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# Isotopic niche segregation during the non-breeding period in Black-faced Cormorants (*Phalacrocorax fuscescens*)

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**ABSTRACT**

Due to environmental changes, prey distribution and availability are predicted to change. This is expected to impact their predators, especially in the highly dynamic and fast-changing marine environment. To predict these impacts, knowledge of predator diets throughout the annual cycle is needed. During the breeding season, collecting diet samples from seabirds is relatively simple, but data on other periods are harder to obtain. To study trophic niche during the non-breeding period, stable isotopes extracted from feathers can be used as a proxy. Bulk stable isotope ratios of carbon ($^{13}C/^{12}C$), nitrogen ($^{15}N/^{14}N$) and sulphur ($^{34}S/^{32}S$) of feathers ($n = 96$), blood ($n = 10$) and gut content ($n = 56$) were combined with GPS tracking data ($n = 30$) to study the trophic niche, individual niche consistency and the link between non-breeding trophic niche and habitat use in Black-faced Cormorants (*Phalacrocorax fuscescens*). On the population level, a large range in isotope compositions (combination of C, N and S isotope ratios) was observed, indicating that individuals exploit diverse prey and habitats. However, comparing blood (breeding) and feather (non-breeding) stable isotope data from the same individuals revealed little within-individual variation in isotope compositions, indicating individual consistency in exploited prey or habitats. Tracking data revealed that $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values in feathers reflected whether an individual foraged in shallow or deeper habitats during the non-breeding period and may be used to monitor habitat use. This study provides further insights into the year-round diet and foraging of the poorly studied Black-faced Cormorant.

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Seabird; cormorant; Bass Strait; non-breeding period; stable isotopes

## Introduction

The consequences of climate change are likely to drastically alter the distribution and abundance of prey in many ecosystems, thereby affecting the predators relying on them (Wernberg *et al.* 2011; Bastille-Rousseau *et al.* 2018; Sadykova *et al.* 2020). Climate change can especially affect marine environments, where rapid changes in prey distribution and availability are predicted (Perry *et al.* 2005; Johnson *et al.* 2011). Such alterations to prey species are expected to have effects throughout the trophic web, eventually impacting top predators (Wernberg *et al.* 2011). To accurately predict how top predators might react to such changes in prey availability and distribution, it is crucial to collect data on their diets and trophic niches, as well as the factors influencing them throughout their annual cycle (Young *et al.* 2015).

During the breeding season, seabirds adopt a central place foraging strategy, returning regularly to the colony to provision their chicks (Schreiber and Burger 2001). In consequence, the trophic ecology of seabirds during this season is generally well studied because this behaviour facilitates collecting samples for dietary studies such as regurgitated prey remains, pellets of hard prey remains and scats (Barrett *et al.* 2007; Young *et al.* 2015). In contrast, during the non-breeding period, many seabirds move away from their breeding colony, remaining at sea for long periods, preventing the collection of direct information on their diet (Barrett *et al.* 2007; Young *et al.* 2015). The non-breeding period is typically a period of high nutritional stress and increased mortality due to decreased food availability (Schreiber and Burger 2001; Clairbaux *et al.* 2021). It is, therefore, important to obtain information on the trophic niche of seabird species during the non-breeding period to understand the factors that influence their ecology at this time (Barrett *et al.* 2007; Lewison *et al.* 2012). Such knowledge is important to predict how seabirds may respond to environmental changes (Young *et al.* 2015; Sadykova *et al.* 2020).

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Analysis of bulk stable isotope ratios of $^{13}C/^{12}C$, $^{15}N/^{14}N$ and $^{34}S/^{32}S$ in tissues can be used to study the diet (Hobson and Clark 1992; Hobson *et al.* 1994) and trophic niches of seabirds (Bearhop *et al.* 2004). Stable isotopes are incorporated at different timescales in various tissues and, thus, by analysing multiple tissues it becomes possible to study trophic niche over different time scales within individuals (Hobson and Clark 1992; Bond and Hobson 2012). For example, blood has a half-life of 11 days and integrates information on trophic niche over the previous 2–3-weeks while feathers reflect dietary inputs at the time they were grown (Hobson and Clark 1992; Bond and Hobson 2012). Additionally, data obtained from stable isotopes can be combined with tracking data to investigate whether the trophic niches differ between exploited areas (Meier *et al.* 2017; Campioni *et al.* 2022).

The Black-faced Cormorant (*Phalacrocorax fuscescens*), an Australian endemic seabird, breeds primarily on coastal islands in the south-east of the continent's mainland and Tasmania (Marchant *et al.* 1990; Brothers 2001). Throughout its breeding range, the number of large breeding colonies is limited, and breeding locations are patchily distributed (Marchant *et al.* 1990; Brothers 2001). In Bass Strait, the species is a winter breeder (June–October) which is thought to be linked to food availability (Taylor *et al.* 2013). During the non-breeding period (October–May), some Black-faced Cormorants remain in the area used during the breeding period (Cansse *et al.* 2024). However, other individuals have been recorded to move up to 320 km from the breeding colony, resulting in individuals being observed at low densities in coastal areas throughout their range (Marchant *et al.* 1990; Cansse *et al.* 2024).

Studies during the breeding season have revealed Black-faced Cormorants forage mainly on benthic fish (Taylor *et al.* 2013) and the areas they can exploit are restricted to shallow coastal areas by their aerobic dive limit (Cansse *et al.* 2024a). As the species is sexually dimorphic, the larger-sized males generally forage further from the coast and at deeper depths than females, leading to spatial sexual segregation in foraging habitat during both the breeding season and the non-breeding period (Cansse et al. 2024, 2024a). In addition, high individual foraging site fidelity has been observed during the breeding season both for males and females (Cansse *et al.* 2025). However, while inter-individual variation has been observed in the movements of both males and females from the natal colony during the non-breeding period (Cansse *et al.* 2024), it is not known whether these reflect individual trophic specialisations at this time.

