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Spatial consistency affects foraging effort in a benthic diving seabird, the Black-faced Cormorant

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For animals which exploit predictable food resources, greater foraging site fidelity has been hypothesized to lead to increased foraging efficiency. However, evidence for this in free-ranging species is limited. In the present study, foraging site fidelity, the factors influencing it and its effect on foraging effort were investigated in the Black-faced Cormorant *Phalacrocorax fuscescens*, a predominantly benthic forager occurring in southeastern Australia. While the study population was found to have a relatively large foraging range, individuals were highly consistent in the smaller foraging areas which they used. Foraging effort was lower in individuals with a higher foraging site fidelity, which is likely to indicate increased foraging efficiency. Foraging site fidelity differed greatly between individuals but none of the assessed factors (sex, mass, size or year of study) were found to have a significant influence. This might indicate that intrinsic factors which could not be assessed, such as personality or experience, may influence the degree to which individuals exploit known habitats. The findings suggest that changes in prey availability or distribution could result in reduced foraging efficiency and, consequently, negative impacts for the species. Further investigation is required to assess within-individual foraging plasticity to predict potential responses to changing prey availability and distribution.

Keywords: biologging, cormorant, foraging consistency, foraging effort, seabird.

Optimal foraging theory predicts that animals will aim to optimize their foraging efficiency, both by minimizing time and energy invested in foraging, as well as by maximizing collected resources over time (Schoener 1971, Ydenberg *et al.* 1994). To do so, individuals can employ different strategies, such as targeting prey with a high energetic content, targeting patches of high prey abundance, and specialization towards certain foraging habitats or prey types, to minimize the time needed to find or capture prey (MacArthur & Pianka 1966, Stephens *et al.* 2008, Baert *et al.* 2021). Species with a large niche width are considered to be generalists while those with a narrow niche width are classified as specialists (Bolnick *et al.* 2003). Some species have a large niche width at the species level but have populations comprising individuals with narrow niche widths that each exploit different resources (Araújo *et al.* 2011).

When the abundance and distribution of resources is highly variable, generalist individuals are believed to have an advantage over specialists as their capacity to switch between available resources can lead to more consistent reproductive outputs (Partridge & Green 1987, Terraube *et al.* 2011, Korpimäki *et al.* 2020). Conversely, when resources are limited in abundance but have a high spatial and temporal predictability, it can be advantageous for individuals to exhibit high levels of foraging site fidelity (i.e. revisit the same location repeatedly for foraging) and resource specialization (Switzer 1993, Tinker *et al.* 2008).

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[Correction added on 21 January 2025, after first online publication: The copyright line was changed.]

Such specialization can reduce the time and energy spent searching for prey, for example through increased site familiarity or through an increase in prey capture success, thereby increasing foraging efficiency (Switzer 1993, Terraube *et al.* 2014, Araujo & Moura 2022).

As a consequence of anthropogenic impacts on the environment, individual foraging specialization and the associated site fidelity potentially could have deleterious effects, both at the individual and population levels (Merkle *et al.* 2022). For example, Northern Elephant Seal *Mirounga angustirostris* individuals with a high and low site fidelity performed similarly over the long term. However, having a high site fidelity became maladaptive under anomalous climate conditions, whereas low site fidelity became advantageous (Abrahms *et al.* 2018). Consequently, site fidelity can act as an ecological trap in some species, for example as a result of a decline in habitat quality or food availability at formerly good-quality sites (Ekroos *et al.* 2012, Kloskowski 2021).

Foraging site fidelity between individuals can differ by underlying factors such as individual experience (Votier *et al.* 2017), personality (Harris *et al.* 2020) and sex (Phillips *et al.* 2017). However, these individual differences are often closely tied to the foraging ecology of the species as well as the habitat type they use (Phillips *et al.* 2017). Consequently, the level of specialization, the factors influencing it or its consequences on their foraging behaviour are not well understood for most species (Ceia & Ramos 2015). The degree of foraging site fidelity can be used as a metric to quantify individual foraging specialization (Carneiro *et al.* 2017). This can subsequently be linked to intrinsic (such as sex, size or mass) or extrinsic (such as year of study) factors to understand the drivers of individual differences, as well as to foraging effort to understand the consequences of foraging specialization on foraging efficiency (Toscano *et al.* 2016, Carneiro *et al.* 2017, Ramellini *et al.* 2022).

