarctic islands span the Antarctic Polar Front (APF), a key hydrographic feature separating cold Antarctic water from warm sub-Antarctic and temperate

water, with only South Georgia, the South Sandwich Islands and Bouvetøya residing to its south. Antarctic krill, *Euphausia superba* (hereafter "krill"), constitutes the main food resource for most marine predators below the APF (e.g. whales, seals, and seabirds), which operates as a natural barrier for this cold-adapted food web key species (Croxall *et al*., 1988; Davis & Darby, 1990; Atkinson *et al*., 2004; 2006; 2008; Reid & Croxall, 2001). Bathymetric features such as ocean slopes and shelf areas aggregate high densities of krill (Atkinson *et al*., 2004; 2008; Cresswell *et al*., 2007; Krafft *et al*., 2010). Still, the local abundances of krill may vary enormously on a temporal scale and low krill events can lead to reduced reproductive performance in krill-dependent predators (Croxall *et al*., 1999; Reid & Croxall, 2001; Barbosa *et al*., 2012; Horswill *et al*., 2017). The Southern Ocean has experienced rapid warming during the second half of the twentieth century (Gille, 2002; Vaughan *et al*., 2003). Thus, krill is facing rising ocean temperatures in addition to increasing predation pressure from Antarctic fur seal (*Arctocephalus gazelle*)- and whale- populations re-establishing after uncontrolled harvesting during the 18th and 19th centuries, commercial fishing and ocean acidification, all of which may produce significant reductions in the biomass of krill (Reid & Croxall 2001; Atkinson *et al*., 2004; 2008; Flores *et al*., 2012; Klein *et al*., 2018). As a result, low krill events may become more regularly common and cause cascading effects throughout the marine ecosystems (Reid & Croxall, 2001; Thorpe *et al*., 2007; Trivelpiece *et al*., 2011).

Penguins are the most numerically-abundant group of predators in the Southern Ocean (Davis & Darby, 1990). During breeding, penguins are central place foragers that attends their nest to feed the land-based dependent chicks (Barlow & Croxall, 2002a; Ichii *et al*., 2007; Thiebot *et al*., 2011; Clewlow *et al*., 2019). Unlike sympatrically-breeding Antarctic fur seals, penguins cannot store food for their offspring as energy rich milk, nor are the penguins able to cover the same geographical distances as flying seabirds when constrained by nest duties (Barlow *et al*., 2002; Ichii *et al*., 2007). Consequently, penguins' foraging range is spatiotemporally restricted, likely making them vulnerable to competition (Waluda *et al*., 2010; Polito *et al*., 2015; Clewlow *et al*., 2019). The macaroni *Eudyptes chrysolophus* and chinstrap penguin *Pygoscelis antarcticus* are present in great numbers in the Southern Ocean (Birdlife International 2019), and both species are large consumers of krill (Croxall *et al*., 1988; Adams & Brown *et al*., 1989). However, unlike the chinstrap penguin, the macaroni penguin is a generalist predator, known to readily switch to other preys when krill are in low abundances (Lynnes *et al*., 2002; Miller *et al*., 2010; Rombola *et al*., 2010; Whitehead *et al*., 2017). The global populations of macaroni and chinstrap penguins are

estimated at approximately 6.3 million and 8 million, respectively (Birdlife International, 2019), though both populations are decreasing (Trivelpiece *et al*., 2011; Lynch *et al*., 2012; Birdlife International, 2019). Unlike macaroni penguins which breeds on most sub-Antarctic islands, chinstrap penguins breeds primarily on islands around the Antarctic Peninsula and on sub-Antarctic islands south of the APF (Birdlife International, 2019). At Bouvetøya, the geographical range of macaroni and chinstrap penguins meet, with the two species breeding sympatrically during the austral summer (Isaksen *et al*., 2000; Biuw *et al*., 2010). In addition, the island is home to the world's second largest breeding colony of Antarctic fur seals, currently counting 66,000 individuals (Hofmeyr *et al*., 2005).

At Bouvetøya, the penguin breeding season spans from December to early March. Egg laying and hatching are relatively synchronous within both species (Haftorn, 1989; Trivelpiece *et al*., 1987). Some days after egg laying, female macaroni penguins leaves to forage at sea while the males incubate the eggs alone until hatching. After hatching, the male macaroni penguins will continue to brood and guard the chicks while the females undertakes short foraging trips for chick provisioning (Haftorn, 1989; Barlow & Croxall, 2002b; Green *et al*., 2002; Blanchet *et al*., 2013). Unlike macaroni penguins, both male and female chinstrap penguins will undertake alternate, long (several days) foraging trips during incubation and alternate, short foraging trips during the brood and guard phase (Haftorn, 1989; Jansen *et al*., 2002; Blanchet *et al*., 2013). Twenty to thirty days after egg hatching, chicks of both species are old enough to thermoregulate on their own and they stay in groups with chicks from other nests, known as crèches (Haftorn, 1989; Jansen *et al*., 2002). During the crèche phase, both male and female macaroni and chinstrap penguins undertake continuously short foraging trips, only attending the colony to feed their offspring. As a result, the amount of food brought back from the sea increases in accordance to the increasing energy demands of the now almost fully-grown chicks (Barlow & Croxall, 2002b; Green *et al*., 2002; Jansen *et al*., 2002). Sixty to seventy days after egg hatching, the chicks fledge and leaves for sea (Barlow & Croxall, 2002b).

Penguins breed on Bouvetøya in a mixed colony on a rocky beach called Nyrøysa, located on the west coast of the island. At this site, macaroni and chinstrap penguins are currently showing differing population trajectories. During the last three decades, the number of macaroni penguins has remained stable at approximately 1100 breeding pairs (Isaksen *et al*., 2000; Biuw *et al*., 2010). Over the same period, the number of breeding chinstrap penguins has decreased from about 200 pairs to 40 pairs (Isaksen *et al*., 2000; Biuw *et al*., 2010),

though the cause of decline remains uncertain (Blanchet *et al*., 2013; Niemandt *et al*., 2016). However, as chinstrap penguins are obligate krill feeders, the decrease may be a result of reduced reproductive performances caused by either competition with other krill foragers or, in combination with other factors, low krill abundances in the waters around Bouvetøya during breeding. Blanchet *et al*. (2013) investigated the potential for prey competition between the three main krill predators at the island (i.e. macaroni penguins, chinstrap penguins and Antarctic fur seals) over a single summer season. The authors concluded that spatiotemporal segregation in foraging niches was sufficient to avoid interspecific competition and that none of the three species faced food shortage during breeding (Blanchet *et al*., 2013). Yet, as the study only looked at one season, it does not out rule the possibility of interannual variation in prey availability, nor changes in the species' foraging niche over time (see Waluda *et al*., 2010; Horswill *et al*., 2017 for examples). Moreover, krill may become sporadically less abundant and the nearshore marine environment around Bouvetøya may face future low krill events. In such a scenario, generalist predators, capable of rapidly switching to other available prey species, are likely to gain a competitive advantage over krill specialists (Forcada & Trathan, 2009; Trivelpiece *et al*., 2011; Blanchet *et al*., 2013; Niemandt *et al*., 2016). Thus, the mixed breeding colony of macaroni and chinstrap penguins may serve as an appropriate system to study the temporal dynamics of niche overlap between centrally foraging generalist and specialist predators in a changing Southern Ocean.

For long, our knowledge regarding at-sea behavior of marine top predators were restricted to occasionally observations along the shoreline and from marine vessels in the open sea. Now, new technology in biotelemetry has enhanced our abilities to follow these species also outside our visual range of direct observations (Cooke *et al*., 2004; Cooke, 2008; Rutz & Hays, 2009; Lowther *et al*., 2014; Wilmers *et al*., 2015). In the study of penguins, which spends most of their time submerged, biotelemetry has improved our understanding of these marine predators' at sea-habitat exploitation, long-range migrations, and dive behavior (Trivelpiece *et al*., 1986; Trathan *et al*., 1998; Biuw *et al*., 2010; Forin-Wiart *et al*., 2019). Further, when combined with proxies of dietary measurements such as from the stable isotope analysis (SIA) of body tissues, it is possible to create a detail description of a penguin's foraging niche, and to determine niche overlap between co-breeding marine species (Cherel *et al*., 2007; Ratcliffe *et al*., 2018). The method of SIA is centered on heavier isotopes being discriminated over lighter forms in biological reaction processes at predictable rates, leading to enriched levels of heavier isotopes when moving up through the food chains

(Cherel & Hobson, 2007; Inger & Bearhop, 2008). Furthermore, as different animal tissues have different turnover rates of stable isotopes (e.g. 4 weeks for red blood cells and 3 to 4 day for plasma), one may use SIA to measure a specie's diet over several temporal scales (Bearhop *et al*., 2004; Cherel & Hobson, 2007; Inger & Bearhop, 2008). The two most commonly used isotopic ratios in animal ecology are $\delta^{15}N$ ($^{15}N/^{14}C$) and $\delta^{13}C$ ($^{13}C/^{12}C$) (Cherel & Hobson, 2007; Inger & Bearhop, 2008). $\delta^{15}N$ increases at a rate of ~2–5‰ for each trophic level in marine ecosystems, and SIA of nitrogen predicts the trophic position of predators and their prey (Hobson & Welch, 1992; Post, 2002; Cherel *et al*., 2005a). In contrast, $\delta^{13}C$ increases at a lower rate, approximately 0-1‰ for each trophic level, and reflects the carbon source at the base of the food chain (Cherel *et al*., 2007; Inger & Bearhop, 2008). Thus, SIA of carbon predicts spatiotemporal variation in species' foraging areas (Tierney *et al*., 2008 Dimitrijević *et al*. 2018).