South-eastern Australia is one of the fastest warming oceanic regions (Wernberg *et al.* 2011; Hoegh-Guldberg *et al.* 2019) and the anticipated oceanographic changes are expected to alter prey diversity, distribution and abundance (Perry *et al.* 2005; Johnson *et al.* 2011; Sadykova *et al.* 2020). Such changes to prey diversity, distribution and abundance could potentially greatly impact marine predators in the region. This is of particular concern for species which exhibit individual foraging specialisations in the diet or areas they exploit, as has been shown for Black-faced Cormorants during the breeding season, which are often less flexible in their foraging behaviour (Crawford *et al.* 2015; Merkle *et al.* 2022; Cansse *et al.* 2025). However, to predict how these species with individual foraging specialisations may respond to the anticipated environmental changes within its ecosystem, information on their trophic niche during the non-breeding period, as well as the temporal extent of individual specialisations in their trophic niche, is urgently needed (Chambers *et al.* 2011; Wernberg *et al.* 2011). Therefore, the aims of the present study were to investigate: the trophic niche; the individual trophic niche consistency; and the link between trophic niche and foraging habitat in Black-faced Cormorants during the non-breeding period.

## Materials and methods

### *Study site and field procedures*

The fieldwork was conducted on Notch Island (38°56′25″S 146°40′33″E), northern Bass Strait (south-eastern Australia), which hosts a Black-faced Cormorant colony of approximately 950 nests (Taylor *et al.* 2013). The Notch Island colony is the largest Black-faced Cormorant colony in northern Bass Strait (Brothers 2001; Taylor *et al.* 2013). Data collection occurred during chick-rearing (September–October) in 2020–2022. Adults rearing chicks aged approximately 20–40 days were captured with a noose-pole while attending the breeding colony.

After capture, a uniquely numbered metal leg band was applied to the left tarsus to identify individuals. Two body contour feathers were collected for molecular sexing and up to six body contour feathers were collected for stable isotope analysis. For five individuals in 2020, only one feather was available. Post-breeding moult of flight feathers for Black-faced Cormorants occurs between January and March (Marchant *et al.* 1990). Body contour feathers are assumed to moult at the same time and, therefore, reflect diet at the time of formation (Marchant *et al.* 1990; Hobson and Clark 1992; Bond and Hobson 2012). No moult was observed

in any captured individuals during the breeding period. Additionally, from a subset of individuals in 2022, a 1 mL blood sample was collected from a tarsus vein by venipuncture and stored in 70% ethanol to allow comparison of blood and feather stable isotopes for these individuals and assess individual trophic niche consistency (Hobson *et al.* 1997). If cormorants regurgitated voluntarily during handling, complete prey items were photographed and stored frozen (−20°C) for identification and stable isotope analysis.

To investigate potential links between trophic niche and foraging areas during the non-breeding period, a subset of 30 individuals (11 male, 19 female) was instrumented with GPS data loggers to determine their post-breeding movements over the three years of study (2020–2022) (Supplementary Table S1). Importantly, while feathers give information about the non-breeding period before deployment, GPS data loggers provide information about the non-breeding period after deployment and therefore information from these sources does not overlap in time. A solar-powered GSM-linked GPS data logger (Technosmart Gipsy (25 g, 1.4 ± 0.1% of body mass; 2020), Pathtrack GEO+GSM (20 g, 1.1 ± 0.1% of body mass; 2021, 2022) or Ornitela ornitrack 25 (25 g, 1.4 ± 0.1% of body mass; 2022) was attached to the central tail feathers with waterproof tape (TESA® 4651, Beiersdorf AG, Germany) or between the scapula with a harness that contained a weak link (Wilson *et al.* 1997; Clewley *et al.* 2021). GPS-GSM loggers were programmed to record a location every 10 min (2020 and 2022) or every 20 min (2021). Depending on the type of logger, the recorded GPS locations were transmitted every 12–96 h when within GSM range. The data loggers continued to transmit data until the device was lost due to moulting, tape detachment, device failure or breakage of the weak link. After all handling procedures, individuals were released near the edge of the colony to resume normal behaviour.

All animal handling procedures were in accordance with Deakin University Animal Ethics committee approvals (B12–2020, B34–2022) and Department of Energy, Environment and Climate Action (Victoria, Australia) wildlife research permits (10009521, 10010406). Access to the island was provided through a parks Victoria access agreement (AA0001127).

### Sample processing

Regurgitated prey were thawed and identified to the lowest taxonomic level possible with relevant guides and, where possible, confirmed with extracted otoliths (Lu and Ickeringill 2002; Gomon *et al.* 2008; Bray and Gomon 2023). Information on the habitat of occurrence for each prey species was obtained from the literature (Lu and Ickeringill 2002; Gomon *et al.* 2008; Bray and Gomon 2023). Only prey items which could be identified to sufficiently detailed taxonomical levels were incorporated in further analyses. All fish samples were identified at the minimum to the family level and, where possible, to the species level. Cephalopod samples were identified to the order. For identified samples, 1–4 g of flesh tissue was collected. Tissue from fish was sampled from one side of the body, posterior to the anus and above the lateral line. Tissue from cephalopods was taken from the base of the mantle. Tissue was only collected from prey items for which the sampling area was not damaged to avoid sample contamination with cormorant gastric juices. Subsequently, the tissue was dried at 50°C for 24–48 h in an oven. After drying, the sample was ground to a fine powder using a mortar and pestle.

Similarly, blood samples from the cormorants were dried at 50°C for 24–48 h before being ground to a fine powder. Feathers were rinsed in a 2:1 chloroform: methanol solution to clean and eliminate grease and subsequently air dried under a fume hood for 24–48 h (Hobson 1999). Subsequently, all samples were weighed and packed into individual tin cups for stable isotope analysis. For prey samples and a subset of feather samples for which $\delta^{34}S$ was analysed, an equal mass of tungsten trioxide ($WO_3$) powder was added to the tin cup.

Bulk stable isotope ratios of carbon ($^{13}C/^{12}C$), nitrogen ($^{15}N/^{14}N$) and sulphur ($^{34}S/^{32}S$) were measured in continuous flow using an elemental analyser coupled to an isotopic ratio mass spectrometer (EA-IRMS). When both bird blood and feathers were available, analyses were conducted at the Farquhar Laboratory of the Research School of Biology, Australian National University (Canberra, Australia) using CE1110 elemental analyser (Thermofisher, Italy) coupled with a Isoprime IRMS (Elementar, Germany). All other bird feather and prey samples were analysed for carbon ($^{13}C/^{12}C$), nitrogen ($^{15}N/^{14}N$) and sulphur ($^{34}S/^{32}S$) at the Laboratoire d'Ecologie Trophique et Isotopique (LETIS), University of Liège (Liège, Belgium) using a VarioMICRO Cube elemental analyser (Elementar, Germany) coupled with a PrecisION IRMS (Elementar, Germany).

