RESEARCH ARTICLE

Foraging behaviour of sympatrically breeding macaroni (*Eudyptes chrysolophus*) and chinstrap (*Pygoscelis antarcticus*) penguins at Bouvetøya, Southern Ocean

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Abstract

Species with similar ecological requirements that overlap in range tend to segregate their niches to minimize competition for resources. However, the niche segregation possibilities for centrally foraging predators that breed on isolated Subantarctic islands may be reduced by spatial constraints and limitations in the availability of alternative prey. In this study we examined spatial and trophic aspects of the foraging niches of two sympatrically breeding penguin species, macaroni (*Eudyptes chrysolophus*; MAC) and chinstrap (*Pygoscelis antarcticus*; CHIN) penguins, at Bouvetøya over two breeding seasons. To measure at-sea movements and diving behaviour, 90 MACs and 49 CHINs were equipped with GPS loggers and dive recorders during two austral summer breeding seasons (2014/15 and 2017/18). In addition, blood samples from tracked birds were analysed for stable isotopes to obtain dietary information. CHINs displayed marked interannual variation in foraging behaviour, diving deeper, utilizing a larger foraging area and displaying enriched values of $\delta^{15}N$ in 2014/15 compared to the 2017/18 breeding season. In contrast, MACs dove to similar depths and showed similar $\delta^{15}N$ values, while consistently utilizing larger foraging areas compared to CHINs. We suggest that low krill abundances in the waters around Bouvetøya during the 2014/15 season resulted in CHINs shifting toward a diet that increased their niche overlap with MACs. Our findings may partly explain the decreasing number of breeding CHINs at the world's most remote island, Bouvetøya, while also highlighting the importance of characterizing niche overlap of species using multi-season data sets.

Keywords

Ecological niche; niche overlap; central place foraging; competition; stable isotope analysis; biotelemetry

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Abbreviations

ANOVA: analysis of variance
APF: Antarctic Polar Front
CHIN: chinstrap penguin
GIS: geospatial information system
GPS: global positioning system
HSD: honestly significant difference test
MAC: macaroni penguin
SEAc: standard ellipse area corrected for small sample size
SIA: stable isotope analyses
TDR: time–depth recorders
UD: utilization distribution

Introduction

In the Southern Ocean, all centrally foraging species are air-breathing marine predators (such as otariid seals and seabirds), many of which utilize remote Subantarctic islands as terrestrial breeding grounds (Barlow et al. 2002; Lowther et al. 2014; Petry et al. 2018). Upwelling of minerals and organic matter caused by internal waves, in addition to influxes of nutrients from land, creates conditions promoting high productivity over the shelf areas of Subantarctic islands (Park et al. 2008; Meyer et al. 2015). Offering predictable food availability, these islands support large multispecies marine predator guilds (Trivelpiece et al. 1987; Adams & Brown 1989; Reid & Croxall 2001; Petry et al. 2018). Intensified competition for food between various predators, resulting from both high predation pressure and spatiotemporal changes in prey availability, may arise in nearshore waters during the breeding season (Dann & Norman 2006; Elliot et al. 2009).

Subantarctic islands are distributed close to the APF, which separates warm temperate waters from colder Subantarctic and Antarctic waters. Only South Georgia, the South Sandwich Islands and Bouvetøya are south of this key hydrographic feature within the ACC. South of the APF, Antarctic krill (*Euphausia superba*; hereafter 'krill') is the main food resource for most marine predators (Croxall et al. 1988; Davis & Darby 1990; Atkinson et al. 2004; Atkinson et al. 2006; Atkinson et al. 2008; Reid & Croxall 2001). However, the local abundance of krill can vary enormously, introducing considerable variability to food web structure and concomitantly the foraging ecology of krill predators (Croxall & Davis 1999; Reid & Croxall 2001; Barbosa et al. 2012; Horswill et al. 2017). Additionally, some sectors of the Southern Ocean, including the

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ACC, have experienced rapid warming since the second half of the 20th century (Gille 2002; Vaughan et al. 2003), causing concern for future krill abundance and possible cascading effects throughout marine food webs (Reid & Croxall 2001; Thorpe et al. 2007; Trivelpiece et al. 2011).

Penguins are the most abundant group of air-breathing marine predators in the Southern Ocean (Davis & Darby 1990) and constitute a significant group of krill consumers (de Brooke 2004). During breeding, penguins are central place foragers that attend their nest for chick provisioning (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—they must bring prey back promptly to feed their chicks—nor do they have the mobility of their flying seabirds' counterparts. Consequently, penguins are spatially constrained during breeding (Barlow et al. 2002; Ichii et al. 2007) and likely vulnerable to the effects of trophic competition (Waluda et al. 2010; Polito et al. 2015; Clewlow et al. 2019). The similar-sized MAC and CHIN both occur in great numbers throughout the Southern Ocean (BirdLife International 2019a, b). However, CHINs are obligate krill feeders, while MACs are more opportunistic and switch readily to other prey types when krill abundance is low (Lynnes et al. 2002; Miller et al. 2010; Rombolá et al. 2010; Niemandt et al. 2016; Whitehead et al. 2017). At Bouvetøya the two species breed sympatrically during the austral summer (Isaksen et al. 2000; Biuw et al. 2010; Blanchet et al. 2013). The penguin breeding season at Bouvetøya spans from December to early March, and the nesting cycle of MACs and CHINs is relatively synchronous, as it is throughout their range (Trivelpiece et al. 1987; Haftorn 1986).Following egg laying, female MACs leave the nest to forage at sea, with the males incubating the eggs alone until hatching. After hatching, male MACs brood and guard the chicks while the females undertake short foraging trips for chick provisioning (Haftorn 1986; Barlow & Croxall 2002b; Green et al. 2002; Blanchet et al. 2013). Unlike MACs, both male and female CHINs undertake incubation and chick provisioning, alternately taking long (multi-day) foraging trips during incubation and short foraging trips during the chick brooding and guarding phase (Haftorn 1986; Jansen et al. 2002; Blanchet et al. 2013). After 20 to 30 days of egg hatching, chicks from different nests gather in crèches (Haftorn 1986; Jansen et al. 2002). Finally, 60 to 70 days after egg hatching, the chicks of both species fledge and go to sea (Barlow & Croxall 2002b).