In this study, we combined the two different, but mutually supportive methods of biotelemetry and SIA to examine the foraging niche of macaroni and chinstrap penguins at Bouvetøya over two nonconsecutive breeding seasons. We used SIA of carbon and nitrogen in blood and plasma for dietary studies and archival global positioning system data-loggers (GPS) and time-depth recorders (TDR) to determine the penguins' three-dimensional distribution during foraging. Our goal was to determine whether the niche segregation between macaroni and chinstrap penguins described by Blanchet *et al*. (2013) remains constant over time. We predicted that overlap in the two species' foraging niche would vary with potentially dynamic changes in prey abundances, with niche segregation still being present either spatially, temporally or trophically as a limiting factor to interspecific competition.

Material and methods

This study was carried out in Nyrøysa, Bouvetøya (54°25'S, 3°20'E; Fig.1) between mid-December to early February in 2014/2015 and in 2017/2018 (hereafter "2015" and "2018") during the austral summer breeding season. All fieldwork was a part of the Norwegian Antarctic Research Expedition (NARE) and animal experimentation was conducted under Norwegian Food Safety Authority Permit numbers 2014/230385 and 17/105553.

Figure 1. Map of Bouvetøya (54°25'S, 3°20'E), its position in the Southern Ocean (top right), and the location of Nyrøysa were all fieldwork took place (red square).

A total of 139 adult breeding penguins (90 female macaroni penguins and 49 chinstrap penguins of unknown sex) were instrumented across both seasons (Table. 1). A GPS-logger (nano-Fix®, Pathtrack Ltd., UK, 64x20x17mm, 22g) and a TDR (G5 DST, CEFAS Technology Limited, 31x8mm, 2,7g) were attached to the dorsal feathers with the use of waterproof tape (Tesa© 4651) and rapid-setting glue (Loctite® 323) (Wilson & Wilson 1989; Wilson *et al*., 1997). GPS and TDR tags were programmed to record a location every 4min and depth every 2s, respectively. Animal handling took less than 10 minutes, after which all individuals returned immediately back to their nests. The two instruments were deployed for

5-10 days on each individual equating to 1-13 foraging trips (covering late incubation to early crèche), after which the animal was recaptured and the instrument package removed.

On retrieval, a blood sample was taken from the brachial vein using a 0.6 x 25 mm needle (Fine-Ject®; Henke Sass Wolf, Tuttlingen, Germany) and a 2 ml (3 ml) syringe (BD Emerald™). In addition, blood samples from five breeding macaroni penguins and three breeding chinstrap penguins from a concurrently running scientific study in 2015 were included in our study (Table. 1). In 2018 samples were centrifuged for 5 minutes at 3000 rpm (Hettich® EBA 20 Centrifuge) and blood and plasma separated using a 100-1000µl pipette (BioPette A™, Labnet International Inc., USA) and a 1-200 µl pipette tip (VWR™). However, due to equipment failure in 2015 centrifuging was not possible. Whole blood from 2015 and red blood cells (RBC) from 2018 were stored with 98% ethanol in heparinized blood containers (BD Vacutainer®; Becton Dickinson, Plymouth, UK), while plasma from 2018 were stored with 98% ethanol in 1.5 ml sterile micro tubes (VWR™). All samples were kept at -18°C until further analysis.

Isotope analysis of $\delta^{15}N$ ($^{15}N/^{14}C$) and $\delta^{13}C$ ($^{13}C/^{12}C$) was carried out for samples of whole blood in 2015 and for separated plasma and RBC in 2018 (Table. 1). Isotope ratios in whole blood closely resemble ratios in RBC (Cherel *et al*., 2005a) and henceforth we refer to both RBC and whole blood as "blood". Lipid extraction was not conducted on blood as it is generally lipid-poor in birds, having little impact on measurements of $\delta^{13}C$ (Bearhop *et al*., 2000; Cherel *et al*., 2005b). Samples of blood and plasma were dried at 50°C, pulverized, and weighed in tin capsules. Further, dried samples were combusted in an Elemental Analyzer (Thermo Scientific Flash HT Plus) at 1020 °C and analyzed on an Isotope Ratio Mass Spectrometer (Thermo Scientific MAT253). $\delta^{15}N$ and $\delta^{13}C$ was determined by normalization to international scales for atmospheric nitrogen and Vienna PeeDee Belemnite carbonate. Ratios of stable isotopes are calculated from the following equation:

$$\delta X = [(R_{sample} / R_{standard}) - 1] \times 1000$$

and expressed as per mil units (‰). X represent ^{13}C or ^{15}N, while R correspond to the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$ (Polito *et al*., 2015; Ratcliffe *et al*., 2018). Instrument uncertainty for $\delta^{15}N$ and $\delta^{13}C$ is standard deviation ≤0.15 per mil (ThermoScientific) for perfectly homogenous materials. All analyses of stable isotopes were conducted at The Stable Isotope Laboratory at CAGE – Centre for Arctic Gas Hydrate, Environment and Climate, located at UiT – The Arctic University of Norway, Tromsø.

Table 1. Adult breeding macaroni (MAC) and chinstrap (CHIN) penguins deployed with GPS and TDR for which data amenable for further analysis were collected over two austral summer breeding seasons (2015 and 2018). Numbers in parentheses represent the total number of samples collected including those for which either insufficient data or blood volume were available, or the electronic instruments failed during deployment.

Species (Year)	GPS	TDR	Blood	Plasma
MAC (2015)	24 (50)	21 (50)	55 (55)	-
MAC (2018)	27 (40)	19 (40)	33 (40)	31 (40)
CHIN (2015)	16 (19)	14 (19)	22 (22)	-
CHIN (2018)	23 (30)	19 (30)	25 (30)	30 (30)

All data from both years were processed and analyzed using R statistical software version 3.5.2 (R Development Core Team 2018). All geospatial and biogeochemical data were defined as representing either early (incubation –early brood) or late (late brood – crèche) breeding by the date of instrumentation and the observed breeding state of the adults immediately prior to instrumentation. Both GPS and TDR data were downloaded using proprietary software (Sirtrack & PathTrack Archival GPS v.1.20, and Pathtrack Ltd TDR Host v.7.6.2, respectively). Dive events were defined using a zero-offset correction of 5 meters (Clewlow *et al*., 2019) and dive statistics extracted using the package *diveMOVE* (Luque & Fried, 2011). Raw GPS data were treated with a speed filter (McConnell *et al*., 1992) set to $20ms^{-1}$ to remove locations due to improbable speeds and then manually removed locations closer than 200m to land (representing the accuracy of the GPS), resulting in discrete at-sea foraging trips for each individual. A continuous-time model of each foraging trip was created using the package *crawl* (Johnson *et al*., 2008), which was then used to estimate a location for each dive. Further, spatially-resolved dive data were clustered into foraging dives or transition dives using the package *mclust* (Scrucca *et al*., 2016), with the expectation that foraging dives are both deeper and of longer durations (Williams *et al*., 1992; Hart *et al*., 2010). Foraging dives were partitioned into those conducted during daytime or nighttime by using the package *suncalc* (Agafonkin & Thieurmel, 2017). Dives were also partitioned by species, year, and breeding stage. Differences in mean maximum dive depth (m) and mean dive duration (s) were then subsequently tested for between groups with non-parametric Wilcoxon signed-rank tests. For spatially-resolved foraging dives 95% kernel Utilization Distribution (UD) were created for species separated by year and breeding stage using the package *adehabitatHR* (Calenge, 2015). In addition, sizes and overlap of foraging areas between species, breeding stage and year were calculated. Foraging areas were visualized using a collection of Antarctic geographical datasets from *Quantarctica* in QGIS

version 3.6.3 (QGIS Development Team, 2019) while foraging dive behavior and stable isotope data were visualized using *ggplot* from the package *ggplot2*. Stable isotope data were tested for normality using *qqplots.* Differences in $\delta^{15}N$ and $\delta^{13}C$ were determined between species and year for blood, and between species and breeding stage for plasma, using Student's t-Tests. In addition, isotopic data were visualized by drawing 100 elliptical projections with a 95% confidence interval (CI) under a Bayesian framework using *niche.plot* from the package *niche.ROVER* (Swanson *et al*., 2015) (Appendix Fig. B & C). All values are presented as mean (± Standard Deviation), and differences are considered significant at $P < 0.05$ unless otherwise stated.