Bulk stable isotope values were expressed in δ-notation as the deviation from standards in parts per mil (‰) according to the following equation:

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

where X is $^{13}C$, $^{15}N$ or $^{34}S$ and R is the corresponding ratio of $^{13}C$:$^{12}C$, $^{15}N$:$^{14}N$ or $^{34}S$:$^{32}S$. Rstandard values

were based on the international standards Vienna Pee Dee Belemnite for $\delta^{13}C$, atmospheric nitrogen ($N_2$) in air for $\delta^{15}N$ and the Canyon Diablo troilites for $\delta^{34}S$.

Certified reference materials from the International Atomic Energy Agency (IAEA), IAEA *N*-1 (ammonium sulphate; $\delta^{15}N = 0.4 \pm 0.2‰$; mean ± SD) and IAEA C-6 (sucrose; $\delta^{13}C = -10.8 \pm 0.5‰$) were included in the batch. Laboratory sulfanilic acid (Sigma-Aldrich; $\delta^{13}C = -28.5 \pm 0.3‰$; $\delta^{15}N = -0.4 \pm 0.3‰$; $\delta^{34}S = 1.3 \pm 0.5‰$) was used as quality control every 10 samples for sulphur. Replicated measurements spread every 10 samples provided standard deviations of ±0.3‰ for $\delta^{13}C$ and $\delta^{15}N$ and ± 0.4‰ for $\delta^{34}S$.

Where bird blood and feathers were available, six feathers were analysed for stable isotopes, as well as a blood sample. Preliminary analyses of these results, where values were obtained for six feathers for each bird, indicated little intra-individual variation within individuals (range individual SD $\delta^{13}C_{feathers}$: 0.08–0.72‰; range individual $\delta^{15}N_{feathers}$: 0.08–1.18‰) and subsequently only four feathers were analysed for the remainder of the birds sampled. Feather stable isotope samples were collected for a total of 96 individuals, including 10 individuals for which blood samples were also collected (Table 1). $\delta^{13}C$ and $\delta^{15}N$ values were available for all individuals. $\delta^{34}S$ data were only obtained for 59 individuals.

### Tracking data processing

The collected GPS tracks were split into trips using the *track2kba* package (Beal *et al.* 2021), with a 500 m buffer around the colony used as the threshold for the start and end of trips. During the post-breeding period, 22 individuals moved away from the colony to new roosts, which were islands and small islets (Cansse *et al.* 2024), from which they undertook central place foraging. For individuals which moved to a new roost, post-breeding foraging trips were considered to start and end at this location. Missing GPS points were linearly interpolated using the 'redisltraj' function in the *adehabitatLT* package (Calenge 2006) to match the programmed schedule (10 min in 2020 and 2022, and 20 min in 2022). Across all tracks, 20 ± 3.7% of the GPS points were missing (mean ± standard error). It was assumed that the non-breeding period started when the individuals that moved away from the breeding colony arrived at a new central place. In cases where this arrival was not on the same day they left the breeding colony, the period between leaving the breeding colony and arriving at the new central place was classified as the staging period. The non-breeding period of individuals which did not leave the breeding colony before the GPS logger ceased working was assumed to start at the median date other individuals left the breeding colony.

### Statistical analyses

A Shapiro-Wilk test was used to test for normal distribution of bulk stable isotope ratio in blood ($\delta^{13}C_{blood}$ and $\delta^{15}N_{blood}$) and feathers ($\delta^{13}C_{feathers}$, $\delta^{15}N_{feathers}$ and $\delta^{34}S_{feathers}$). This indicated that, except for $\delta^{34}S_{feathers}$, data were not normally distributed (see Results). Therefore, to determine whether bulk stable isotope values differed between males and females in blood, a Mann-Whitney-Wilcoxon test was used, with $\delta^{13}C_{blood}$ or $\delta^{15}N_{blood}$ as the dependent variable and sex as the grouping variable. Similarly, to investigate whether bulk stable isotope values differed between males and females in feathers, a Mann-Whitney-Wilcoxon test with $\delta^{13}C_{feathers}$ or $\delta^{15}N_{feathers}$ as dependent variables and sex as the grouping variable was used. As data for $\delta^{34}S_{feathers}$ was normally distributed, a Welch's t-test with $\delta^{34}S_{feathers}$ as dependent variable and sex as the grouping variable was used to test for differences between sexes. As multiple feathers were collected for most birds, the dependent variable ($\delta^{13}C_{feathers}$, $\delta^{15}N_{feathers}$ or $\delta^{34}S_{feathers}$) was the mean of all feathers collected for an individual bird.

For ten individuals where both feathers and blood were collected, the Pearson's correlation in bulk stable isotope values between feathers and blood was calculated, to investigate whether a shift in tropic niche

**Table 1.** Summary of the number of Black-faced Cormorant (*Phalacrocorax fuscescens*) individuals for which feather and blood samples were collected at Notch Island (Victoria, Australia) during the breeding season. A total of 96 feather samples and 10 blood samples were collected.

| | Male | | Female | |
|---|---|---|---|---|
| | Feathers | Blood | Feathers | Blood |
| 2020 | 4 | – | 11 | – |
| 2021 | 17 | – | 9 | – |
| 2022 | 28 | 4 | 27 | 6 |

occurred between the breeding season (blood) and the non-breeding period (feathers). Feathers are typically enriched in $^{13}C$ and $^{15}N$ compared to blood in seabirds (i.e. higher $\delta^{13}C$ and $\delta^{15}N$ values) (Quillfeldt *et al.* 2008). Therefore, to allow comparison of $\delta^{13}C_{blood}$ and $\delta^{15}N_{blood}$ values to those in feathers, the trophic discrimination factors for Kerguelen shags (*Leucocarbo verrucosus*) were used to obtain this correlation ($\delta^{13}C$: 1.55; $\delta^{15}N$: 1.04) (Cherel *et al.* 2014). This discrimination factor was chosen as Kerguelen shags are a marine cormorant of comparable size to Black-faced Cormorants. The TDF was added to the raw $\delta^{13}C$ and $\delta^{15}N$ values obtained from the blood samples. Unless mentioned otherwise, these corrected values are used in all analyses and reported values.