In the marine environment, prey resources are highly variable in their distribution and abundance. This is especially the case for pelagic prey which can reach high abundances but are highly variable, both spatially and temporally (Gende & Sigler 2006, Dänhardt & Becker 2011). In contrast, benthic prey have lower abundances but their distribution is predictable at smaller spatial scales than pelagic prey (Litzow *et al.* 2004, Riverón *et al.* 2021, Filatova *et al.* 2022). Consequently, through experience, benthic foragers may gain knowledge of profitable foraging patches which, in turn, can lead to the development of foraging specializations which enhance efficiency (Werner *et al.* 1981, Hines *et al.* 1997, Riverón *et al.* 2021). However, due to oceanographic impacts of climate change, the distribution, diversity and abundance of prey in the marine environment are expected to be altered (Perry *et al.* 2005, Johnson *et al.* 2011). These changes could especially impact benthic foragers, which can exhibit foraging specializations at smaller spatial scales than pelagic foragers (Weimerskirch 2007, Ceia & Ramos 2015, Merkle *et al.* 2022).

Cormorants are a group of diving birds living in marine and freshwater environments across the world (Nelson 2005). The majority of species exclusively exploit marine environments where they feed predominantly on benthic fish species (Nelson 2005). As benthic foragers feeding on prey with relatively high levels of predictability, several species of cormorants have been shown to have high levels of individual foraging specializations at several temporal scales (Bearhop *et al.* 2006, Camprasse *et al.* 2017, Morgan *et al.* 2019, Fijn *et al.* 2022). While this foraging specialization and consistency is often assumed to have positive impacts on foraging efficiency, its effects have only rarely been studied in cormorants (Morgan *et al.* 2019).

The Black-faced Cormorant *Phalacrocorax fuscescens*, Australia's only endemic cormorant species, has a breeding distribution stretching across the continent's southeastern coast (Nelson 2005). This region is experiencing some of the fastest oceanic warming in the world, which is predicted to impact the distribution, diversity and abundance of marine prey (Perry *et al.* 2005). The species forms colonies on offshore islands ranging in size from a few birds to more than a thousand breeding pairs (Marchant *et al.* 1990), and forages exclusively in the marine environment (Nelson 2005). Previous studies have revealed that the Black-faced Cormorant is primarily a benthic forager, with maximum foraging depths constrained by its body mass-influenced aerobic dive limit (Cansse *et al.* 2024). The species is sexually dimorphic (Riordan & Johnston 2013) and, consequently, the larger males can forage in deeper regions which results in sexual segregation of foraging areas during the breeding season. Preliminary reports suggest that the Black-faced Cormorant displays individual consistency in its spatial habitat use and dive depths during the breeding season (Cansse *et al.* 2024), yet the degree of inter-individual variability in specialization, or its consequences, are not known. Such information is crucial for understanding foraging efficiency and predicting potential responses of the Black-faced Cormorant to the anticipated climate change-induced alterations in the southeastern Australia oceanic region (Chambers *et al.* 2011, Hobday & Lough 2011, Merkle *et al.* 2022).

The aims of the present study, therefore, were to: (1) determine the level of individual foraging site fidelity; (2) investigate potential factors influencing such behavioural consistency; and (3) assess its consequences for foraging effort and efficiency in Black-faced Cormorants.

METHODS

Fieldwork data collection

The study was conducted at Notch Island (38°56′25″S, 146°40′33″E), northern Bass Strait, southeastern Australia. The island hosts a Black-faced Cormorant colony of approximately 950 nests (Taylor *et al.* 2013). Data collection occurred during chick-rearing (September to October) between 2020 and 2023. Adults rearing chicks aged approximately 20–40 days were captured with a noose-pole when they returned to the breeding colony after a foraging trip. Individuals were weighed in a cloth bag using a spring scale (±25 g, Salter, Bristol, UK) and morphometric measurements (culmen length, bill length, tarsus length and bill depth) were taken using vernier callipers (±0.1 mm). Two body contour feathers were collected for molecular sexing and a uniquely numbered metal leg band was applied. A combined remote download pressure-GPS logger (Pathtrack nanoFix® GEO + RF (20 g, 1.1 ± 0.1% of body mass; 2020, 2021, 2022, 2023)) or remote download GPS-GSM logger (Technosmart Gipsy (25 g, 1.4 ± 0.1%; 2020) or Pathtrack GEO + GSM (20 g, 1.1 ± 0.1% of body mass; 2021, 2022)) was then attached to two central tail feathers with waterproof tape (TESA® 4651, Beiersdorf AG, Germany (Wilson *et al.* 1997)) before individuals were released near the edge of the colony to resume normal behaviour.

Pressure data were collected at 4-s intervals, and GPS location data were collected every 5 min (2020, 2022 and 2023) or 10 min (2021) for the combined GPS-pressure loggers, or every 10 min (2020 and 2022) or 20 min (2021) for the GPS-GSM loggers. In order to reduce energy consumption, loggers were programmed to stop collecting GPS data at night between 8:00 PM and 4:00 AM local time. Pressure data were collected at 4-s intervals as a consequence of limitations in battery and memory size. Similarly, differences in GPS collection intervals between years and loggers were a consequence of limitations in battery capacity. Data were remotely downloaded with a base station at the colony (Pathtrack nanoFix® GEO + RF loggers), or over the GSM network (Technosmart Gipsy and Pathtrack GEO + GSM loggers) until the logger battery expired, the device was shed or the bird was out of reception range.