Results

In 2015, individual breeding macaroni and chinstrap penguins were instrumented for a mean 7.9 (±2.0) and 6.2 (±4.6) days, respectively, while in 2018 it was 8.9 (±4.8) and 6.0 (±3.5) days. The resulting location data resulted in a mean 3.1 (±1.5) and 2.7(±2.0) foraging trips per individual macaroni and chinstrap penguin in 2015, and 3.3 (±1.7) and 2.6 (±2.1) for the two species respectively in 2018 (Appendix Fig. A). During early breeding season, mean trip durations for the macaroni and chinstrap penguins were 3.1 (±3.7) and 1.4 (±1.4) days during 2015, and 5.4 (±5.5) and 1.1 (±0.8) days during 2015, respectively. Chinstrap penguins decreased their mean foraging trip durations significantly as they progressed through their breeding season in both years (2015: 0.7 (±0.4) days. 2018: 0.5 (±0.4) days), as did macaroni penguins in 2018 (1.8 (±1.3) days) (Wilcoxon Rank Sum, $P<.05$ in all cases) but not in 2015 (1.6 (±2.0) days). Across both years, chinstrap penguins consistently conducted significantly shorter foraging trips than macaroni penguins during late breeding (Wilcoxon Rank Sum, $P<.05$ in all cases). The deepest dive detected for the macaroni penguins were 116m in 2015 and 123m in 2018, while the longest dive lasted for 186s and 170s in the first- and second year, respectively. Chinstrap penguins exhibited generally similar maximum dive depths and durations with the deepest and longest dives being 120m and 160s in 2015, and 85m and 160s in 2018. Transition dives were both significantly shallower and of shorter durations than foraging dives (Wilcoxon Rank Sum, $P <.001$). Between 40% and 53% of the dives conducted by macaroni penguins ($n_{(2015)}$=10,478 and $n_{(2018)}$=11,187), and between 38% and 43% of those conducted by chinstrap penguins ($n_{(2015)}$=4341 and $n_{(2018)}$=4961), were classified as transiting dives, with the remainder as foraging dives ($n_{(\text{macaroni 2015})}$=15,717, $n_{(\text{macaroni 2018})}$=9,921, $n_{(\text{chinstrap 2015})}$=7083, $n_{(\text{chinstrap 2018})}$=6577).

As the breeding season progressed in both years, macaroni and chinstrap penguins conducted significantly deeper and longer daytime foraging dives, with the exception of chinstrap penguins in 2018 (Wilcoxon Rank Sum, $P<.001$; Fig. 2A & B; Table. 2). Between years there were intraspecific differences in dive behavior, with chinstrap penguins in 2015 diving significantly deeper (mean difference 12.1m and 36.4m, respectively) and longer (31.0sec and 65.7sec, respectively) than during the same stages of breeding in 2018 (Wilcoxon Rank Sum, $P<.001$; Fig. 2A & B; Appendix Table A). For macaroni penguins the interannual differences in daytime dive behavior between early and late breeding season were less clear, with individuals diving significantly longer (4.3s and 7.0s, respectively) in 2015,

but deeper (1.9m and 1.7m, respectively) in 2018 (Wilcoxon Sum Rank, P<.005; Fig. 2A & B; Appendix Table A). Interestingly, chinstrap penguins in 2015 dove significantly deeper and longer than macaroni penguins during nighttime, and during daytime in the late breeding season, in either year (Wilcoxon Rank Sum, P <.001 in all other cases; Fig. 2A & B; Table; Appendix Table A). Conversely, macaroni penguins in both years conducted consistently deeper and longer daytime dives compared to chinstrap penguins in 2018 (Wilcoxon Rank Sum W <.001 in all cases; Fig 2A & B; Appendix Table A), though no clear pattern was detected during nighttime.

Table 2. Intra-annual and diurnal comparison of mean maximum A) dive depths and B) durations within groups of macaroni (MAC) and chinstrap (CHIN) penguins instrumented during early (incubation-early brood) and late (late brood-creche) breeding at Bouvetøya during 2015 and 2018. Results are presented as N, mean (± SD). Matched superscript symbols denote nonsignificance of paired tests. All other Wilcoxon W test statistics were significant at $\alpha = 0.05$.

A)

	Max depth (m)				Wilcoxon W			
	Day		Night		Early	Late	Day	Night
Species (Year)	Early	Late	Early	Late	Day~Night	Day~Night	Early~Late	Early~Late
MAC (2015)	2276, 36.0 (±17.3)	10295, 44.3 (±18.6)	800, 16.2 (±12.2)	2346, 12.8 (±11.2)	1559500	22751000	8523400	1125500
MAC (2018)	5507, 37.9 (±16.5)	4012, 46.3 (±22.4)	46, 6.97 (±2.08)	356, 10.7 (±7.69)	252620	1369700	8601100	5334,5
CHIN (2015)	2991, 36.8 (±17.3)	3441, 63.8 (±21.3)	44, 21.9 (±9.73)	637, 29.7 (±22.9)	98880	1857800	1724800	12875[¥]
CHIN (2018)	3422, 24.7 (±11.5)	2938, 27.4 (±14.9)	175, 15.2 (±7.62)	42, 9.99 (±4.26)	447519	113530	4696900	5018,5

B)

	Dive duration (s)				Wilcoxon W			
	Day		Night		Early	Late	Day	Night
Species (Year)	Early	Late	Early	Late	Day~Night	Day~Night	Early~Late	Early~Late
MAC (2015)	2276, 100.0 (±21.5)	10295, 109 (±21.9)	800, 61.5 (±28.5)	2346, 52.8 (±27.4)	1560400	22699000	9039100	1105400
MAC (2018)	5507, 95.7 (±23.8)	4012, 102 (±24.7)	46, 24.5 (±18.0)	356, 43.2 (±21.5)	250160	1368700	9132400	4097
CHIN (2015)	2991, 101 (±25.2)	3441, 132 (±26.1)	44, 81.1 (±28.2)	637, 86.7 (±37.2)	90324	1805500	1972300	13464[¥]
CHIN (2018)	3422, 70.0 (±22.2)	2938, 66.3 (±21.7)	175, 62.6 (±35.0)	42, 35.0 (±17.4)	321150[¥]	107400	5545500	5377