Subsequently, the link between non-breeding habitat (movement niche) and trophic niche was assessed. Although Black-faced Cormorants from the study site display different post-breeding movement strategies, individuals stay in small geographical areas during the non-breeding period (Cansse *et al.* 2024). Consequently, the collected GPS tracking data were used to categorise the non-breeding habitats of individuals as either migratory (individuals which left the area of the breeding colony) or as resident (individuals that stayed near the colony during the non-breeding period) (Cansse *et al.* 2024). As earlier analyses indicated that resident individuals either forage in shallow seagrass dominated areas or in areas further offshore (Cansse *et al.* 2024a), the resident individuals were divided into an inshore group (individuals foraging in the shallow Corner Inlet region during the non-breeding period) and coastal (individuals foraging in deeper areas). As no good habitat maps are available for the region, these classifications were based on the general area these individuals used. No individuals switched areas over the course of tracking data collection. The 50% kernel core range for all GPS locations during the non-breeding period was determined using the *adehabitatHR* package (Calenge 2011). Kernel core ranges were calculated for each non-breeding category (migratory, resident inshore or resident coastal) and the smoothing factor (*h*) was set to 0.1 to standardise it across groups.

A Shapiro-Wilk test was used to test for normal distribution of bulk stable isotope ratio in feathers ($\delta^{13}C_{feathers}$, $\delta^{15}N_{feathers}$ and $\delta^{34}S_{feathers}$) for the different non-breeding categories. As $\delta^{15}N_{feathers}$ values were not normally distributed (see Results), a Kruskal-Wallis test with mean individual $\delta^{15}N_{feathers}$ as the dependent variable, and non-breeding category as the grouping variable, was used to assess whether values in the feathers differed between the different categories of non-breeding behaviour. Subsequently, a Dunn's test with Bonferroni correction was used as a *post-hoc* test to assess between which spatial categories the $\delta^{15}N_{feathers}$ stable isotope values differed. $\delta^{13}C_{feathers}$ and $\delta^{34}S_{feathers}$ values were normally distributed for this subset of individuals (see Results). Hence, a one-way ANOVA was used to assess whether these values in the feathers differed between the different categories of non-breeding behaviour. Subsequently, a Tukey HSD test was used as a *post-hoc* test to assess between which spatial categories the $\delta^{13}C_{feathers}$ and the $\delta^{34}S_{feathers}$ stable isotope values differed.

Lastly, the stable isotope composition from collected prey samples was assessed to investigate the link between prey species, their habitat and potential links to the trophic niche during the non-breeding period. Due to a lack of data of where prey was captured, as well as a lack of trophic discrimination factors which allow to accurately compare prey tissue and feathers, this section was limited to visual comparisons of isotopic composition of prey species and feathers from individuals with tracking data. All data were processed and analysed in the R statistical environment (R Core Team 2022) (version 4.1.3).

## Results

Feather and blood bulk stable isotope values were distributed along a gradient from low $\delta^{13}C$ and high $\delta^{15}N$ values to high $\delta^{13}C$ and low $\delta^{15}N$ values (Figures 1 and 2). A Shapiro-Wilk test indicated $\delta^{13}C_{blood}$ and

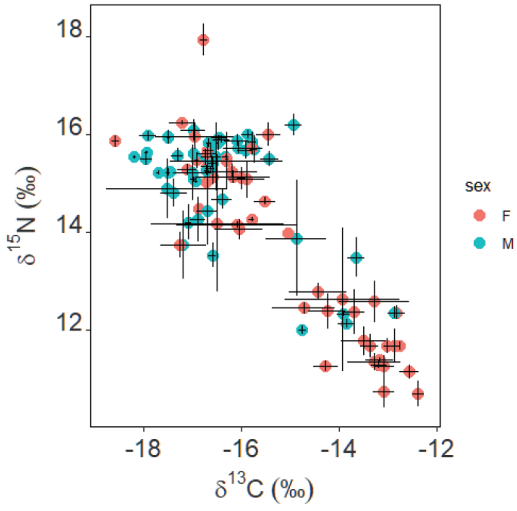


**Figure 1.** Mean bulk stable isotope values and their standard deviation for all Black-faced Cormorant (*Phalacrocorax fuscescens*) individuals for which feathers were collected at Notch Island (Victoria, Australia) over the three years of study. A total of 96 feather samples were collected. For five individuals, only one feather was collected and, hence, these have no standard deviation.

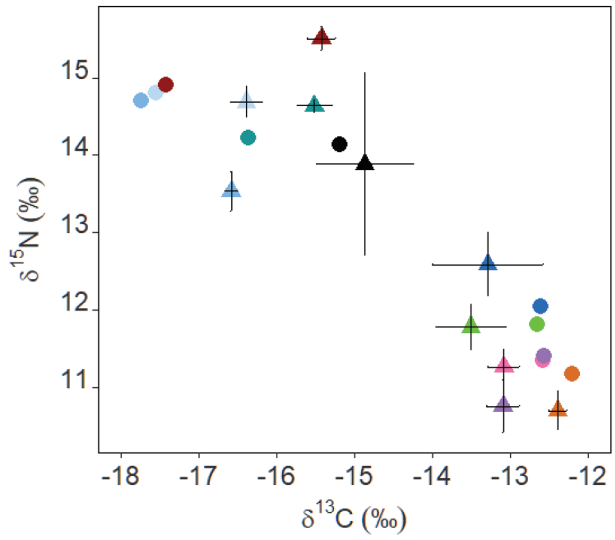


**Figure 2.** The $\delta^{13}C$ and $\delta^{15}N$ values for the 10 Black-faced Cormorants (*Phalacrocorax fuscescens*) for which both blood (circles) and feather (triangles) samples were collected in 2022 on Notch Island (Victoria, Australia). Different individuals are represented by different colours. To account for differences in fractionation between blood and feathers, $\delta^{13}C$ and $\delta^{15}N$ for blood were corrected using the discrimination factors for Kerguelen shags from Cherel *et al.* (2014). Corrected values for blood are plotted.