At Nyrøysa, a rocky beach located on the west coast of Bouvetøya, MACs and CHINs currently show differing population trajectories. During the last three decades the number of MACs has remained stable (1100 breeding pairs), while the number of CHINs has decreased from about 200 to 40 pairs (Isaksen et al. 2000; Biuw et al. 2010). Bouvetøya is located at the distributional limit of CHINs, possibly leaving the species in suboptimal conditions with less tolerance to changes in the local ecosystem (Fig. 1; Strycker et al. 2020). The underlying cause of this decline remains uncertain (Blanchet et al. 2013; Niemandt et al. 2016), with potential prey competition not to be excluded as a driving factor. As a result of increasing ocean temperatures, krill abundance may decline and the frequency of low krill events around Bouvetøya may increase in the future (Atkinson et al. 2004; Atkinson et al. 2006; Atkinson et al. 2019; Trivelpiece et al. 2011). In such a scenario, generalist predators, capable of rapidly switching to other available prey species, may gain a competitive advantage over krill specialists (Forcada & Trathan 2009; Trivelpiece et al. 2011; Blanchet et al. 2013; Niemandt et al. 2016). The mixed breeding colony of MACs and CHINs is therefore an interesting system to study the temporal dynamics of niche overlap between a foraging generalist and a foraging specialist in a changing Southern Ocean.

In the present study, we combine biotelemetry with SIA to examine the foraging niche of MACs and CHINs at Bouvetøya over two non-consecutive breeding seasons. Signatures of $\delta^{15}N$ are used as tracers for trophic levels, while those of $\delta^{13}C$ typically reflect the carbon source at the base of the food chain (Bearhop et al. 2000; Cherel & Hobson 2007). By combining SIA of blood and biotelemetry we can characterize the spatial and trophic dimensions of the two species' foraging niches on intra- and interseasonal time scales. Our goal was to determine whether the overlap in foraging niches between the two species remains consistent across years in terms of habitat use and trophic ecology.

Material and methods

Field site

Our study was conducted at Nyrøysa, Bouvetøya (54°25′S, 3°20′E; Fig. 1), during the austral summer breeding season (mid-December to early February) in 2014/15 and in 2017/18 (hereafter '2015' and '2018'). All fieldwork was undertaken as part of the Norwegian Antarctic Research Expedition programme, and animal experimentation was conducted under permits from the Norwegian Food Safety Authority (permit numbers 2014/230385 and 17/105553).

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Fig. 1 The location of Bouvetøya (54°25'S, 3°20'E) and Nyrøysa (red square), where all fieldwork took place. The inset shows the global distribution of CHIN (red dots) and MAC (blue dots) breeding colonies (Strycker et al. 2020).

Movement and diving behaviour

A total of 139 breeding penguins (90 female MACs and 49 CHINs of unknown sex) were instrumented during the two seasons (Table 1). Only female MACs were tagged as the male stays at the nest during most of the breeding season (Barlow & Croxall 2002b). A Pathtrack GPS-logger (nanoFix® model 64 × 20 × 17 mm, 22 g) and a CEFAS Technology TDR (G5 Data Storage Tag model 31 × 8 mm, 2.7 g) were attached to the dorsal feathers using Tesa© 4651 waterproof tape and Loctite® 323 rapid-setting glue (Wilson & Wilson 1989; Wilson et al. 1997). GPSs were programmed to record a location every four minutes and the TDRs recorded depth every 2 s. The two instruments were deployed for 5–10 days on each individual, corresponding to 1–13 foraging trips (covering late incubation through to early crèche), after which the animal was recaptured and the instrument package removed. Upon retrieval, a blood sample was taken from the brachial vein using a 0.6 × 25 mm needle (FineJect®; Henke Sass Wolf) and a 2-ml syringe (BD Emerald™). Animal handling, during deployment or recovery, took less than 10 minutes, after which all individuals returned immediately to their nests.

Stable isotope sample preparation

In 2018, samples were centrifuged for five minutes at 3000 rpm (Hettich® EBA 20 Centrifuge) and plasma was separated from the cell pack using a 100–1000-µl pipette (BioPette A™, Labnet International Inc.) and a 1–200-µl pipette tip (VWR™). Whole blood from 2015 and red blood cells from 2018 were stored in 98% ethanol in heparinized blood containers (BD Vacutainer®; Becton Dickinson). All samples were kept at −18°C until further analysis.

Table 1 Breeding MACs and CHINs deployed with GPSs and TDRs for which data amenable for further analysis were collected over two austral summer breeding seasons (2015 and 2018) at Bouvetøya.