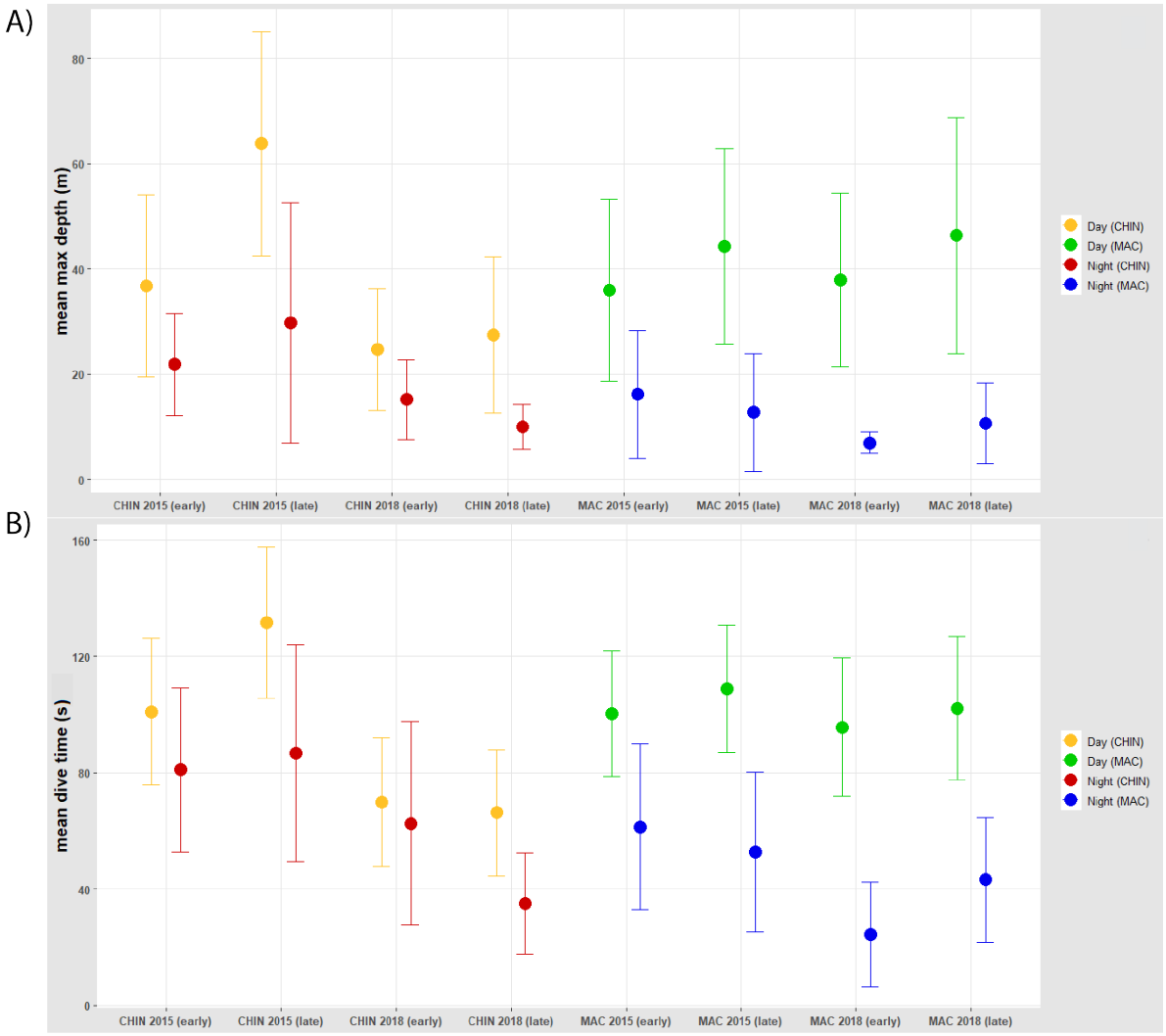

Figure 2. Mean A) maximum dive depth (m) and B) dive duration (s), with associated standard deviation bars, for macaroni (MAC) and chinstrap (CHIN) penguins on Bouvetøya during early – (incubation early brood) and late – (late brood – crèche) breeding season in 2015 and 2018.

Both species differed markedly in the area of foraging habitat utilized, with macaroni penguins typically exploiting an area more than six times larger than chinstrap penguins (Fig. 3; Appendix Table B). Across both years, the 95% UD of both macaroni and chinstrap penguins decreased as breeding progressed, though the difference between early- and late-breeding season was less pronounced in 2015 (early breeding: macaroni$_{(2015/2018)}$, 140,653.5km^2/382,128.9km^2; chinstrap$_{(2015/2018)}$, 22,640km^2/43,985km^2; late breeding: macaroni $_{(2015/2018)}$, 54,252km^2/20,840.4km^2; chinstrap$_{(2015/2018)}$, 4,362.9km^2/1,584.5km^2) (Fig. 3; Appendix Table B). Importantly, during late breeding chinstrap penguins utilized ~175% larger area in 2015 compared to in 2018 (Fig. 3; Appendix Table B). There was also considerable overlap in the 95% UD of both species, with macaroni penguins occupying between 88-100% of the habitat exploited by chinstrap penguins in both years (Fig. 3; Appendix Table B).

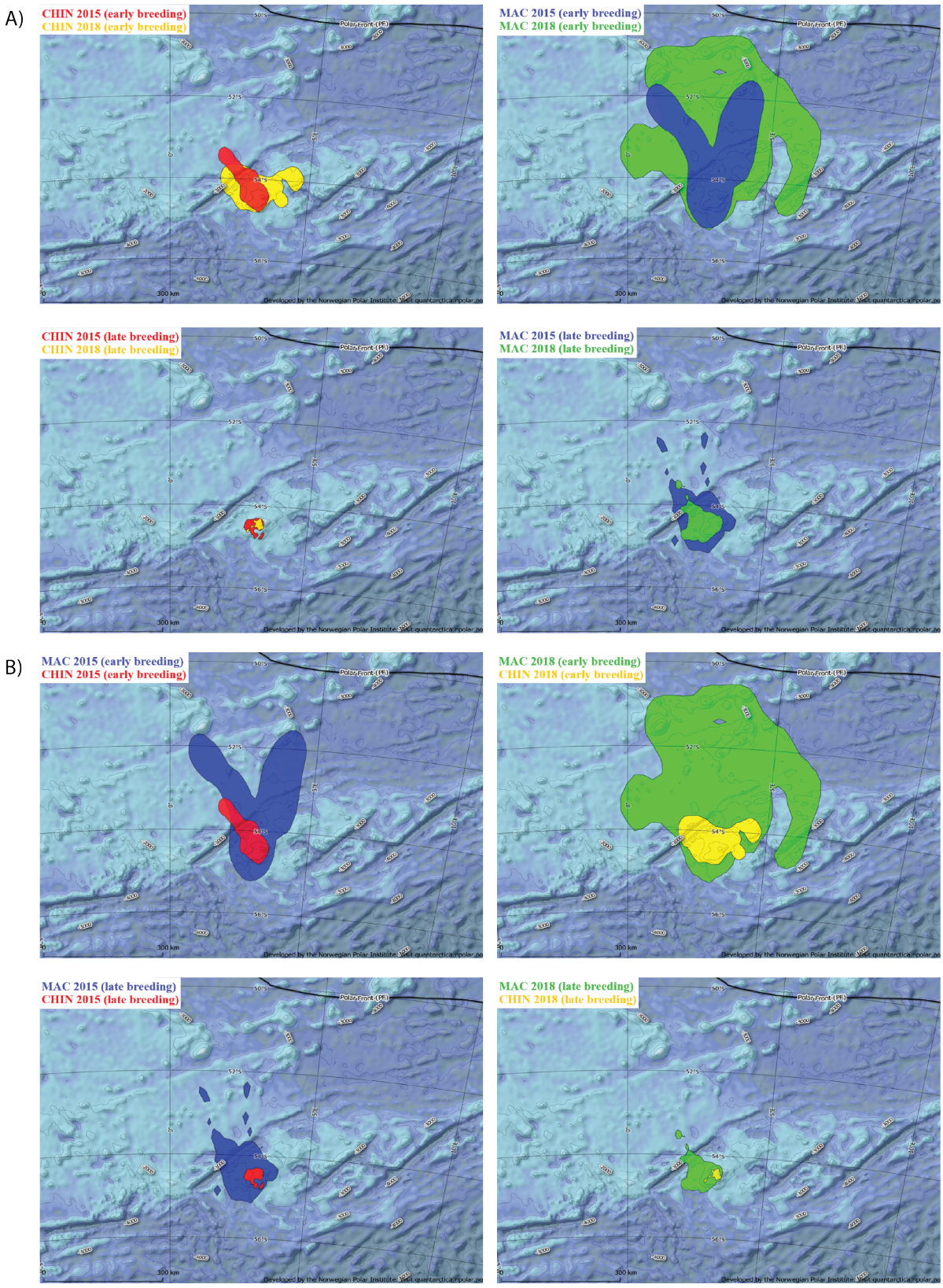

Figure 3. Comparisons of estimated 95% kernel UDs for macaroni (MAC) and chinstrap (CHIN) penguins on Bouvetøya A) at the intraspecific level and B) the interspecific level during early – (incubation – early brood) and late – (late brood – crèche) breeding season in 2015 and 2018.

During early breeding season in 2018, macaroni penguins displayed significantly higher values of $\delta^{15}N$ (11.3‰ ±0.3) compared to their conspecifics in late breeding season (10.0‰ ±0.5) and the chinstrap penguins throughout the season ($\delta^{15}N_{(early)}$, 9.8‰ ±0.4; $\delta^{15}N_{(late)}$, 8.2‰ ±0.7) (Student's t-Test, P<.001 in all cases; Fig. 4A; Appendix Table C & D). Further, chinstrap penguin values of $\delta^{15}N$ in late breeding season were the lowest of all other groups by a significant margin (Student's t-Test, P<.001 in all cases; Fig. 4A; Appendix Table C & D), while macaroni penguins in late- and chinstrap penguins in early-breeding season in 2018 appeared to occupy the same trophic niche (Student's t-Test, P>0.2; Fig. 4A; Appendix Table C & D).

At a broader temporal scale, $\delta^{15}N$ ratios of chinstrap penguins in 2015 were significantly higher compared to their conspecifics in 2018 ($\delta^{15}N_{(2015)}$, 11.1‰ ±0.3; $\delta^{15}N_{(2018)}$, 9.4‰ ±0.6) and of macaroni penguins across both years ($\delta^{15}N_{(2015)}$, 10.7‰ ±0.2; $\delta^{15}N_{(2018)}$, 10.4‰ ±0.3) (Student's t-Test, P<.001 in all cases; Fig. 4B; Table 3; Appendix Table E). Conversely, chinstrap penguins in 2018 had significantly the lowest values of $\delta^{15}N$ of all other groups (Student's t-Test, P<.001 in all cases; Fig. 4B; Table 3; Appendix Table E). Similar to chinstrap penguins, macaroni penguin $\delta^{15}N$ were elevated in 2015 compared to in 2018 (Student's t-Test, P<.001; Fig. 4B; Table 3; Appendix Table E). Of note were the interannual patterns of $\delta^{13}C$, which was significantly lower during 2015 for both species ($chinstrap_{(2015)}$, -23.6‰ ±0.3; $chinstrap_{(2018)}$, -25.3‰ ±0.3; $macaroni_{(2015)}$, -22.6‰ ±0.3; $macaroni_{(2018)}$, -23.5‰ ±0.5) (Student's t-Test, P<.001; Fig. 4B; Table 3; Appendix Table E).