$\delta^{15}N_{blood}$ values were not normally distributed for males and $\delta^{13}C_{blood}$ values were not normally distributed for females [$\delta^{13}C_{blood}$ (Male: n = 4, W = 0.588, $p < 0.001$; Female: n = 6, W = 0.731, $p = 0.025$) and $\delta^{15}N_{blood}$ (Male: n = 4, W = 0.745, $p = 0.019$; Female: n = 6, W = 0.846, $p = 0.214$)]. In feathers, $\delta^{13}C$ and $\delta^{15}N$ values were not normally distributed for both sexes [$\delta^{13}C_{feathers}$ (Male: n = 45, W = 0.914, $p = 0.002$; Female: n = 41, W = 0.898, $p < 0.001$) and $\delta^{15}N_{feathers}$ (Male: n = 45, W = 0.921, $p = 0.003$; Female: n = 41, W = 0.792, $p < 0.001$)], however, they were normally distributed for $\delta^{34}S_{feathers}$ (Male: n = 31, W = 0.968, $p = 0.521$; Female: n = 28, W = 0.939, $p = 0.078$). A Mann-Whitney-Wilcoxon test indicated all stable isotope values differed significantly between males and females in feathers [$\delta^{13}C_{feathers}$ (W = 1703, $p < 0.001$), $\delta^{15}N_{feathers}$ (W = 643.5, $p < 0.001$)] and blood [$\delta^{13}C_{feathers}$ (W = 23, $p = 0.019$) and $\delta^{15}N_{feathers}$ (W = 1, $p = 0.019$)] (Supplementary Figures S1 and S2). A two-sided Welch's t-test indicated a significant difference in $\delta^{34}S_{feathers}$ values between male and female feathers (t = 4.056, df = 44.09, $p < 0.001$) (Supplementary Figure S1). Male feather samples were predominantly characterised by higher $\delta^{15}N_{feathers}$, higher $\delta^{34}S_{feathers}$ and lower $\delta^{13}C_{feathers}$ values, compared to female samples (Table 2, Figure 1). Similarly male blood samples were characterised by higher $\delta^{15}N_{blood}$ and lower $\delta^{13}C_{blood}$ values in comparison to female samples (Table 2). After application of the trophic discrimination factor (Cherel *et al.* 2014), comparisons of the stable isotope values for blood and feathers indicated that $\delta^{15}N$ and $\delta^{13}C$ values within individuals were similar between the two tissues (Figure 2, Supplementary Figure S3). Both the Pearson's correlation in $\delta^{15}N$ ($r = 0.95$, $p < 0.001$) and $\delta^{13}C$ ($r = 0.97$, $p < 0.001$) between blood, corrected for trophic enrichment, and feathers were high within individuals.

Post-breeding tracking data were available for 30 individuals for an average of 83.9 ± 11.2 days (range = 21–276 days) after the nominal end of chick-rearing. Individuals were categorised as resident inshore [8: 8 female (resident individuals foraging in the shallow Corner Inlet area)], resident coastal [15: 7 male, 8 female (resident individuals foraging further offshore)] and as migratory [7: 4 male, 3 female (individuals which left the area used during the breeding season)] (Figure 3a, Supplementary Table S1). A Shapiro-Wilk test indicated $\delta^{15}N_{feathers}$ values were not normally distributed for the resident inshore non-breeding category ($n = 8$, W = 0.784, $p = 0.019$) but were normally distributed for the other categories (migratory: $n = 7$, W = 0.981, $p = 0.965$; resident coastal: $n = 15$, W = 0.915, $p = 0.161$). Values were normally distributed for $\delta^{13}C_{feathers}$ (migratory: $n = 7$, W = 0.966, $p = 0.867$; resident inshore: $n = 8$, W = 0.879, $p = 0.186$; resident coastal: $n = 15$, W = 0.926, $p = 0.240$) and $\delta^{34}S_{feathers}$ (migratory: $n = 3$, W = 0.786, $p = 0.080$; resident inshore: $n = 5$, W = 0.887, $p = 0.344$; resident coastal: $n = 10$, W =

**Table 2.** Mean ± standard deviation of bulk stable isotopes ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$) for feathers and blood collected during the breeding season from Black-faced Cormorants (*Phalacrocorax fuscescens*) at Notch Island (Victoria, Australia). The number of individuals for which data for a specific isotope is available is reported next to the mean ± standard deviation. To account for differences in fractionation between blood and feathers, $\delta^{13}C$ and $\delta^{15}N$ for blood were corrected using the discrimination factors for Kerguelen shags from Cherel *et al.* (2014).

| | Male | | Female | |
|---|---|---|---|---|
| | Feather | Blood (corrected) | Feather | Blood (corrected) |
| $\delta^{13}C$ (‰) | −16.4 ± 1.2 ($n = 45$) | −17.0 ± 1.2 ($n = 4$) | −15.1 ± 1.7 ($n = 41$) | −13.2 ± 1.6 ($n = 6$) |
| $\delta^{15}N$ (‰) | 15.0 ± 1.1 ($n = 45$) | 14.6 ± 0.3 ($n = 4$) | 13.7 ± 1.9 ($n = 41$) | 12.0 ± 1.1 ($n = 6$) |
| $\delta^{34}S$ (‰) | 14.9 ± 1.8 ($n = 31$) | - | 12.3 ± 2.9 ($n = 28$) | - |