Species (year)	GPS[a]	TDR[a]	Blood[a]
CHIN (2015)	16 (19)	14 (19)	19 (19)
CHIN (2018)	23 (30)	19 (30)	25 (30)
MAC (2015)	24 (50)	21 (50)	50 (50)
MAC (2018)	27 (40)	19 (40)	33 (40)

[a] Numbers in parentheses represent the total number of samples collected, including those for which either insufficient data or blood samples were available or the electronic instruments failed during deployment.

Statistical analysis of movement and diving behaviour

All data from both breeding seasons were processed and analysed using R statistical software version 3.5.2 (R Development Core Team 2018). All geospatial data 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 m (Clewlow et al. 2019) and dive statistics were extracted using the package *diveMOVE* (Luque & Fried 2011). Raw GPS data were treated with a speed filter (McConnell et al. 1992) set to 20 ms^{-1} to remove extreme outliers and then locations closer than 200 m to land (representing the accuracy of the GPS) were removed manually, resulting in discrete at-sea foraging trips for each individual. Interspecific differences in trip duration were subsequently tested for using non-parametric Wilcoxon signed-rank tests. 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 via temporal interpolation.

Further, spatially resolved dive data were clustered into two categories, namely, foraging dives and transit dives, using the package *mclust* (Scrucca et al. 2016). Here foraging dives are defined as being deeper, and of longer durations, compared to transit dives. Penguins are known to undertake deeper and longer dives when searching for, and approaching, prey in foraging locations, while short and shallow dives resemble travelling between discrete foraging areas and the nest site (Williams et al. 1992; Hart et al. 2010). Differences between foraging and transit dives were tested for using Wilcoxon signed-rank tests. Next, foraging dives partitioned by species, breeding season and early/late breeding stages were subsequently tested for differences in mean maximum dive depth (m) and mean dive duration (s) using two-way ANOVAs and Tukey's HSD tests.

Statistical analysis of habitat utilization distributions

Using the estimated locations of foraging dives, 95% kernel UDs were created for groups of MACs and CHINs separated by breeding season and early/late breeding stages using the package adehabitatHR (Calenge 2015), with a smoothing parameter for bivariate normal distribution. In addition, the size and overlap of UDs were calculated. Polygons of estimated foraging areas were visualized using a GIS software, QGIS version 3.6.3 (QGIS Development Team 2019). Foraging dive behaviour and stable isotope data were visualized using *ggplot* from the package *ggplot2*. Differences in $\delta^{15}N$ and $\delta^{13}C$ were explored between species and breeding seasons using two-way ANOVAs and Tukey's HSD tests. SEAcs were calculated for stable isotope data using the package *SIBER* (Jackson et al. 2011). Values are presented as mean (±standard deviation) and differences were considered to be significant at $p < 0.05$.

SIA

Isotope analyses of $\delta^{15}N$ ($^{15}N/^{14}C$) and $\delta^{13}C$ ($^{13}C/^{12}C$) were carried out for samples of whole blood in 2015 and for red blood cells in 2018 (Table 1). Isotope ratios in whole blood closely resemble ratios in red blood cells (Cherel et al. 2005) and henceforth both red blood cells and whole blood are referred to as 'blood'. In blood, the turnover rate of stable isotopes of nitrogen and carbon is approximately four weeks, with levels of $\delta^{15}N$ ($^{15}N/^{14}N$) and $\delta^{13}C$ ($^{13}C/^{12}C$) increasing between 2–4‰ and 0–1‰ respectively per trophic level in marine ecosystems (Post 2002; Inger & Bearhop 2008). Blood samples were dried at 50°C, pulverized and weighed in tin capsules. Dried samples were then combusted in an elemental analyzer (Thermo Scientific Flash HT Plus) at 1020°C and analysed on an isotope ratio mass spectrometer (Thermo Scientific MAT253). $\delta^{15}N$ and $\delta^{13}C$ were determined by normalization to international scales for atmospheric nitrogen and Vienna PeeDee Belemnite carbonate. Ratios of stable isotopes were calculated using the following equation:

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

and expressed as per mil units (‰) (Polito et al. 2015; Ratcliffe et al. 2018). All SIAs were conducted at the Stable Isotope Laboratory at CAGE—Centre for Arctic Gas Hydrate, Environment and Climate, at UiT The Arctic University of Norway, Tromsø. Differences in $\delta^{15}N$ and $\delta^{13}C$ were then explored between species and breeding seasons using two-way ANOVAs and Tukey's HSD tests. SEAcs were calculated for stable isotope data using the package *SIBER* (Jackson et al. 2011).

Results

Movement and diving behaviour

In 2015, MACs and CHINs were instrumented for a mean period of 7.9 (± 2.0) and 6.2 (± 4.6) days, respectively. In 2018 the mean instrumentation periods were 8.9 (± 4.8) days for MACs and 6.0 (± 3.5) days for CHINs. This led to individual MACs and CHINs conducting a mean 3.1 and 2.7 foraging trips in 2015, and 3.3 (± 1.7) and 2.6 (± 2.1) in 2018, respectively. Mean trip durations for MACs were 3.1 (± 3.7) days in 2015 and 5.4 (± 5.5) days in 2018, while the mean trip durations for CHINs were 1.4 (± 1.4) and 1.1 (± 0.8) days, respectively, during the same period. The mean foraging range decreased for both species as the breeding season progressed, and it

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Table 2 Mean (with associated standard deviation), minimum and maximum foraging range (km), for MACs and CHINs in early (incubation and early brood) and late (late brood and crèche) breeding at Bouvetøya during the austral summers of 2015 and 2018.