Table 3 Estimated mean values of (±) of δ^{15}N and δ^{13}C from blood samples taken from macaroni (MAC) and chinstrap (CHIN) penguins on Bouvetøya during the austral summer breeding seasons of 2015 and 2018. All groups had sigficantly different isotope ratios at $\alpha = 0.05$ with the exception of CHIN in 2015 sharing similar δ^{13}C values to MAC in 2018 (denoted by matched superscript symbols).

	MAC			CHIN		
Year	**N**	**δ^{15}N**	**δ^{13}C**	**N**	**δ^{15}N**	**δ^{13}C**
2015	55	10.7‰ (±0.24)	-22.6‰ (±0.34)	22	11.1‰ (±0.31)	-23.6‰ (±0.27)[¥]
2018	33	10.4‰ (±0.28)	-23.5‰ (±0.47)[¥]	25	9.4‰ (±0.57)	-25.3‰ (±0.28)

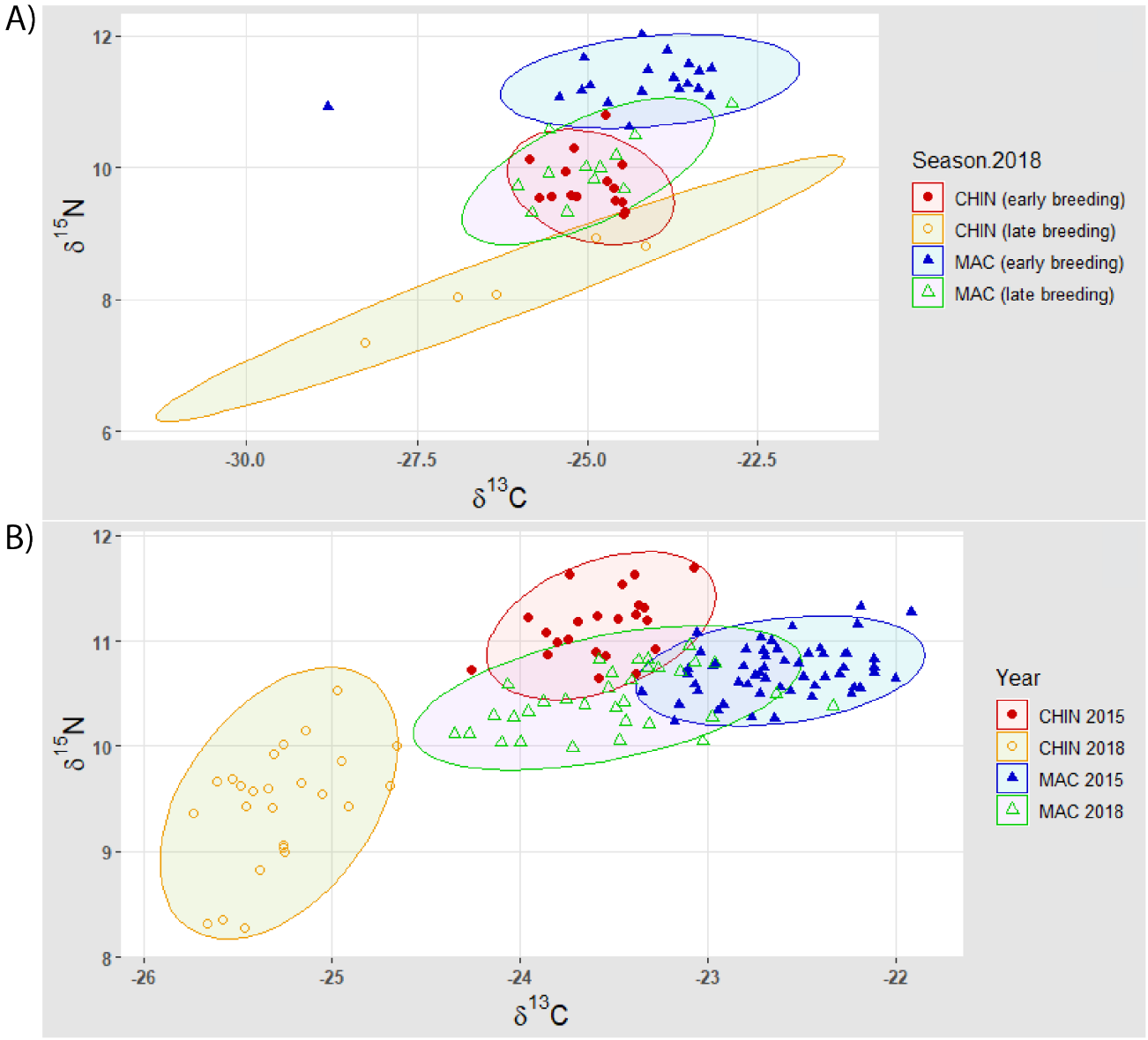

Figure 4. A) Intra-annual variation in δ^{15}N and δ^{13}C values, with 95% CI ellipses drawn for means, in plasma of macaroni (MAC) and chinstrap (CHIN) penguins on Bouvetøya during early – (incubation – early brood) and late – (late brood – crèche) breeding season in 2018. B) Inter-annual variation in δ^{15}N and δ^{13}C values, with 95% CI drawn for means, in blood of MAC and CHIN on Bouvetøya during the austral summer breeding season of 2015 and 2018.

Discussion

Our study shows clear, consistent, and substantial spatial overlap in foraging habitat between two sympatrically breeding penguin species at Bouvetøya. Only one other study has examined spatial niche segregation of macaroni and chinstrap penguins on the island, though the authors did not capture the entire breeding season, nor did they distinguish foraging from transiting dives (Blanchet *et al*., 2013). Thus, by capturing information on patterns of at-sea habitat use throughout the entire breeding season and supplementing it with biogeochemical data as a proxy for feeding behavior, our study gives a more realistic interpretation of the at-sea foraging dynamics of both species. Furthermore, by including multiple years, we provide a clearer picture of the degree and stability of niche segregation between the macaroni and chinstrap penguins and a more thorough interpretation of the trophic overlap between them over time.

Our study indicates that about 40-50% of all dives were likely to represent transiting behavior. Consequently, the failure to partition out transit dives by Blanchet *et al*. (2013) may have led to the bimodal pattern of dive depths (10m and 70m) described for macaroni penguins in 2007. Nevertheless, our study shows that both macaroni and chinstrap penguins dove deeper and longer in both years, compared to their conspecifics in 2007 (Blanchet *et al*., 2013). Most notably though, chinstrap penguins dove up to 43m deeper and 73s longer in 2015 compared to their conspecifics in 2007. In contrast, macaroni penguins displayed less variation in dive behavior between years, including 2007 (Blanchet *et al*., 2013), suggesting that they targeted similar prey in all seasons. Further, penguins typically forage at shallower depths and reduce their foraging activity during low light intensity (Croxall *et al*., 1988; Wilson *et al*., 1993; Barlow & Croxall, 2002; Blanchet *et al*., 2013), and the same pattern were visible for the penguins on Bouvetøya in 2007, 2015, and 2018 (Blanchet *et al*., 2013). Likely, the daily vertical migration of krill and, to some extent, of myctophids (Miller *et al*., 2008) increases the availability of prey closer to the sea surface during the night, making deeper foraging dives unnecessary (Lishman *et al*., 1983; Croxall *et al*., 1988; Jansen *et al*., 1998; Wilson *et al*., 1993; Ichii *et al*., 2007). Still, the chinstrap penguins displayed large interannual variation in dive behavior during both day- and night-time, and dove significantly deeper in 2015 compared to in 2007 and 2018 (Blanchet *et al*., 2013), which emphasizes the importance of prey vertical migration for breeding top predators on Bouvetøya. Given that macaroni and chinstrap penguins occupied similar vertical niches during 2015, our data

suggests that this was an outlier year in the terms of how chinstrap penguins exploited the water column.