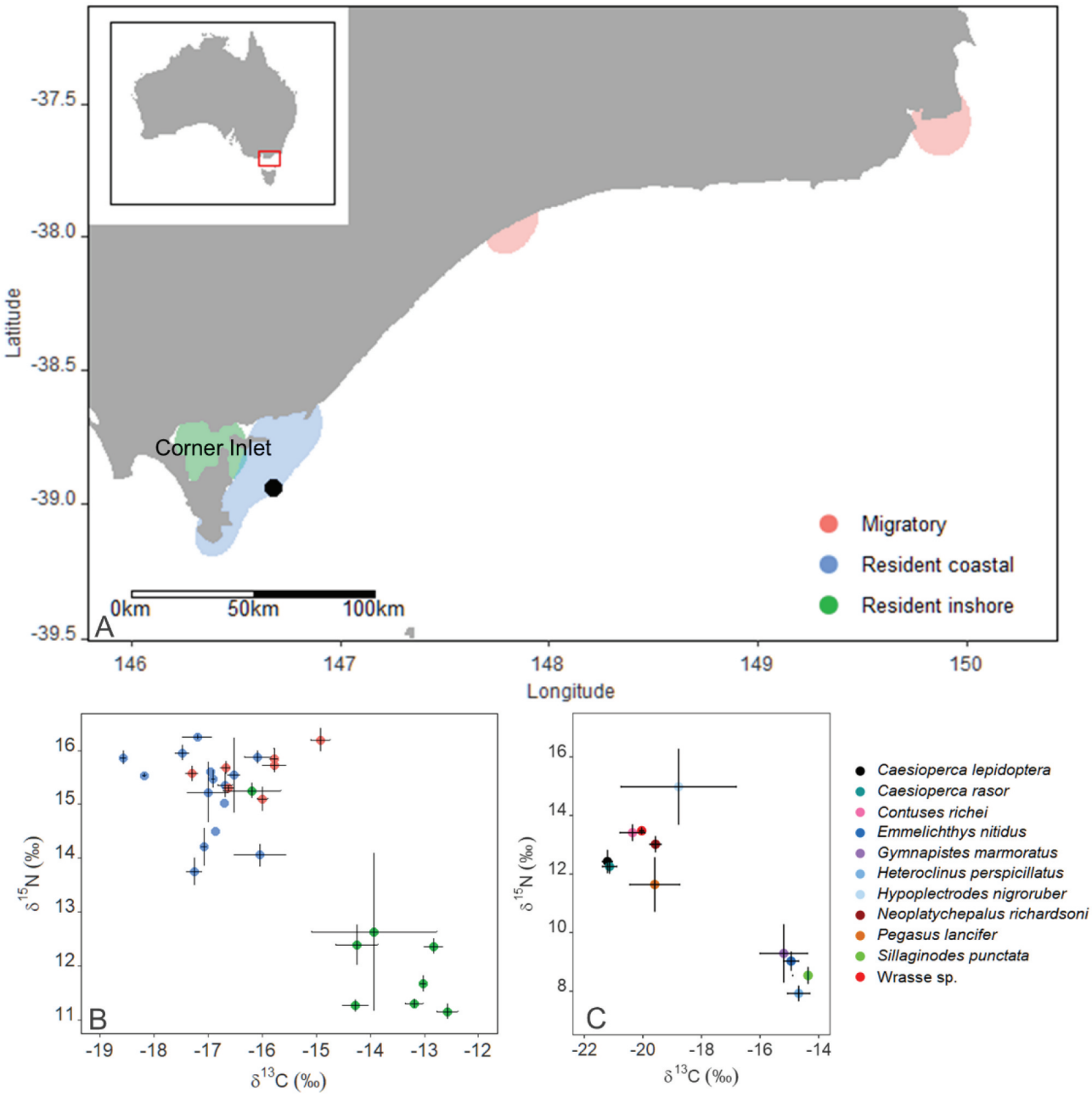


**Figure 3.** (a) The 50% kernel utilisation distribution for GPS locations collected from 30 Black-faced Cormorants (*Phalacrocorax fuscescens*) (11 male and 19 female) in each non-breeding category during the early non-breeding period. The categories are: resident inshore (green), resident coastal (blue) and migratory (red). Tracking data for males and females was combined. The black circle represents the breeding colony on Notch Island (Victoria, Australia); (b) relationship between $\delta^{13}C$ and $\delta^{15}N$ values observed in feathers and the locations used during the non-breeding period: resident inshore (green), resident coastal (blue) and migratory (red); and (c) mean bulk stable isotope values for prey species and taxonomic groups where multiple samples were available.

0.928, $p = 0.432$) for all non-breeding categories. A Kruskal-Wallis test indicated significant effects of the non-breeding category on $\delta^{15}N_{feathers}$ values ($\chi^2 = 18.40$, df = 2, $p < 0.001$). The Dunn's post-hoc test with Bonferroni correction indicated significant differences in $\delta^{15}N_{feathers}$ ($Z = 3.55$, $p_{adj} = 0.001$) values between migratory and resident inshore birds (Supplementary Figure S4). There were significant differences in $\delta^{15}N_{feathers}$ ($Z = -3.29$, $p_{adj} = 0.003$) between resident coastal birds and resident inshore birds. However, there were no differences for $\delta^{15}N_{feathers}$ ($Z = 0.87$, $p_{adj} = 1.000$) values between resident coastal birds and migratory birds (Table 3, Figure 3b). A one-way ANOVA indicated significant effects of the non-breeding category on $\delta^{13}C_{feathers}$ ($F_{2,27} = 38.2$, $p < 0.001$) and $\delta^{34}S_{feathers}$ ($F_{2,15} = 11.67$, $p < 0.001$) values. The Tukey post-hoc test indicated significant differences in $\delta^{13}C_{feathers}$

**Table 3.** Mean ± standard deviation of bulk stable isotopes ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$) for feathers collected from Black-faced Cormorants (*Phalacrocorax fuscescens*) at Notch Island (Victoria, Australia) during the breeding season for each non-breeding category. The number of individuals for which data for a specific isotope is available is reported next to the mean ± standard deviation.

| | Resident inshore | Resident coastal | Migratory |
|---|---|---|---|
| $\delta^{13}C$ (‰) | −13.78 ± 1.17 ($n = 8$) | −17.03 ± 0.68 ($n = 15$) | −16.15 ± 0.78 ($n = 7$) |
| $\delta^{15}N$ (‰) | 12.25 ± 1.34 ($n = 8$) | 15.21 ± 0.75 ($n = 15$) | 15.63 ± 0.36 ($n = 7$) |
| $\delta^{34}S$ (‰) | 11.63 ± 1.45 ($n = 5$) | 15.01 ± 1.30 ($n = 10$) | 14.49 ± 0.78 ($n = 3$) |

(95% CI = 1.28–3.47, $p < 0.001$) and $\delta^{34}S_{feathers}$ (95% CI = −5.30–−0.40, $p = 0.021$) values between migratory and resident inshore birds (Supplementary Figure S4). There were also significant differences in $\delta^{13}C_{feathers}$ (95% CI = 1.28–3.47, $p < 0.001$) and $\delta^{34}S_{feathers}$ (95% CI = −4.18–2.33, $p < 0.001$) between resident coastal birds and resident inshore birds (Supplementary Figure S4). However, there were no differences in $\delta^{13}C_{feathers}$ (95% CI = −1.85–0.09, $p < 0.079$) and $\delta^{34}S_{feathers}$ (95% CI = −1.68–2.73, $p = 0.813$) values between resident coastal birds and migratory birds (Table 3, Figure 3b, Supplementary Figure S4). All but one of the resident inshore birds had lower $\delta^{15}N_{feathers}$ and higher $\delta^{13}C_{feathers}$ values compared to resident coastal and migratory birds (Table 3, Figure 3b). Resident inshore birds were generally characterised by lower $\delta^{34}S_{feathers}$ values compared to resident coastal birds and migratory birds (Table 3).