All GPS loggers used in the present study weighed substantially less than the recommended 3% of the body mass, a limit which has been shown to have negligible effects (Wilson *et al.* 2002, Vandenabeele *et al.* 2012). However, owing to logistical constraints, no comparisons could be made between tagged and untagged birds. Therefore, tag effects on the diving and foraging effort of individuals cannot be excluded (Vandenabeele *et al.* 2015). However, as such tag effects are likely to have been negligible and similar for all tagged individuals, they should not affect the interpretation of the reported results.

Data processing

The collected GPS tracks were split into individual foraging trips using the *track2kba* package (Beal *et al.* 2021) in the R statistical environment (R Core Team 2022). A buffer of 0.5 km around the colony was used as a threshold to start and end trips. This buffer was chosen to avoid classifying cormorants roosting on Notch Island, which extends roughly 350 m north-west and 300 m south of the colony, as being on a foraging trip. Both visual inspection of the tracks and observations during fieldwork indicated no foraging in the immediate vicinity of the breeding colony. If no data were collected for more than 12 h, or if the return to the colony was not recorded, the trip was considered as incomplete. Although data gaps longer than 1 h were observed in the tracking data of 66% of the individuals in the present study, they were not observed frequently (on average

0.41 ± 0.07 gaps > 1 h day^{-1}). Missing GPS points were linearly interpolated using the 'redisltraj' function in the *adehabitatLT* package (Calenge 2011a) so as to match the programmed schedule. For individuals where pressure data were available, these were processed using the *diveMove* package (Luque 2007), with zero-offset correction using the running quantile method, to obtain dive behaviour summaries. Dive locations were linearly interpolated from the tracking data.

As only a subset of individuals had dive data available, a Hidden Markov Model (HMM) was used to identify the at-sea activities throughout foraging trips in all individuals. This HMM used step length and turning angle derived from the GPS tracks to identify the behavioural states of roosting, foraging (including resting on water) and commuting flight while on a foraging trip. Resting on water was not classified as a separate behaviour as the logger sampling interval did not allow this to be discerned from foraging behaviour. The HMM was first fitted to the subset of individuals for which dive behaviour was available using the *moveHMM* package (Michelot *et al.* 2016) to select the parameter values which resulted in the best-fitting model. After fitting the HMM, tracks were inspected visually, and the collected diving data were used to verify model accuracy. Subsequently, the best-fitting model was fitted to the tracks without dive data. As sampling intervals varied between logger types and years, GPS data were resampled to the largest time interval (20 min) before fitting the HMM.

Data collection periods varied between the various devices used. For birds equipped with GPS-pressure loggers, on average 8.4 ± 0.7 trips were collected (range: 1–28), while for birds with GPS-GSM loggers, on average 15.5 ± 2.1 trips were collected (range: 1–53). Hence, to standardize the amount of data analysed for each bird, as well as to avoid using data collected potentially after chicks had fledged, only the first five foraging trips were analysed for each bird. Birds with fewer than five trips were excluded from further analyses. Subsequently, the 95% kernel utilization distribution (UD) for all locations classified as foraging or commuting was calculated for each trip using the *adehabitatHR* package (Calenge 2011b), and Bhattacharyya's Affinity Index was calculated for each combination of trips (Bhattacharyya 1943, Fieberg & Kochanny 2005). An index of 0 indicates no overlap, while an index of 1 indicates complete overlap. For each individual, the mean overlap of all trips for that individual was calculated to derive a foraging site fidelity index (*FSFI*). In addition, for each trip, the mean overlap with all other trips for the same individual was calculated (*trip FSFI*). Subsequently, for each trip, the individual *FSFI* was subtracted from the *trip FSFI*, which resulted in the Δ*FSFI* (i.e. within-individual centring; see van de Pol and Wright (2009) and Table S1). In this method, a positive Δ*FSFI* indicates that a trip had a higher-than-average overlap with other trips of that individual, while a negative Δ*FSFI* indicates a lower-than-average overlap. By following the framework of van de Pol and Wright (2009), linear mixed models containing *FSFI* and Δ*FSFI* could be applied to discern, respectively, the inter-individual and intra-individual effects of increasing *FSFI* on foraging effort. Using both *FSFI* and Δ*FSFI* in the model allows determination of whether inter- and intra-individual increases in foraging site fidelity affect foraging effort in the same direction.