The different patterns of dive behavior of macaroni and chinstrap penguins reflects the variation in horizontal habitat exploitation across our study. Penguins appear to target oceanographic features, such as ocean currents and temperature gradients that may represent areas of biological productivity (Lowther *et al*., 2014), and the birds may alter their foraging behavior in accordance to the distribution of their prey (Bengtson *et al*., 1993; Meyer *et al*., 1997; Trathan *et al*., 1998; Miller *et al*., 2008). Krafft *et al*. (2010) detected high aggregations of large krill in areas northwest of Bouvetøya, while small krill dominated areas to the south of the island. In line with this study, both species generally travelled in northerly and northwesterly directions during the breeding season in all years, including 2007 (Blanchet *et al*., 2013), presumably taking advantage of these predictable and productive areas. However, in contrast to 2018, we show that macaroni and chinstrap penguins utilized areas further away from the colony during the late breeding season in 2015, during which the chicks' energy demands likely puts further constrains on penguins' foraging abilities. Penguins may increase their foraging ranges and dive depths when prey densities are low, possibly as a counteractive response to increased intra- and inter-specific competition for food (Horswill *et al*., 2017; Ratcliffe *et al*., 2018). Such a response may reduce spatial overlap between sympatrically breeding penguins during foraging and allow for co-existence even when resource partitioning is minimal (Trivelpiece *et al*., 1987; Hindell *et al*., 1995; Mori & Boyd, 2004). Therefore, it is reasonable to believe that both species were searching for prey further offshore in 2015 due to lack of prey closer to the colony, potentially generated by an Ashmole's halo as the season progressed (Birt *et al*., 1987; Elliot *et al*., 2009). Still, the overlap in the two species' foraging areas varied little between years, with the macaroni penguins occupying almost the entire foraging area of the chinstrap penguins. This highlights the general lack of spatial niche segregation between the two species previously described by Blanchet *et al*. (2013).

The isotopic data from 2015 also supports the notion of a very different trophic seascape to 2018. Taken in isolation, the differences in $\delta^{13}C$ between 2015 and 2018 for each species could indicate foraging in different habitats. However, given that our GPS data did not indicate any gross changes in the spatial patterns of habitat exploitation, this is likely not the case. A more appropriate explanation is that the trophic content of the seascape varied, with penguins feeding on prey of different carbon signals between years, which is supported by

our $\delta^{15}N$ data. During 2018, macaroni penguins foraged approximately half a trophic level higher than the chinstrap penguins (assuming a 2‰ increase in $\delta^{15}N$ for each trophic level, Hobson & Welch 1992). However, during the breeding season in 2015, chinstrap penguins exhibited the highest $\delta^{15}N$ values of any group in the study. The bathymetric features around Bouvetøya supports high aggregations of krill (Krafft *et al*., 2010), and earlier dietary studies have found chinstrap penguins in Nyrøysa to mainly forage upon krill during the breeding season (Haftorn, 1986; Niemandt *et al*., 2016). In contrast, breeding macaroni penguins in Nyrøysa have been found to forage upon a wide selection of prey species, including myctophid fishes (>40% of the diet by mass) and two species of euphasiids, *Euphausia superba* (here "krill") and *Thysanoessa macrura* (Niemandt *et al*., 2016). Thus, under the assumption that 2018 reflected a year in which chinstrap penguins fed on krill and macaroni penguins were mixed-prey foragers, there are three possible explanations for the dramatic differences in 2015. Firstly, fish, being situated a trophic level higher than krill, may serve as an alternative food resource for Southern Ocean penguins when krill is rarely encountered (Croxall *et al*., 1988; Ratcliffe *et al*., 1988; Ichii *et al*., 2007; Miller *et al*., 2008). Myctophid fishes have a mesopelagic nature and typically occupy deeper water layers compared to krill (Lishman *et al*., 1983; Miller *et al*., 2008). Thus, the deeper foraging dives of the chinstrap penguins in 2015 may indicate that they may have been searching for fish in deeper water layers, as a complete switch in prey from krill to fish would likely increase the levels of $\delta^{15}N$ in blood by at least 2‰ (Hobson & Welch 1992; Tierney *et al*., 2008). Secondly, given that $\delta^{15}N$ in krill may also vary by as much as 2‰ based on age (Polito *et al*., 2013), variation in the dominant life history stage of krill available around Bouvetøya may have driven the isotopic differences in chinstrap penguins between 2015 and 2018. However, earlier dietary analysis from seals and penguins in Nyrøysa suggests little interannual variation in the size of krill consumed by predators at Bouvetøya (Kirkman *et al*., 2000; Niemandt *et al*., 2016; Tarroux *et al*., 2016), potentially ruling out this being a driving factor. Thirdly, during the synthesis of proteins, ^{15}N are discriminated over ^{14}N (Cherel *et al*., 2005; Cherel & Hobson, 2007; Inger & Bearhop, 2008). As a result, fasting or starving animals which "feed on themselves" are likely to display elevated blood and plasma levels of $\delta^{15}N$ (Cherel *et al*., 2005). Thus, based on interannul variation in $\delta^{15}N$, we propose that chinstrap penguins in 2015 experienced low krill availability and either attempted to switch to alternative prey, such as myctophid fishes, or underwent catabolism as the penguins' energetic demands increased from early to late breeding season. When considering intra-annual variation in $\delta^{15}N$ during the breeding seasons in 2018 both species seemingly targeted more prey from lower

trophic levels as the season progressed, emphasizing the importance of krill as a food resource for both species during breeding. More, the macaroni penguins in late- and the chinstrap penguins in early- breeding season displayed similar values of $\delta^{15}N$, supporting the idea that chinstrap penguins may search for fish when krill is not readily encountered.

Density and distribution of krill are known to vary greatly at local scales between seasons in the Southern Ocean (Brierley *et al*., 2002; Miller *et al*., 2008), but the frequency of such low krill events are unknown at the poorly-studied Bouvetøya. No earlier studies have detected any clear evidences for krill scarcity in the area (Blanchet *et al*., 2013; Niemandt *et al*., 2016). However, based on isotope data, Tarroux *et al*. (2016) proposed that low krill densities in 2015 likely led to antarctic fur seals in Nyrøysa targeting more fish and cephalopods, supporting our contention. The breeding number of chinstrap penguins have been decreasing in Nyrøysa (Isaksen *et al*., 2000; Biuw *et al*., 2010) and competition for breeding space (Hofmeyr *et al*., 2005; Niemandt *et al*., 2016), destruction of nest sites by landslide, and the killing of penguins from rock falls and aggressive encounters by antarctic fur seals (Isaksen *et al*., 2000; Niemandt *et al*., 2016; Pers.Observ) have all been proposed as possible explanations. However, none of these satisfactorily explains the differing population trajectories observed for the macaroni and chinstrap penguins at the site (Biuw *et al*., 2010). Unlike chinstrap penguins, macaroni penguins are known to more readily change between available prey species (Waluda *et al*., 2010), to utilize deeper water layers (Blanchet *et al*., 2013), and to forage over larger areas during breeding (Thiebot *et al*., 2011), possibly making prey like myctophids more accessible for the second species. Moreover, Bouvetøya is located on the distributional limit of chinstrap penguins, suggesting that the species is living on the edge of its ecological niche and with possibly little tolerance for fluctuations in its main prey, krill. Consequently, when both species are constrained in how far they can travel, and under conditions of low krill availability, the mixed-prey foraging macaroni penguin is likely to gain a competitive advantage. Thus, increased interspecific competition or catabolism, arising from krill scarcity, may lead to reduced individual fitness and reproductive performances for chinstrap penguins at Bouvetøya.

Conclusion

By describing the spatial and isotopic foraging ecology of macaroni and chinstrap penguins over two complete breeding seasons, we demonstrate that single-season studies characterizing levels of niche segregation may not be appropriate as they do not fully incorporate dynamic environmental aspects typical of a marine ecosystem, nor do they fully encapsulate the behavioural plasticity of predators. Due to our poor understanding of krill fluctuations at Bouvetøya, low krill events may already be common enough to drive the decline in breeding number of chinstrap penguins in Nyrøysa. The non-static APF is predicted to move southwards as a response to increasing ocean temperatures (Cristofari *et al*., 2018). When coupled with a rapidly warming Southern Ocean (Gille, 2002;), the distribution of krill is likely to continue contracting southwards towards the continent (Atkinson *et al*., 2019). Consequently, Bouvetøya is likely to become geographically closer to temperate waters and thus further outside the geographical distribution of krill (Atkinson *et al*., 2004; 2006; Trathan *et al*., 2015). Thus, low krill events are likely to become more frequent at Bouvetøya, potentially driving the breeding population of chinstrap penguins to local extinction.

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Appendix

Table A. Interannual and diurnal comparisons of mean maximum dive depth (m) and mean dive duration (s) between groups of macaroni (MAC) and chinstrap (CHIN) penguins on Bouvetøya during early- (incubation – early brood) and late- (late brood – crèche) breeding season in 2015 and 2018.