Species/year	Early breeding			Late breeding		
	Mean range (km)	Min. range (km)	Max. range (km)	Mean range (km)	Min. range (km)	Max. range (km)
CHIN 2015	52.2 ± 46.2	8.2	144.6	22.7 ± 16.0	4.8	59.1
CHIN 2018	51.5 ± 40.6	2.2	121.1	8.8 ± 6.1	2.1	37.6
MAC 2015	149.9 ± 1424	23.1	348.5	64.3 ± 41.0	6.2	178.2
MAC 2018	158.1 ± 157.3	3.3	399.0	54.1 ± 57.2	7.2	335.5

was significantly shorter for CHINs than for MACs throughout the study (early breeding in 2015 and 2018: MAC, 149.9 km/158.1 km; CHIN, 52.2 km/51.5 km; late breeding in 2015 and 2018: MAC, 54.1 km/64.3 km; CHIN, 22.7 km/8.8 km) (Wilcoxon rank sum, $p < 0.05$ in all cases; Table 2). CHINs travelled about three times further offshore during the late breeding season in 2015 compared to the late breeding period in 2018 (Wilcoxon rank sum, $p < 0.001$).

Foraging dives were significantly deeper, and of longer duration, compared to transit dives for both MACs and CHINs throughout the breeding seasons of 2015 and 2018 (Wilcoxon rank sum, $p < 0.001$). During foraging, CHINs exhibited maximum dive depths and durations that were generally similar to MACs in 2015, with the deepest and longest dive being 120 m and 160 s for CHINs, and 116 m and 186 s for MACs. A clearer difference in the two dive parameters between the two species was detected in 2018, with the deepest and longest dive being 85 m and 160 s for CHINs, and 123 m and 170 s for MACs. Intraspecific differences in foraging dive behaviour between breeding seasons were detected for both species. This difference was most pronounced for CHINs, which dove significantly deeper (mean difference 12.4 and 31.2 m, respectively) and longer (mean difference 31.4 and 69.1 s, respectively) during foraging in early and late breeding seasons in 2015 compared to the same stages of breeding in 2018 (Tukey's HSD, $p < 0.001$; Fig. 2; Table 3). For MACs the interannual differences in foraging dive behaviour were less pronounced, with individuals diving deeper (mean difference 6.8 and 4.9 m) during both the early and late breeding stages in 2018 compared to the same stages of breeding in 2015 (Tukey's HSD, $p < 0.001$; Fig. 2; Table 3). No specific pattern was observed in mean maximum dive duration for MACs between breeding seasons; however, the species dove longer in late- compared to early breeding (mean difference 8.3 and 2.3 s, respectively) in both 2015 and 2018 (Tukey's HSD, $p < 0.01$; Fig. 2; Table 3). Interestingly, CHINs dove significantly deeper and longer in the late breeding stage in 2015, yet not in 2018, compared to the MACs throughout both breeding seasons (Tukey's HSD, $p < 0.001$; Fig. 2; Table 3).

Habitat UDs

There was a marked difference between the two species in the size of the area used for foraging, with MACs typically exploiting an area more than six times larger than CHINs (Fig. 3). Across both breeding seasons, the 95% UD of both MACs and CHINs decreased as the breeding season progressed, though the difference between early and late breeding season was less pronounced in 2015 (early breeding in 2015 and 2018: MAC, 140 653.5 km^2/382 128.9 km^2; CHIN, 22 640.0 km^2/43 985.0 km^2; late breeding in 2015 and 2018: MAC, 54 252.0 km^2/20 840.4 km^2; CHIN, 4362.9 km^2/1584.5 km^2; Fig.3). Most notably, CHINs utilized an almost three times larger foraging area during late breeding in 2015 compared to the same part of the breeding season in 2018 (Fig. 3). There was also considerable overlap in the 95% UD of the two species, with MACs occupying between 88 and 100% of the habitat exploited by CHINs in both breeding seasons (Fig. 3).

SIAs

Nitrogen ratios of CHINs in 2015 were significantly higher compared to their conspecifics in 2018 (δ^{15}N in 2015 and 2018, 11.1 ± 0.3‰/9.4 ± 0.6‰) and to MACs from both breeding seasons (δ^{15}N in 2015 and 2018, 10.7 ± 0.2‰/10.4 ± 0.3‰; Tukey's HSD, $p < 0.001$ in all cases; Fig. 4, Table 4). Importantly, CHINs in 2018 had the lowest values of δ^{15}N of all groups across breeding seasons (Tukey's HSD, $p < 0.001$ in all cases; Fig. 4, Table 4). Similarly, MACs δ^{15}N were elevated in 2015 compared to in 2018 (Tukey's HSD, $p < 0.05$; Fig. 4, Table 4); however, considering a 2‰ increase in δ^{15}N per trophic level, the difference is of little ecological importance. δ^{13}C values were significantly lower during 2015 for both species (MAC in 2015 and 2018, −22.6 ± 0.3‰/−23.5 ± 0.5‰; CHIN in 2015 and 2018 −23.6 ± 0.3‰/−25.3 ± 0.3‰; Tukey's HSD, $p < 0.001$; Fig. 4, Table 4).