Two variables indicative of foraging effort were used: first, the proportion of time spent foraging, which was calculated as the amount of time foraging in a trip divided by the active trip duration (i.e. trip duration minus time classified as roosting away from the colony). Active trip duration was used instead of trip duration to decrease the variability in foraging proportion between trips, as trip duration was often increased due to birds roosting away from the colony. Secondly, for individuals where dive data were available, the dive rate (m h^{-1}; vertical distance travelled per active trip hour) was also investigated.

Statistical analyses

In a first step, the effects of sex, year, tarsus-length and mass on individual-level foraging site fidelity were tested in a linear model with a beta distribution. Mass and sex were added as earlier research indicated that mass, which is higher for males in this sexually dimorphic species, affects diving behaviour leading to differences in habitat use in sexes (Cansse *et al.* 2024). Thereby, these were added to the model to determine if these differences affected foraging site fidelity. Tarsus-length was added as a measure of individual size to investigate whether this affected site fidelity. Lastly, year of study was added to investigate potential interannual differences in site fidelity.

In a second step, linear mixed models were used to assess the factors influencing foraging effort. Two dependent variables indicative of foraging effort, the proportion of an active trip spent foraging and the dive rate, were used in two separate models as dependent variables. Both models contained *FSFI* and Δ*FSFI* as well as sex, year of study, tarsus-length (as a measure of individual size) and overnight absence from the colony as fixed factors. Overnight absence from the colony was added to the models as some foraging trips involved overnight roosting away from the colony, and it was hypothesized that this prolonged roosting while on a trip could be a factor affecting foraging effort independently from site fidelity. Thus, adding overnight absence to the model allowed this potential effect to be controlled for. Sex was added as earlier research indicated differences in dive depth and habitat use between males and females (Cansse *et al.* 2024), which potentially affect foraging effort. Tarsus-length was added as a measure of individual size to investigate whether size affected foraging effort. Year of study was added to control for potential inter-annual variation in foraging effort. The individual was added as a random factor in both models. The model containing the proportion of time foraging used a beta distribution.

Models which used the beta distribution were fitted using the *glmmTMB* package (Brooks *et al.* 2017). All other linear mixed models were fitted using the *lme4* package (Bates *et al.* 2015). For model selection throughout the study, the full model was specified, and the 'dredge' function in the *MuMIn* package (Barton 2018) was used to compare all possible models. For the models investigating inter- and intra-individual effects of *FSFI*, the *FSFI* and *ΔFSFI* could not be included separately (van de Pol & Wright 2009) and, therefore, only models containing both or none of these variables were compared in the dredge function. Candidate models were compared using Akaike's information criterion corrected for small sample sizes (AICc). Subsequently, the difference in AICc (ΔAICc) was used for model averaging on all models with $\Delta\text{AICc} < 4$ to determine the factors influencing the dependent variables for all models (Burnham & Anderson 2002, Symonds & Moussalli 2011).

RESULTS

Data were obtained from 72 birds (43 males, 29 females) across the 4 years of study (Table 1). Dive behaviour and GPS data were available for 41 individuals (24 males, 17 females), and the remaining birds only had GPS data. Loggers which collected dive behaviour collected data for 8.3 ± 0.5 days while the GPS-only loggers collected data for 20.0 ± 1.9 days. Comparison of the HMM-derived behaviour categories with obtained dive behaviour indicated that the HMM had similar levels of accuracy in each year of the study (Table S2). Although a relatively high proportion of the commuting sections still contained dives (i.e. false negatives for foraging behaviour) (range: 54.8–66.6%, Table S2), the majority of the dives were included in sections classified as foraging (68.7–74.2%, Table S2). This indicated that in the derived HMM, sections classified as foraging were largely representative for the spatial and temporal occurrence of foraging behaviour. The high proportion of commuting sections containing dives is likely to be an effect of the large sampling interval, thereby causing dives to be included at the start or end of commuting intervals. To assess whether model outcomes were affected by the sampling rates, the HMM was used to classify the data collected at 10-min intervals which slightly increased accuracy (Table S3). However, model outcomes were similar, indicating the models were robust to some misclassifications (Table S4).

At the population level, Black-faced Cormorants used a large area for foraging reaching maximum distances of 21.9 ± 0.7 km from the colony (Fig. 1). However, at the individual level, the areas used were much smaller as individuals repeatedly visited the same area for foraging. While there were large inter-individual differences in foraging site fidelity (*FSFI*; range: 0.19–0.96), the median *FSFI* was high (0.73). This indicated that the majority of the Black-faced Cormorants in the present study displayed high foraging site fidelity (Fig. S1). None of the considered variables in the model (sex, year, mass and tarsus-length) had a significant effect on the degree of foraging site fidelity.