	Wilcoxon W							
	Max depth				Dive duration			
	Early		Late		Early		Late	
Species (Year)	Day	Night	Day	Night	Day	Night	Day	Night
MAC (2015) ~ MAC (2018)	6730600	8518.5	21277000	394260¥	5544800	5266.5	17487000	334070
CHIN (2015) ~ CHIN (2018)	7301600	5416	9092700	21142	8359100	4951	9628600	24136
MAC (2015) ~ CHIN (2015)	3523200	24158	26488000	1114800	3454000¥	26847000	24668	1135700
MAC (2015) ~ CHIN (2018)	2197300	73062¥	7049700	47676¥	1285200	2741300	73345¥	29828
MAC (2018) ~ CHIN (2015)	7949000	1838	9855300	177980	9189200	1895.5	11031000	190640
MAC (2018) ~ CHIN (2018)	4567200	2847900	6665.5	175130¥	4001600	1646500	6457.5	5822.5

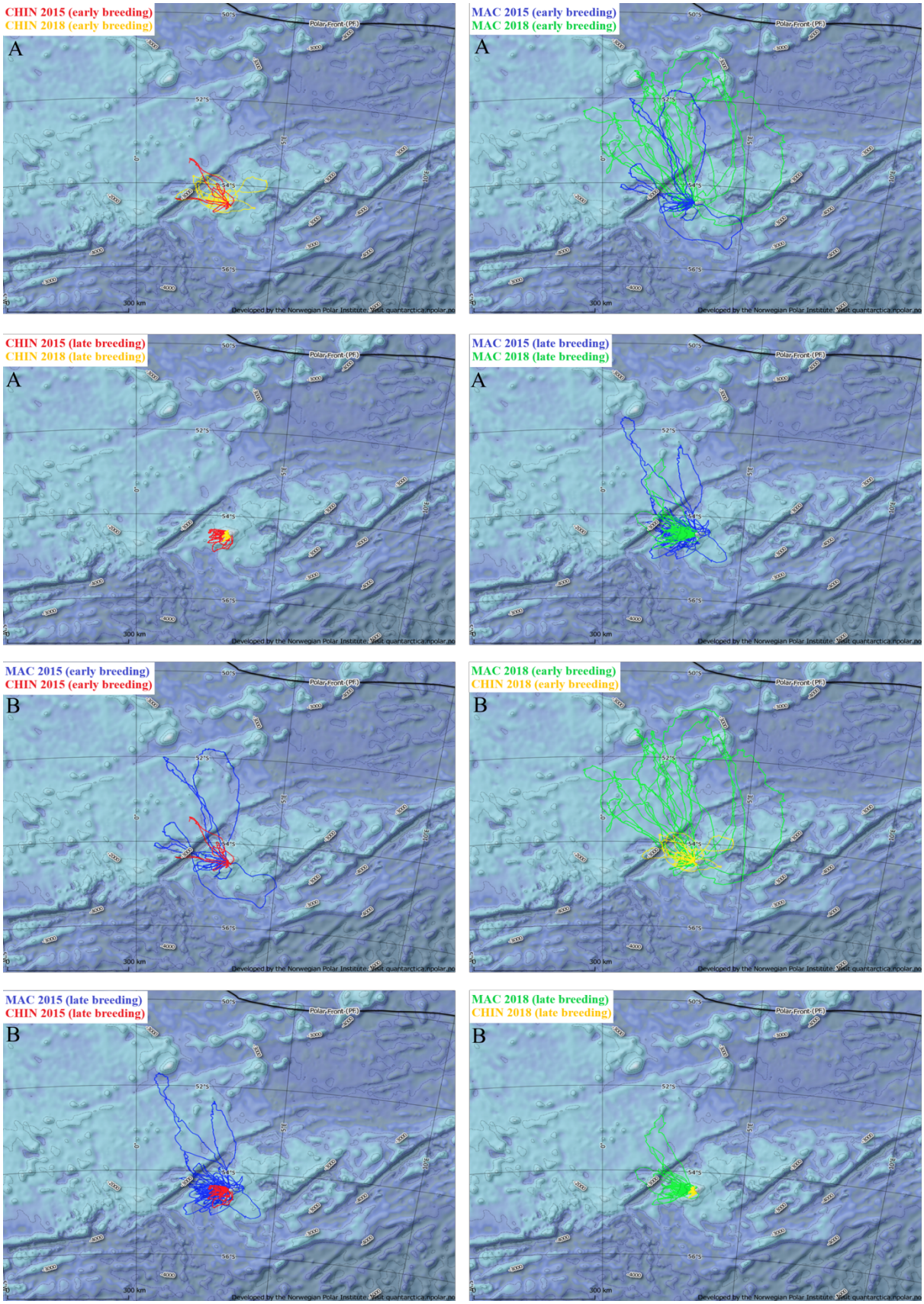

Figure A. Intra- A) and inter-species B) comparisons of foraging trips undertaken by macaroni (MAC) and chinstrap (CHIN) penguins on Bouvetøya during early- (incubation – early brood) and late- (late brood – crèche) breeding season in 2015 and 2018.

Table B. Sizes (km^2) and overlap (%) of estimated 95% Kernel UD for macaroni (MAC) and chinstrap penguins (CHIN) on Bouvetøya during early- (incubation – early brood) or late- (late brood – crèche) breeding season in 2015 and 2018.

Variable	Size (km^2)	% Overlap							
		MAC 2015 (early)	**MAC 2015 (late)**	**MAC 2018 (early**	**MAC 2018 (late)**	**CHIN 2015 (early)**	**CHIN 2015 (late)**	**CHIN 2018 (early)**	**CHIN 2018 (late)**
MAC 2015 (early)	140564.5	-	-	95.4	-	14.3	-	-	-
MAC 2015 (late)	54252.0	-	-	-	37.0	-	7.9	-	-
MAC 2018 (early)	382129.9	35.1	-	-	-	-	-	11.2	-
MAC 2018 (late)	20840.4	-	97.1	-	-	-	-		7.5
CHIN 2015 (early)	22640.0	88.3	-	-	-	-	-	79.3	-
CHIN 2015 (late)	4363.9	-	100	-	-	-	-	-	33.3
CHIN 2018 (early)	43985.0	-	-	96.9	-	40.7	-	-	-
CHIN 2018 (late)	1586.5	-	-	-	99.2	-	90.6	-	-