Discussion

We demonstrate substantial spatial overlap in the foraging niches of sympatrically breeding MACs and CHINs across

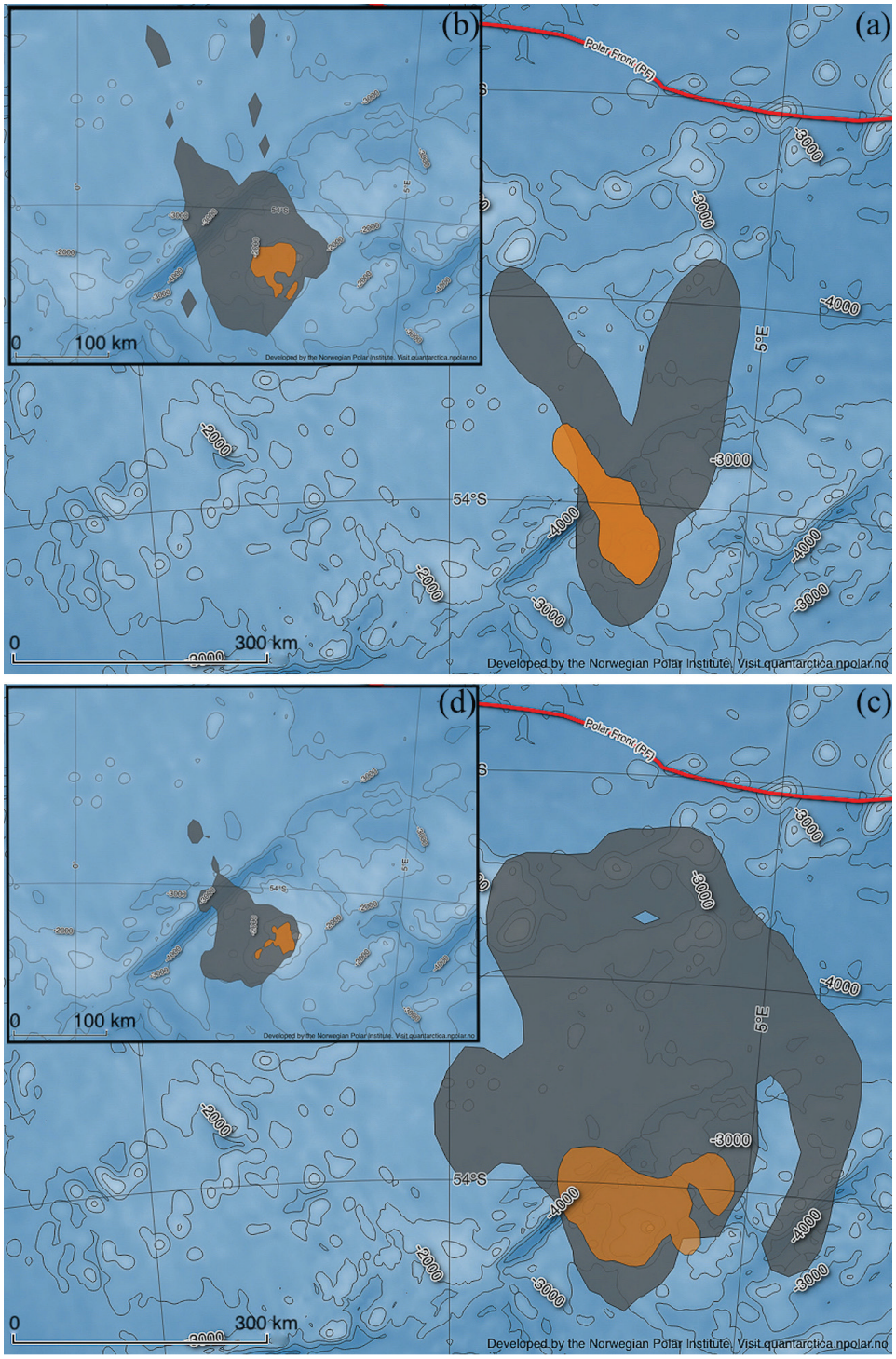

Fig. 2 Comparisons of estimated 95% kernel UDs for MACs (grey) and CHINs (orange) in early (incubation and early brood) and late (late brood and crèche) breeding at Bouvetøya, with the APF visible to the north of Bouvetøya. (a) Early breeding, 2015. (b) Late breeding, 2015. (c) Early breeding, 2018. (d) Late breeding, 2018. The greatest interspecific difference in UDs was observed between MACs and CHINs throughout the breeding season of 2018, while the greatest intraspecific difference in UDs was observed for CHINs between early and late breeding the same year. Compared to the early breeding periods in 2015 and 2018, both MACs and CHINs were foraging closer to the nest site during the late breeding periods in 2015 and 2018. Compared to 2015, both species displayed larger UDs in the early breeding period in 2018 and smaller UDs in the late breeding period in 2018.

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Table 3 Mean maximum dive depth (m) and mean dive duration (s) of foraging dives, with associated standard deviation, undertaken by MACs and CHINs in early (incubation and early brood) and late (late brood and crèche) breeding at Bouvetøya during the austral summers of 2015 and 2018.