On average, Black-faced Cormorants in the present study were found to forage for 65.1 ± 1.1% of their active trip duration. For birds where dive data were available, the average dive rate was

Table 1. Summary information for Black-faced Cormorants *Phalacrocorax fuscescens* instrumented with GPS and dive behaviour data loggers at Notch Island, northern Bass Strait, southeastern Australia.

	Sex					
	Male			Female		
Year	Mass (g)	GPS (*N*)	Dive data (*N*)	Mass (g)	GPS (*N*)	Dive data (*N*)
2020	2082 ± 102	15	6	1699 ± 32	14	8
2021	1892 ± 121	10	6	1658 ± 35	6	2
2022	2094 ± 32	13	7	1625 ± 57	6	4
2023	2050 ± 41	5	5	1716 ± 22	3	3

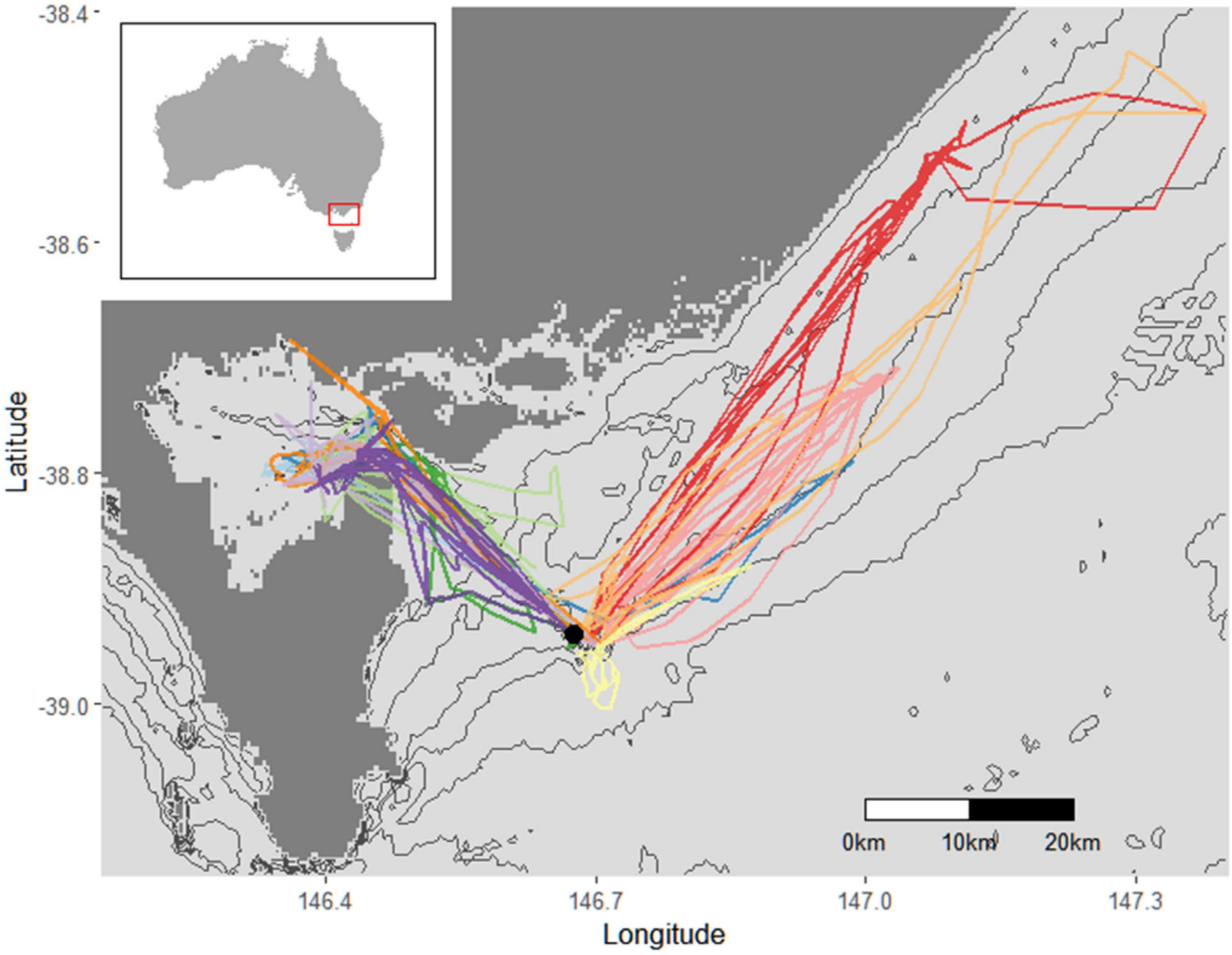

Figure 1. Representative foraging tracks from Black-faced Cormorants breeding at Notch Island displaying the high level of foraging site fidelity. Each colour represents a different individual (*N* = 11). The black dot on the map indicates the location of Notch Island.