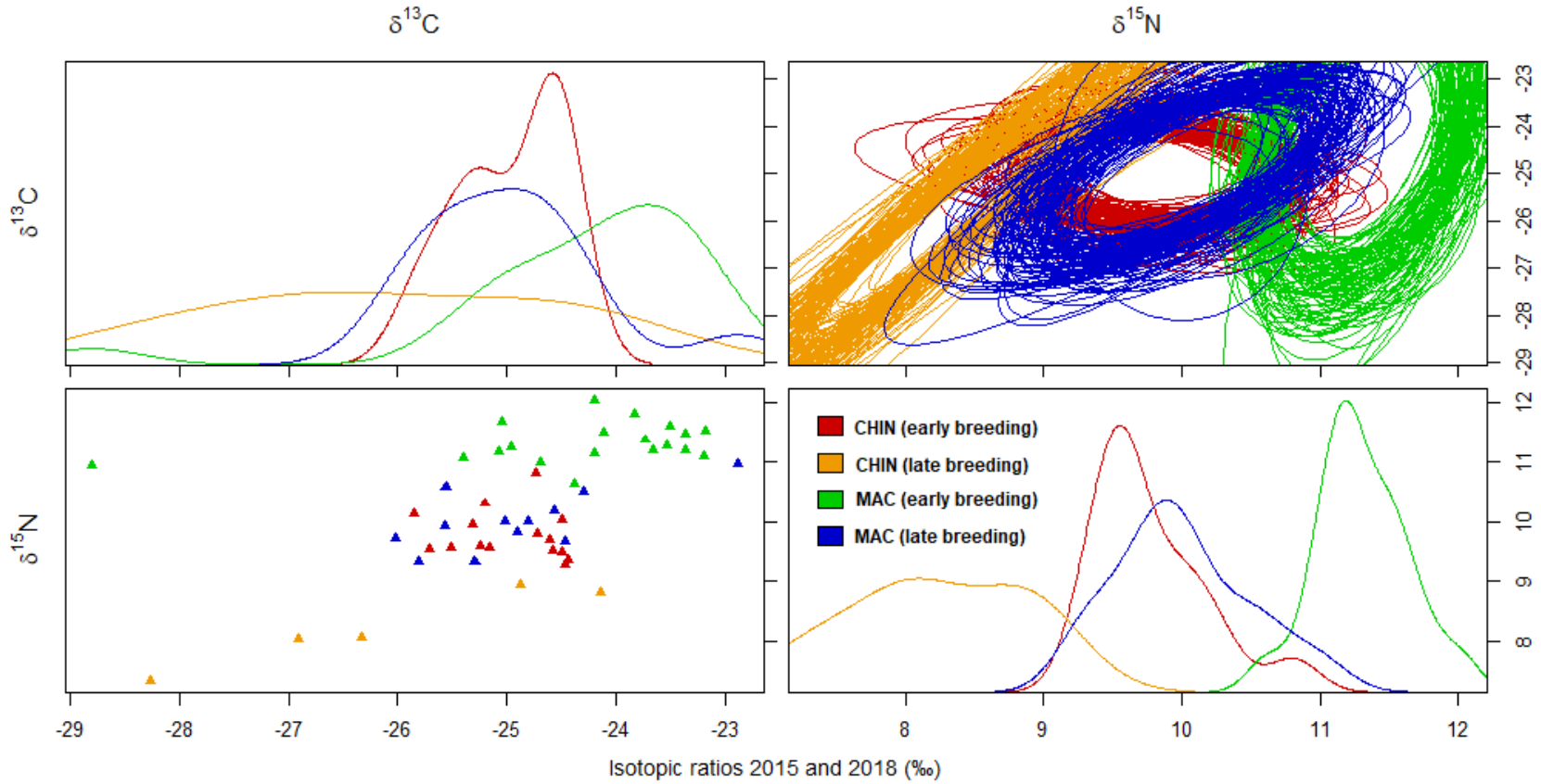

Figure B. Intra-annual variation in isotopic ratios of $\delta^{15}N$ and $\delta^{13}C$ in samples of plasma taken from macaroni (MAC) and chinstrap (CHIN) penguins on Bouvetøya during early- (incubation – early brood) and late- (late brood – crèche) breeding season of 2018. The upper right window shows 100 (95% CI) elliptical projections drawn for niche regions (mean isotopic values of $\delta^{15}N$ and $\delta^{13}C$) for each species in both parts of the season.

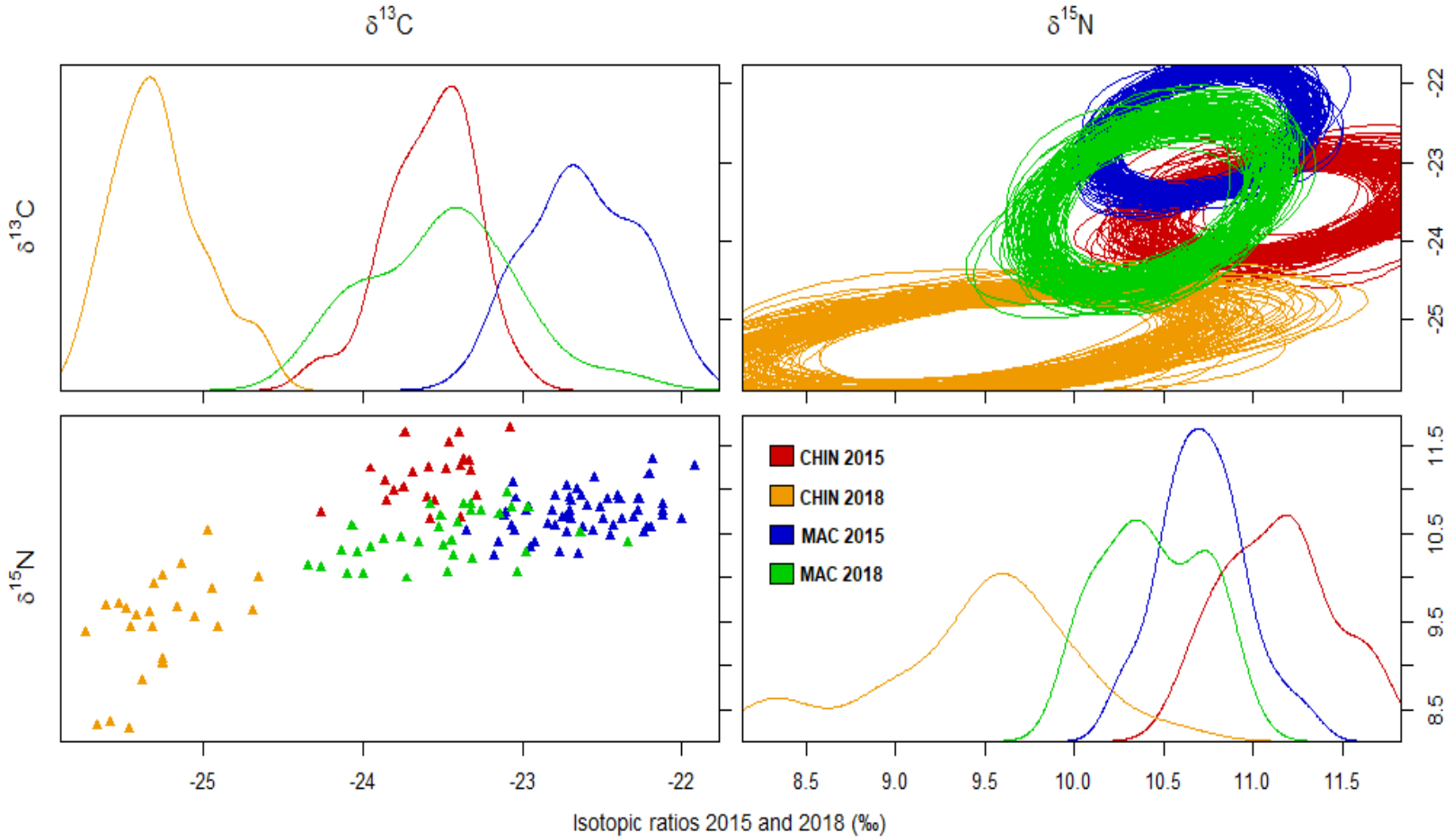

Figure C. Interannual variation in isotopic ratios of $\delta^{15}N$ and $\delta^{13}C$ in blood samples taken from macaroni (MAC) and chinstrap (CHIN) penguins on Bouvetøya during the austral summer breeding season of 2015 and 2018. The upper right window show 100 (95% CI) elliptical projections drawn for niche regions (mean isotopic values of $\delta^{15}N$ and $\delta^{13}C$) for each species in both years.

Table C. Estimated mean values (±SD) of $\delta^{15}N$ and $\delta^{13}C$ in samples of plasma taken from macaroni (MAC) and chinstrap (CHIN) penguins on Bouvetøya during early- (incubation – early brood) and late- (late brood – crèche) breeding season in 2018.

	MAC			CHIN		
Breeding season 2018	**N**	**$\delta^{15}N$**	**$\delta^{13}C$**	**N**	**$\delta^{15}N$**	**$\delta^{13}C$**
Early	19	11.3‰ (±0.33)	-24.3‰ (±1.29)	15	9.77‰ (±0.41)	-25.0‰ (±0.49)
Late	12	10.0‰ (±0.50)	-24.9‰ (±0.85)	5	8.24‰ (±0.65)	-26.1‰ (±1.64)

Table D. Comparisons of estimated means of $\delta^{15}N$ and $\delta^{13}C$ from samples of plasma taken from macaroni (MAC) and chinstrap (CHIN) penguins on Bouvetøya during early- (incubation – early brood) and late- (late brood – crèche) breeding season in 2018.

$\delta^{15}N$	**CHIN (late)**			**MAC (early)**			**MAC (late)**		
	t-test	**Df**	**p-value**	**t-test**	**Df**	**p-value**	**t-test**	**Df**	**p-value**
CHIN (early)	6.272	18	6.488e-06	-12.137	32	1.623e-13	-1.3132	25	0.201
CHIN (late)	-	-	-	-14.988	22	4.99e-13	-6.1187	15	1.965e-05
MAC (early)	-	-	-	-	-	-	8.8544	29	9.648e-10
$\delta^{13}C$									
CHIN (early)	2.4942	18	0.02258	-1.8268	32	0.07707	-0.1421	25	0.8881
CHIN (late)	-	-	-	-2.6072	22	0.01609	-1.9799	15	0.06637
MAC (early)	-	-	-	-	-	-	1.4393	29	0.1608

Table E. Comparisons of estimated means of $\delta^{15}N$ and $\delta^{13}C$ from blood samples taken from macaroni (MAC) and chinstrap (CHIN) penguins on Bouvetøya during the austral summer breeding season of 2015 and 2018.

$\underline{\delta^{15}N}$	**CHIN (2018)**			**MAC (2015)**			**MAC (2018)**		
	t-test	**Df**	**p-value**	**t-test**	**Df**	**p-value**	**t-test**	**Df**	**p-value**
CHIN (2015)	12.569	45	2.535e-16	6.4067	75	1.175e-08	8.6525	53	1.03e-11
CHIN (2018)	-	-	-	-14.279	78	<2.2e-16	-8.8526	56	3.125e-12
MAC (2015)	-	-	-	-	-	-	4.8903	86	4.639e-16
$\underline{\delta^{13}C}$									
CHIN (2015)	20.966	45	<2.2e-16	-11.825	75	<2.2e-16	-0.67529	53	0.5024
CHIN (2018)	-	-	-	-33.973	78	<2.2e-16	-16.756	56	<2.2e-16
MAC (2015)	-	-	-	-	-	-	10.271	86	<2.2-16