Species/year	Early breeding				Late breeding			
	n (trips)	*n* (dives)	Max. depth (m)	Dive duration (s)	*n* (trips)	*n* (dives)	Max. depth (m)	Dive duration (s)
CHIN 2015	10	3035	36.6 ± 17.3	101 ± 25.5	33	4048	58.4 ± 24.8	125 ± 32.5
CHIN 2018	16	3597	24.2 ± 11.6	69.6 ± 23.0	45	2980	27.2 ± 14.9	65.9 ± 21.9
MAC 2015	15	3076	30.8 ± 18.3	90.2 ± 29.1	62	12 641	38.5 ± 21.3	98.5 ± 31.7
MAC 2018	24	5553	37.6 ± 16.7	95.1 ± 24.6	48	4368	43.4 ± 23.7	97.4 ± 29.3

two breeding seasons at Nyrøysa, Bouvetøya. At this location, Blanchet et al. (2013) investigated the potential for prey competition between three main krill predators at Bouvetøya (i.e., MACs, CHINs and Antarctic fur seals) over a single summer breeding season in 2007. These authors concluded that there was potential for competitive overlap among the three species, but that both spatial and temporal partitioning of foraging areas likely reduced direct competition (Blanchet et al. 2013). However, given the short duration of their study, temporal variation in niche overlap between the three species was not evaluated (see Waluda et al. 2010; Horswill et al. 2017 for examples). Our study clearly shows temporal variation in the foraging niche of MACs and CHINs within and between breeding seasons at the island, highlighting the importance of including both intra- and interseasonal variations when considering the possibility for prey competition. The foraging behaviour of breeding penguins is likely to reflect the increasing energy demands of their chicks as the breeding season progresses. In line with this expectation, we found that MACs and CHINs utilized larger foraging areas during early breeding in 2015 and 2018, when being less constrained by nest duties and free to travel for several days before returning. Both species then decreased their foraging range later in the breeding season as a result of having to return more regularly to the breeding site for chick provisioning as the chicks grow older (late brood and crèche) throughout our study. Despite this general trend, we found distinct differences in the foraging range of MACs and CHINs between the two breeding seasons, with both species utilizing larger foraging areas and travelling further offshore from Bouvetøya during late breeding in 2015 compared to late breeding in 2018. When prey is scarce, penguins are likely to increase their foraging range and utilize a larger section of the water column. Such responses to low prey availability have been linked to reduced spatial overlap, and thereby reduced prey competition, between sympatrically breeding penguin species elsewhere (Trivelpiece et al. 1987; Hindell et al. 1995; Mori & Boyd 2004). Hence, the larger foraging range of MACs and CHINs during the late breeding phase in 2015 may signal low prey densities in nearshore waters of Bouvetøya during this period. Still, MACs occupied nearly the entire horizontal foraging area of the CHINs throughout our study, highlighting the latter species' general lack of spatial niche segregation previously described by Blanchet et al. (2013).

As the breeding season progressed and adult penguins became more constrained in how long (and therefore how far) they could travel due to chick provisioning, both species appeared to increase their foraging efforts by diving deeper. CHINs in the latter stage of breeding in 2015 dove approximately 19 m deeper than during the breeding season of 2007 (Blanchet et al. 2013), and 31 m deeper than their conspecifics at the same stage in 2018. Most notably, CHINs in the late breeding season of 2015 dove deeper than MACs in 2007 (Blanchet et al. 2013), 2015 or 2018 (current study). This deeper diving effort was generally matched with longer dive durations of CHINs between 2015 and 2018, though dive durations in 2015 were not notably different from those in 2007 (Blanchet et al. 2013). In contrast, mean maximum dive depth of MACs showed little variation either during the period of this study or in comparison with 2007 (Blanchet et al. 2013), suggesting that MACs were consistently targeting prey at similar depths. In comparison, CHINs were likely searching for prey in deeper water layers in 2015, presumably because less prey were available close to the sea surface. Still, the vertical niche of the two species showed significant overlap throughout the breeding season in 2015, which may have resulted in increased competition for less abundant prey between MACs and CHINs breeding on Nyrøysa. Hence, CHINs may have faced challenges because of the need for increased foraging efforts in combination with interspecific competition during the 2015 breeding season.

The isotopic data support the notion that there was a shift in prey resources around Bouvetøya between 2015 and 2018. Considering each species separately, the differences in $\delta^{13}C$ between 2015 and 2018 could indicate foraging in different habitats. However, a much greater increase in foraging range, with less variability in $\delta^{13}C$, was detected for MACs between the two seasons. Therefore, a more likely explanation is that MACs and