Stable isotope values were collected from 56 prey samples belonging to 19 species/taxonomic groups (Table 4). The $\delta^{13}C$ of prey samples was negatively correlated with $\delta^{15}N$, similarly to those of feather and blood samples (Figure 3c). However, the absolute values differed between feathers and prey, as no trophic discrimination factors were available to allow an exact comparison of prey and feather values. Except for redbait (*Emmelichthys nitidus*) and ocean perch (*Helicolenus percoides*), both infrequently observed prey species, all prey with low $\delta^{15}N$ and high $\delta^{13}C$ values were seagrass or sandy habitat associated species (Table 4, Figure 3c). However, these values could also correspond to shallower and more coastal areas. On the contrary, most species with high $\delta^{15}N$ and low $\delta^{13}C$ were pelagic, reef or rock habitats associated species (Table 4, Figure 3c). This could also correspond to deeper and less coastal zones. Similarly, except for redbait and Australasian snapper (*Pagrus auratus*), species with low $\delta^{34}S$ values were associated to seagrass and sandy habitats, while reef associated species occurring

**Table 4.** Bulk stable isotope values from opportunistically collected prey of Black-faced Cormorants (*Phalacrocorax fuscescens*) at Notch Island, Victoria, Australia. For prey identified to the species level, the habitat is also reported (obtained from Bray and Gomon (2023)).

| Species | Mean $\delta^{13}C$ (‰ VPDB) | SD $\delta^{13}C$ (‰ VPDB) | Mean $\delta^{15}N$ (‰ AIR) | SD $\delta^{15}N$ (‰ AIR) | Mean $\delta^{34}S$ (‰ CDT) | SD $\delta^{34}S$ (‰ CDT) | n | Habitat |
|---|---|---|---|---|---|---|---|---|
| *Caesioperca lepidoptera* (Butterfly perch) | −21.21 | 0.16 | 12.42 | 0.38 | 18.77 | 0.36 | 3 | Rocky reefs, outcrops & drop-offs |
| *Caesioperca razor* (Barber perch) | −21.13 | 0.24 | 12.25 | 0.23 | 19.24 | 0.52 | 3 | Rocky reefs, outcrops & drop-offs |
| *Contusus richei* (Barred toadfish) | −20.35 | 0.42 | 13.41 | 0.27 | 16.67 | 0.86 | 4 | Sandy, weedy areas |
| *Emmelichthys nitidus* (Redbait) | −14.94 | 0.25 | 9.025 | 0.32 | 10.25 | 1.26 | 2 | Pelagic offshore |
| *Gymnapistes marmoratus* (Soldier) | −15.18 | 0.81 | 9.28 | 0.98 | 12.84 | 1.31 | 14 | Seagrass beds, sandy areas |
| *Helicolenus percoides* (Ocean perch) | −15.25 | – | 8.84 | – | 12.35 | – | 1 | Reef associated/sandy areas |
| *Heteroclinus perspicillatus* (Common Weedfish) | −14.68 | 0.38 | 7.92 | 0.25 | 13.84 | 0.45 | 4 | Reef associated, seagrass, algal beds |
| *Hypoplectrodes nigroruber* (Banded seaperch) | −18.78 | 1.96 | 14.98 | 1.28 | 16.88 | 1.07 | 2 | Reef associated |
| *Hyporhamphus* sp. (Halfbeak sp.) | −19.98 | – | 13.22 | – | 17.65 | – | 1 | |
| *Monacanthidae* sp. (Leatherjacket sp.) | −19.57 | – | 12.97 | – | 18.94 | – | 1 | |
| *Neoplatycephalus richardsoni* (Tiger flathead) | −19.57 | 0.19 | 13.01 | 0.26 | 15.95 | 0.99 | 3 | Sandy & silty bottoms |
| Octopus sp. | −18.11 | – | 9.57 | – | 14.75 | – | 1 | |
| *Pagrus auratus* (Australasian snapper) | −16.41 | – | 11.94 | – | 11.84 | – | 1 | Reef associated |
| *Parapercis ramsayi* (Spotted grubfish) | −18.88 | – | 12.96 | – | 19.04 | – | 1 | Reef associated, sandy areas |
| *Parequula melbournensis* (Silverbelly) | −21.06 | – | 14.35 | – | 16.81 | – | 1 | Sandy, silty, seagrass areas |
| *Pegasus lancifer* (Sculptured seamoth) | −19.59 | 0.85 | 11.64 | 0.92 | 16.75 | 1.19 | 7 | Sandy, muddy bottoms |
| *Sillaginodes punctatus* (King George whiting) | −14.36 | 0.52 | 8.53 | 0.28 | 14.88 | 0.80 | 3 | Seagrass, sandy areas |
| *Triglidae* sp. (Gurnard sp.) | −16.19 | – | 10.99 | – | 13.38 | – | 1 | |
| *Labridae* sp. (Wrasse sp.) | −20.04 | 0.07 | 13.48 | 0.11 | 18.03 | 0.51 | 3 | |

in deeper and less coastal zones had higher $\delta^{34}S$ values in comparison (Table 4).

## Discussion

Here, stable isotopes, regurgitated prey and tracking data were used to investigate the trophic ecology of Black-faced Cormorants during the breeding and non-breeding periods. At the population level, a large range in isotope compositions was observed, showing that Black-faced Cormorants exploit diverse habitats and diverse prey. Combining stable isotope data with non-breeding tracking data indicated that $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values differed between resident inshore and resident coastal foraging individuals, and could therefore be used to investigate non-breeding habitat.

### *Trophic niche and niche consistency in Black-faced Cormorants*

Differences in trophic niche were observed between the sexes, with males having significantly lower $\delta^{13}C$ values, and significantly higher $\delta^{15}N$ and $\delta^{34}S$ values than females. In the marine environment, increasing $\delta^{13}C$ values are associated with more inshore and more benthic foraging (Fleming *et al.* 2018). Similarly, increasing $\delta^{34}S$ values indicate an increase in the pelagic influence on the exploited habitat or prey species (Fry and Chumchal 2011). This is consistent with previous studies that have shown Black-faced Cormorant males forage in deeper water habitats than females during both the breeding season and non-breeding period (Cansse et al. 2024, 2024a). $\delta^{15}N$ values were higher for males than females, which could indicate a higher trophic position (Hobson *et al.* 1994). However, no habitat specific baseline data were available and, therefore, differences in $\delta^{15}N$ values might predominantly be affected by habitat type in the present study. Sex differences in trophic niche have also been observed in South Georgian Shags (*Leucocarbo georgianus*), Kerguelen Shags (*Leucocarbo verrucosus*) and Imperial Shags (*Leucocarbo atriceps*) (Bearhop *et al.* 2006; Michalik *et al.* 2013). Such differences in trophic niche could potentially lead to sex-specific impacts of alterations to prey availability or distribution due to environmental perturbations (Gianuca *et al.* 2019); for example, when the habitat or prey species exploited by one sex is more vulnerable to environmental changes. Such impacts of changing prey availabilities on a single sex could affect population sex ratios and eventually lead to reductions in reproductive success on the population level.