370.3 ± 20.5 m h^{-1}. In the models assessing which factors (sex, mass, tarsus-length, year of study, *FSFI*, Δ*FSFI* and overnight absence from the colony) influenced these considered measures of foraging effort (i.e. proportion of time foraging and dive rate), *FSFI* and Δ*FSFI* were consistently included in all of the top candidate models (ΔAICc < 4), indicating that these factors affected foraging effort (Table S5). Year of study and overnight absence were included in all of the top candidate models for dive rate. The presence or absence of other predictor variables in candidate models was more variable (Table S5). As multiple candidate models with ΔAICc < 4 were found, model averaging was conducted for all dependent variables.

The proportion of time spent foraging in a trip decreased both with increasing *FSFI* (95% confidence interval (CI) (−1.84 to −0.67)) and with increasing Δ*FSFI* (95% CI (−2.97 to −0.90)) (Table 2). This indicates that increasing the foraging site fidelity leads to a decrease in the proportion of a trip which is spent on foraging both within and between individuals (Fig. 2a). No other factors were found to have a consistent effect on the proportion of time spent foraging (Table 2).

For the subset of individuals where diving data were available, the dive rate decreased as *FSFI* increased (95% CI (−565.0 to −33.1)) indicating an inter-individual effect, where individuals with a higher *FSFI* had a lower dive rate (Fig. 2b). As Δ*FSFI* increased, the dive rate decreased (95% CI (−740.5 to −258.4)). This indicates that, as individuals increased their foraging site fidelity, they reduced diving effort (intra-individual effect) (Fig. 2b). Dive rate was lower when an individual was absent from the colony overnight (95% CI (−275.2 to −170.8)), indicating that overnight roosting may decrease effort, potentially as a consequence of roosting in areas with good prey availability. Dive rate was observed to be higher than in other years of study in 2021 (95% CI (73.7–402.1)) and lower in 2022 (95% CI (−305.4 to −18.1)), potentially indicating inter-annual differences in prey availability.

DISCUSSION

Foraging site fidelity can lead to increases in foraging efficiency, but evidence for this in free-ranging species is limited. In the present study, a high consistency in spatial habitat-use and foraging site fidelity was quantified in the Black-faced Cormorant, a predominantly benthic forager occurring in southeastern Australia. This behavioural consistency was associated with reduced foraging effort, suggesting that individuals foraging in familiar locations may experience increased foraging efficiency.

Individual variation in site fidelity

At the population level, Black-faced Cormorants in the present study were observed to use a relatively large area for foraging. However, individuals foraged repeatedly in the same restricted location, indicating a high level of individual specialization in foraging sites. Similar specialization in foraging locations has been observed in other cormorant and shag species (Potier *et al.* 2015, Camprasse *et al.* 2017, Morgan *et al.* 2019), as well as in benthic foragers in general (Riverón *et al.* 2021, Filatova *et al.* 2022).

The factors year of study, morphometrics (i.e. mass or tarsus-length) or sex were not found to have a significant influence on foraging site fidelity. However, large inter-individual differences were

Table 2. Results from the models examining the factors influencing foraging proportion and dive rate.

	Proportion foraging (%)			Dive rate ($m\ h^{-1}$)		
Predictors	Est	sd	95% CI	Est	sd	95% CI
Intercept	1.21	1.02	−0.78 to 3.22	600.9	333.5	−56.5 to 1258.4
FSFI	**−1.26**	**0.29**	**−1.84 to −0.67**	**−299.5**	**135.0**	**−565.0 to −33.1**
Δ*FSFI*	**−1.92**	**0.52**	**−2.97 to −0.90**	**−499.4**	**122.2**	**−740.5 to −258.4**
Overnight	0.04	0.08	−0.12 to 0.21	**−223.0**	**26.5**	**−275.2 to −170.8**
Year (2021)	0.07	0.15	−0.22 to 0.36	**237.9**	**83.3**	**73.7 to 402.1**
Year (2022)	0.05	0.12	−0.18 to 0.29	**−161.8**	**72.8**	**−305.4 to −18.1**
Year (2023)	−0.03	0.13	−0.29 to 0.21	−51.1	87.0	−222.8 to 120.4
Sex (M)	−0.12	0.15	−0.42 to 0.18	83.8	73.0	−59.7 to 227.3
Tarsus-length (mm)	0.00	0.01	−0.03 to 0.04	0.6	5.5	−10.1 to 11.5

The reported values were obtained after model averaging of all candidate models (ΔAICc < 4). Reported are the parameter estimates (est), their standard deviation (sd) and 95% confidence interval (95% CI). When the CI did not cross 0 (i.e. there was an effect of the predictor), this is indicated in bold.