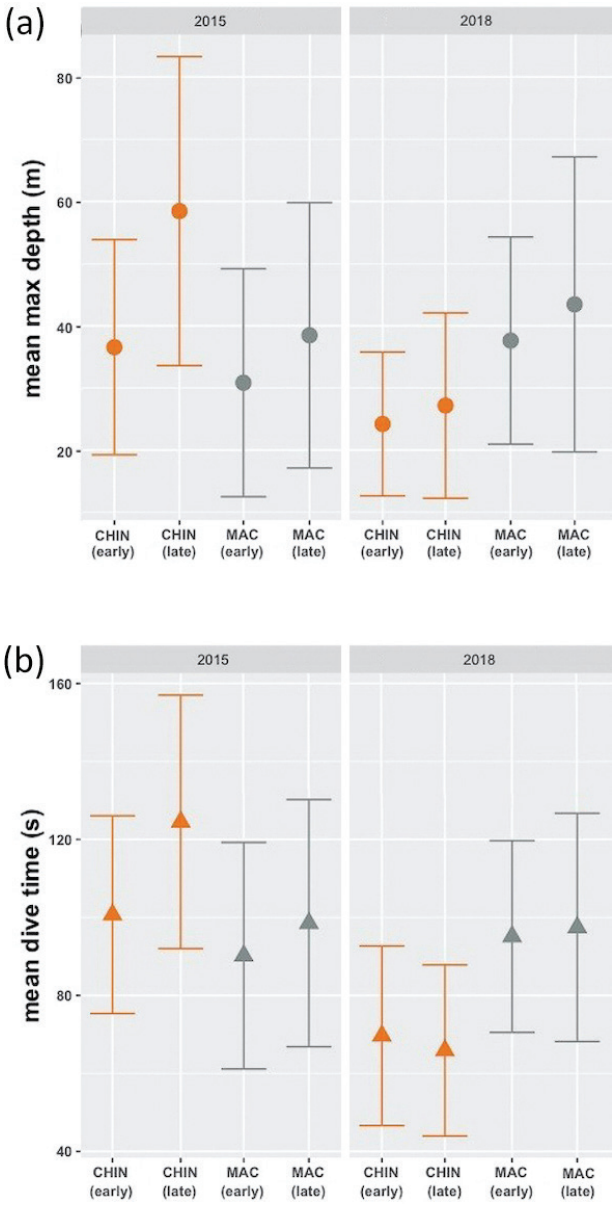

Fig. 3 Mean (a) maximum dive depth (m) and (b) dive duration (s), with associated standard deviation bars, for MACs and CHINs in early (incubation and early brood) and late (late brood and crèche) breeding at Bouvetøya during the austral summers of 2015 and 2018. The CHINs showed the greatest variation in dive behaviour (mean maximum depth and mean dive duration) between the two breeding seasons, while the MACs showed little variation in dive behaviour between 2015 and 2018.

CHINs were feeding on prey with slightly different carbon signals between breeding seasons. This assumption was supported by a clear difference in CHINs $\delta^{15}N$ data between 2015 and 2018. Assuming a 2‰ increase in $\delta^{15}N$ for each trophic level (Hobson & Welch 1992), during 2018 MACs likely consumed more prey from higher trophic levels compared to CHINs. Conversely, during the breeding season in 2015, CHINs exhibited the highest $\delta^{15}N$ values of any group in the study. The bathymetric features around Bouvetøya are thought to support high aggregations of krill (Krafft et al. 2010), and earlier dietary studies have found that CHINs nesting on Nyrøysa forage mainly on krill during the breeding season (Haftorn 1986; Niemandt et al. 2016). In contrast, MACs nesting on Nyrøysa have been found to forage on a wide selection of prey species, including myctophid fishes (>40% of the diet by mass) as well as krill and the abundant Southern Ocean krill (*Thysanoessa macrura*; Niemandt et al. 2016). Under the assumption that 2018 reflected a breeding season in which CHINs fed on krill and MACs were mixed-prey foragers, there are three possible explanations for the significant differences in $\delta^{15}N$ observed for CHINs in 2015. First, fish, being generally situated at a trophic level higher than krill, may serve as an alternative food resource for some species of Southern Ocean penguins when krill is at low densities (Croxall et al. 1988; Ichii et al. 2007; Miller & Trivelpiece 2008; Ratcliffe et al. 2018). As a result of the mesopelagic nature of myctophid fish, this alternative food resource is typically found in deeper water layers (Lishman & Croxall 1983; Miller & Trivelpiece 2008). Hence, the deeper foraging dives of the CHINs in 2015 could indicate that they were foraging on myctophid fish (Hobson & Welch 1992; Tierney et al. 2008). Second, 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 CHINs between 2015 and 2018. However, earlier dietary analysis of seals and penguins on Nyrøysa suggests little interannual variation in the size (a close proxy for age) of krill consumed by predators at Bouvetøya (Kirkman et al. 2000; Niemandt et al. 2016; Tarroux et al. 2016). Third, fasting or starving penguins are likely to display elevated blood and plasma levels of $\delta^{15}N$ (Cherel et al. 2005). Variation in $\delta^{15}N$ seen between study breeding seasons is also consistent with CHINs experiencing greater catabolism of their own tissues during the breeding season of 2015.

The annual density and distribution of krill are known to vary greatly at local scales in the Southern Ocean (Brierley et al. 2002; Miller & Trivelpiece 2008), but the frequency of low krill abundance events is unknown around Bouvetøya. Two earlier studies of predator diets did not detect clear evidence for krill scarcity in the area (Blanchet et al. 2013; Niemandt et al. 2016). Conversely, based on isotope data, Tarroux et al. (2016) proposed that low krill densities in 2015