The low standard deviation in feather $\delta^{15}N$ and $\delta^{13}C$ values observed in individual Black-faced Cormorants in the present study suggests low variation in trophic niche throughout the period feathers were moulted and synthesised. This low standard deviation is consistent with previous studies which revealed both male and female Black-faced Cormorants largely remain within a narrow geographic area throughout the non-breeding period (Cansse *et al.* 2024). For individuals where bulk stable isotope data for both blood and feathers were available, fractionation-corrected $\delta^{15}N$ and $\delta^{13}C$ levels were found to be comparable between these tissues. This similarity between tissues likely indicates that, on the individual level, birds feed on similar prey, and likely also in similar habitats during the breeding season and the non-breeding period. This is consistent with previous tracking studies which have shown that Black-faced Cormorants feed at comparable depths between the breeding season and non-breeding period (Cansse *et al.* 2024), and the larger size of males allows them to dive deeper than females (Cansse *et al.* 2024a). Similar findings have also been reported for South Georgian and Kerguelen shags (Bearhop *et al.* 2006).

The individual consistency in trophic niche (this study) and the similarity in habitat use between the breeding season and non-breeding period (Cansse *et al.* 2024) suggests long-term individual consistency in trophic niche and habitat use in Black-faced Cormorants. However, there was high inter-individual variation in trophic niche and habitats used (Cansse et al. 2024, 2024a). This is consistent with Black-faced Cormorants being individually specialised in the prey or habitat they exploit, while being part of a generalist population (Bolnick *et al.* 2003).

### *Habitat use and prey species*

For the 30 individuals for which tracking data were available during the non-breeding period, all individuals which had low $\delta^{15}N$, low $\delta^{34}S$ and high $\delta^{13}C$ values foraged in shallow inshore areas characterised by extensive seagrass fields during the non-breeding period (Lucieer *et al.* 2019). These differences in stable isotope values can be explained by the link of $\delta^{34}S$, which increases with increases in the pelagic influence on the food web, and $\delta^{13}C$, which decrease with increasing distance from the coast (Connolly and Schlacher 2013; Fleming et al. 2018; Fry and Chumchal 2011). The stable isotope composition for these resident inshore individuals differed from those of migratory and resident coastal birds, indicating individuals foraging in these areas likely consumed different prey. Migratory individuals and resident coastal individuals did not show significant differences for any stable isotopes. This

suggests that differences in stable isotope values can be partly driven by exploited habitat types in different areas, but differences could also be partly driven by differences in baseline values between areas and further research is required to elucidate this.

The stable isotope values in the sampled feathers represent the trophic niche of individuals in the year prior to when the GPS tracking data were collected. Previous studies have suggested Black-faced Cormorant individuals display inter-annual consistency in non-breeding period habitat use (Cansse *et al.* 2024). Therefore, the link between stable isotope compositions and foraging location (inshore or deeper coastal regions) likely indicates individuals consistently use either inshore or deeper coastal regions across multiple non-breeding periods. For most individuals, tracking data was only available for the early non-breeding period due to the device being lost or due to the device ceasing to transmit data. However, tracking data collected for the entire non-breeding period indicates individual animals stay within the same area for the entire non-breeding period (Cansse *et al.* 2024). Therefore, the areas used during the early non-breeding period are likely representative for the entire non-breeding period of an individual.

Stable isotope values for prey samples were distributed along the same gradient which was observed for feather and blood samples. However, due to a lack of baseline data, or trophic discrimination factors between prey and feathers, no detailed comparisons in values could be made. Similarly to the feather and blood samples, most prey species either had high $\delta^{15}N$, high $\delta^{34}S$ and low $\delta^{13}C$ values or low $\delta^{15}N$, low $\delta^{34}S$ and high $\delta^{13}C$ values. While prey species with higher $\delta^{13}C$ and lower $\delta^{34}S$ values are predominantly associated with seagrass habitats (Bray and Gomon 2023), species with low $\delta^{13}C$ and high $\delta^{34}S$ values are predominantly associated with rocky habitats, reefs or soft sediments (Bray and Gomon 2023). This is consistent with expected trends in $\delta^{13}C$ and $\delta^{34}S$ values in the marine environment (Fry and Chumchal 2011; Fleming *et al.* 2018).

Although little information on baseline stable isotope levels is available from the region, earlier work indicated high $\delta^{13}C$ values in particulate organic matter outflow from Corner Inlet, a shallow bay to the northwest of the colony which contains extensive seagrass fields (Davenport and Bax 2002; Lucieer *et al.* 2019). This area is intensively used as a foraging habitat during the breeding season and during the non-breeding period by the resident inshore birds (Cansse et al. 2024, 2024a). Therefore, this is likely where the seagrass associated prey species were captured, which is also indicated by the observation that the majority of the birds which spent the non-breeding period in this area had high $\delta^{13}C$ and low $\delta^{34}S$ values in their feathers. However, further work on stable isotope baseline values in the region is required to confirm if differences in values between individual exploiting different areas are a result of a different diet or if these are driven only by differences in the baselines.

In summary, Black-faced Cormorants breeding at Notch Island were found, at the population level, to feed on a large range of prey inhabiting different coastal habitat during the non-breeding period. However, individual birds showed limited variation in their trophic niche over the moulting period and between the breeding season and the non-breeding period, suggesting long-term individual trophic specialisations. Lastly, feather stable isotope values reflected whether Black-faced Cormorants foraged inshore or in deeper coastal regions during the non-breeding period and indicated a potential inter-annual consistency in habitat use. Therefore, stable isotope composition of tissues could potentially be used to monitor and assess future changes in habitat use in Black-faced Cormorants during the breeding and non-breeding period.

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## Disclosure statement

No potential conflict of interest was reported by the author(s).

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## Data availability statement

Part of the tracking data used in this study were collected as part of an environmental impact assessment for a proposed offshore windfarm development. Contractual obligations require the raw data to be kept confidential until the impact assessment is complete. Once this process is complete, we intend to make the data available in the Birdlife International seabird tracking data base. Stable isotope data presented in this study are available as supplementary material.

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