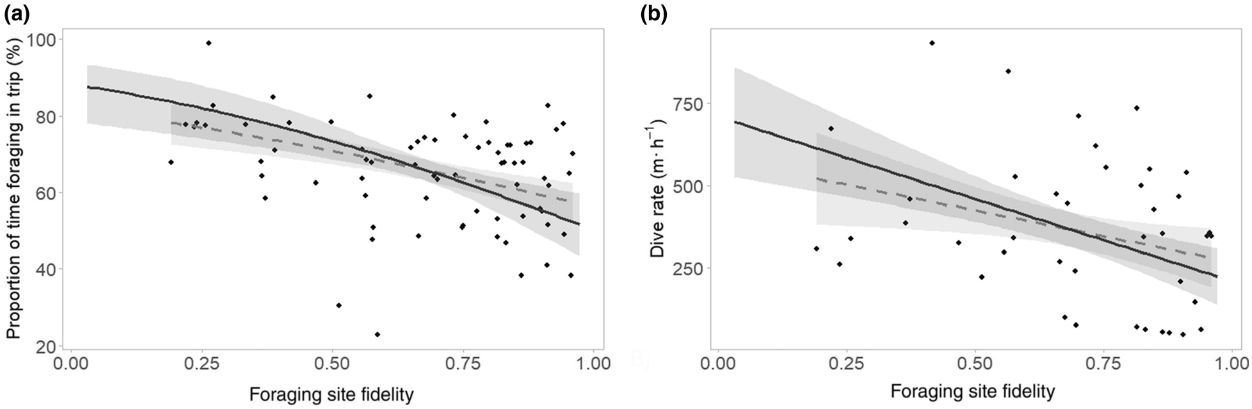

Figure 2. Model-predicted effects of foraging site fidelity on (a) proportion of time spent foraging in a trip (%) and (b) dive rate (m h^{-1}). Within-individual effects are indicated in dark grey (full line) and between-individual effects are indicated in light grey (dashed line).

observed in foraging site fidelity. This could indicate that other factors which are related to the individual, but which could not be assessed in the present study, may influence site fidelity. For example, in Black-legged Kittiwakes *Rissa tridactyla*, bolder individuals were found to have a higher foraging site fidelity (Harris *et al.* 2020). In Northern Gannets *Morus bassanus*, foraging site fidelity was higher for adults than for immatures, indicating that age, potentially through individual familiarity with the environment, could influence this behavioural consistency (Votier *et al.* 2017).

Changing environmental conditions could potentially influence the distribution and abundance of prey species for marine predators (Perry *et al.* 2005, Johnson *et al.* 2011). Consequently, the level of foraging site fidelity, and its adaptive value, might differ between years if prey conditions change (Switzer 1993, Foo *et al.* 2020, Michelot *et al.* 2021). While in the present study no significant differences in foraging site fidelity were found between years, a greater range in fidelity was observed, and lower fidelity was more common in 2022 and 2023 than in other years. In addition, dive rate (m h^{-1}) was lower in 2022, suggesting greater prey availability (Womble *et al.* 2014). Furthermore, a concurrent study (Cansse *et al.* 2024), observed a higher proportion of pelagic dives in 2022, potentially reflecting a change in prey distribution and/or type. These results could indicate that where prey is present in high abundance but under low spatial predictability, such as pelagic prey types (Riverón *et al.* 2021), foraging site fidelity becomes less important for Black-faced Cormorants to achieve high foraging efficiency.

Influence of foraging site fidelity on foraging efficiency

When interpreting the effects on foraging effort in the present study, it was assumed that a lower proportion of time at sea spent foraging was indicative of a higher foraging efficiency. This was assumed because benthic foraging cormorants do not locate prey while commuting (Harris *et al.* 2012) and, as such, the commuting time to and from the foraging spot will have little variation. As a result, if more time was spent on foraging, as a consequence of low capture success or more time needed to locate prey, the proportion of time spent foraging would increase and, therefore, foraging efficiency can be assumed to be lower. Similarly, a lower dive rate was assumed to be indicative of a higher foraging efficiency. This was assumed as individuals with a lower dive rate are likely to need fewer dives to search and capture sufficient prey.

No data are available for Black-faced Cormorants linking the proportion of time spent foraging or dive effort to prey capture success, so it cannot be excluded that more time foraging indicates a higher efficiency, as found for Scopoli's Shearwaters *Calonectris diomedea* (Padget *et al.* 2017). However, available data for the closely related Double-crested Cormorants *Phalacrocorax auratus* indicate an increase in catch per unit effort and a decrease in search time when prey density increases (Enstipp *et al.* 2007). Therefore, in the present study on Black-faced Cormorants, it was assumed that a lower dive rate and a lower proportion of time spent foraging indicate higher prey capture rates and, therefore, a higher foraging efficiency.