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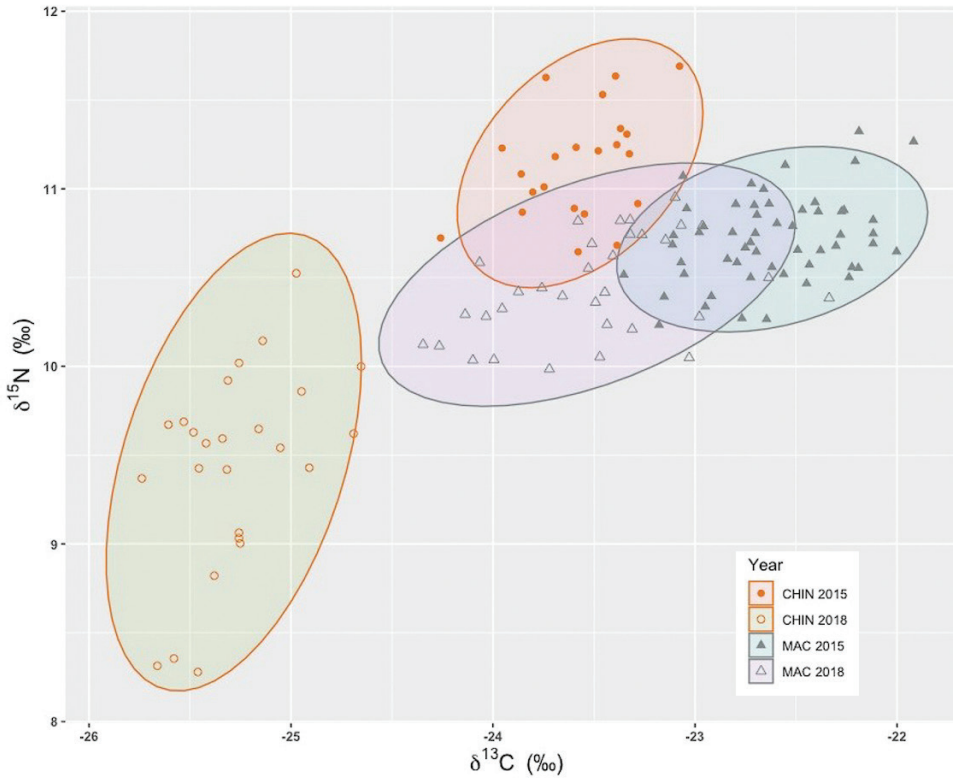

Fig. 4 Interannual variation in $\delta^{15}N$ and $\delta^{13}C$ values, with 95% confidence intervals drawn for means, in blood of MACs and CHINs breeding at Bouvetøya during the austral summers of 2015 and 2018. The CHINs showed the greatest variation in $\delta^{15}N$ and $\delta^{13}C$ between the two breeding seasons, suggesting a shift in prey consumed by the species in 2015 and 2018.

Table 4 Mean stable isotope measurements of $\delta^{15}N$ and $\delta^{13}N$ (‰), with associated standard deviation bars, and SEAc for MACs and CHINs breeding at Bouvetøya during the austral summers of 2015 and 2018.

Species/year	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	SEAc
CHIN 2015	11.1 ± 0.3	−23.6 ± 0.3	0.27
CHIN 2018	9.4 ± 0.6	−25.3 ± 0.3	0.46
MAC 2015	10.7 ± 0.2	−22.6 ± 0.3	0.24
MAC 2018	10.4 ± 0.3	−23.5 ± 0.5	0.39

likely led to Antarctic fur seals breeding on Nyrøysa targeting more fish and cephalopods, supporting the underlying mechanism that we suggest drove the behaviour of CHINs in 2015 in our study. The number of breeding pairs of CHINs has been decreasing on Nyrøysa over recent decades, during which intermittent monitoring has been taking place (Isaksen et al. 2000; Biuw et al. 2010). Competition for breeding space (Hofmeyr et al. 2005; Niemandt et al. 2016), destruction of nest sites by landslides and the killing of penguins in rockfalls, as well as aggressive encounters by Antarctic fur seals (Isaksen et al. 2000; Niemandt et al. 2016; pers. obs.), have all been proposed as possible explanations for the decreasing number of breeding CHINs at the Nyrøysa study site. However, given that these pressures are likely to impact both species equally, they fail to explain the differing population trajectories observed for MACs and CHINs at Nyrøysa (Biuw et al. 2010). Unlike CHINs, MACs are known to readily prey switch (Waluda et al. 2010), in addition to utilizing deeper water layers (Blanchet et al. 2013) and larger foraging areas during breeding (Thiebot et al. 2011; this study). This makes MACs potentially more flexible to changes in prey community composition and prey density while raising offspring. Another consideration is that Bouvetøya is located at the eastern distributional limit for CHINs. This could mean that at this site this species is living at the edge of its ecological niche, with little tolerance for fluctuations in krill densities. Consequently, when both species are constrained in how far they can travel, and under conditions of low krill availability, the mixed-prey foraging MACs are likely to gain a competitive advantage. Thus, increased interspecific competition arising from krill scarcity may lead to reduced individual fitness and reproductive performances for CHINs at Bouvetøya.

Conclusion

By describing the spatial and isotopic foraging ecology of MACs and CHINs over two complete breeding seasons, this study demonstrates that single-season studies characterizing levels of niche segregation may not be appropriate as they do not fully incorporate dynamic aspects typical of marine ecosystems. Although little is known regarding krill fluctuations/availability at Bouvetøya, low krill events may already be common enough to have driven the decline in breeding number of CHINs on Nyrøysa, possibly exacerbated by competition for food from sympatrically breeding MACs. The APF is predicted to move southwards as a response to increasing ocean temperatures (Gille 2002; Cristofari et al. 2018), resulting in a southward contraction of krill distribution towards the continent (Atkinson et al. 2019). Only a few hundred kilometres south of the APF, Bouvetøya is likely to fall outside the distribution range of krill in the future (Atkinson et al. 2004; Atkinson et al. 2006; Trathan et al. 2015), which may drive the breeding population of CHINs, the easternmost distributed of the species, to local extirpation.

Disclosure statement

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