Foraging site fidelity was found to affect the proportion of time spent foraging in a trip and dive rate, both decreasing as foraging site fidelity increased. These results indicate that more spatially consistent individuals are likely to be more efficient foragers. This is consistent with previous research linking foraging site fidelity and foraging behaviour in marine predators. For example, in Australian Fur Seals *Arctocephalus pusillus doriferus* individuals with a higher foraging site fidelity were found to have a higher proportion of successful dives, indicating a higher foraging efficiency (Speakman *et al.* 2021).

Additionally, in the present study, a within-individual effect of increasing foraging site fidelity was found with individuals increasing their foraging efficiency (i.e. lower proportion of the trip spent foraging and lower dive rate) when they revisited previously exploited sites compared to when they visited new or less familiar sites. This suggests that, within individuals, increased familiarity of foraging sites results in beneficial foraging outcomes or that individuals actively revisit locations where they have previously been successful. Similar findings have been reported in Little Penguins *Eudyptula minor*, where foraging site fidelity was found to be higher after trips with higher prey capture success (Carroll *et al.* 2018).

Combined, the between- and within-individual effects of foraging site fidelity suggest that a higher foraging efficiency is obtained by foraging in more familiar locations. Such increased efficiency could result in higher reproductive success, as has been shown in European Shags *Gulosus aristotelis* (Morgan *et al.* 2019), African Penguins *Speniscus demersus* (Traisnel & Pichegru 2019) and Lesser Black-backed Gulls *Larus fuscus* (van den Bosch *et al.* 2019). However, a consequence of such foraging site fidelity is that negative influences on foraging site prey availability, either by natural or anthropogenic factors, will decrease foraging efficiency and, consequently, reproductive success may decline (Merkle *et al.* 2022). Thereby, if prey distributions shift, and no alternative prey is available, foraging sites might become unsuitable for foraging.

The temporal extent of foraging site fidelity in Black-faced Cormorants is not yet known. The present study occurred during late chick-rearing when provisioning of offspring is assumed to be maximal. By collecting data in different parts of the breeding season or in different years of study for the same individual, it would be possible to determine the intra- and inter-annual foraging plasticity in Black-faced Cormorants. Data on within-breeding season plasticity could help to unravel the potential effects of sudden events, such as marine heatwaves, on foraging efficiency and reproductive success (Woehler & Hobday 2023). Inter-annual information on foraging plasticity could help us to understand the extent to which individuals can adapt to changing environmental conditions, such as climate change, over longer timespans (Chambers *et al.* 2011).

CONCLUSION

In summary, as a population, Black-faced Cormorants were found to use a relatively large area for foraging, but individuals were highly consistent in the areas they exploited. While variation in foraging site fidelity was observed, no measured factors were found which could explain these differences. Importantly, modelling results indicated that increasing foraging site fidelity, both within and between individuals, increased foraging efficiency. This indicates that disturbances to foraging habitat could have negative impacts on individuals owing to a reduction in foraging efficiency. Further investigation is required to determine plasticity in foraging behaviour within individuals over greater temporal scales. Such information would enable better predictions about the effects of habitat disturbance on foraging efficiency of Black-faced Cormorants.

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AUTHOR CONTRIBUTIONS

Thomas Cansse: Conceptualization; investigation; writing – original draft; writing – review and editing; methodology; formal analysis; data curation. **Luc Lens:** Investigation; writing – original draft; writing – review and editing; formal analysis; methodology. **Grace J. Sutton:** Investigation; writing – review and editing; data curation. **Jonathan A. Botha:** Data curation; writing – review and editing; investigation. **John P.Y. Arnould:** Conceptualization; investigation; funding acquisition; writing – original draft; writing – review and editing; methodology; formal analysis; data curation.

CONFLICT OF INTEREST

The authors declare no competing interests.

ETHICAL NOTE

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).

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Data Availability Statement

Part of the 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 database (https://www.seabirdtracking.org/).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Violin plot for the mean *FSFI* for all Black-Faced Cormorants in this study.

Table S1. Example of calculation of *FSFI* and *ΔFSFI* from trip overlaps obtained with the Bhattacharyya Affinity Index.

Table S2. Accuracy of the Hidden Markov Models for the different years of study for data resampled at a 20-min interval.

Table S3. Accuracy of the Hidden Markov Models for the different years of study for data resampled at a 10-min interval.

Table S4. Results from the models examining the factors influencing foraging proportion and dive rate (m h^{-1}). These models used data which were classified with the Hidden Markov Model at a 1-min interval.

Table S5. Candidate models (ΔAICc < 4) for which model averaging was applied for proportion of time foraging and dive rate.