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Maternal effects and fitness consequences of individual variation in bottlenose dolphins' ecological niche

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Abstract

1. The niche describes the ecological and social environment that an organism lives in, as well as the behavioural tactics used to interact with its environment. A species niche is key to both ecological and evolutionary processes, including speciation, and has therefore been a central focus in ecology.
2. Recent evidence, however, points to considerable individual variation in a species' or population's niche use, although how this variation evolves or is maintained remains unclear.
3. We used a large longitudinal dataset to investigate the drivers and maintenance of individual variation in bottlenose dolphins' *Tursiops aduncus* niche. Specifically, we (a) characterised the extent of individual differences in habitat use, (b) identified whether there were maternal effects associated with this variation and (c) investigated the relationship between habitat use and calving success, a component of reproductive fitness.
4. By examining patterns of habitat use, we provide evidence that individual dolphins vary consistently between one another in their niche. We further show that such individual variation is driven by a strong maternal effect. Finally, habitat use and calving success were not related, suggesting that use of different habitats results in similar fitness outcomes.
5. Niche partitioning, maintained by maternal effects, likely facilitates the coexistence of multiple ecotypes within this population.

1 | INTRODUCTION

The niche is a multidimensional phenomenon describing an organism's ecological and social environment, as well as the behavioural tactics used to interact with the environment. Niche partitioning, where animals use resources differently to each other in time and space to reduce competition, is thought to be key to speciation, due to the effect of niche-specific selective pressures on character displacement, reproductive isolation and adaptive diversification (Dieckmann & Doebeli, 1999; Schoener, 1974). Characterisation of a species' or population's niche therefore remains important for both ecologists and evolutionary biologists. However, in recent years it has emerged that, in many species, there is extensive variation in the niche that conspecifics occupy (Bolnick et al., 2003). Nonetheless, we do not yet fully understand the evolution, maintenance and importance of this variation. Clarifying this would not only assist in gaining a more realistic and meaningful understanding of the niche concept, but also in understanding the coexistence of species, and evolution of biodiversity (Bolnick et al., 2011; Costa-Pereira et al., 2018).

Habitat use, a major component of the ecological niche (Morris, 2003), varies among conspecifics (e.g. individual specialisation; Bolnick et al., 2003) and shapes the density and distribution of individuals, their behaviour, resource competition and population dynamics (Morris, 2011; van Beest et al., 2014; Webber & Vander Wal, 2018).

Some causes of this variation are well known. For instance, males and females often use habitat differently (McCorquodale, 2003; Safi et al., 2007; Sprogis et al., 2018) and habitat use can also change throughout ontogeny (Matich & Heithaus, 2015; Rosenberger & Angermeier, 2003). For individual variation in habitat use to affect evolutionary or population dynamics, though, it should not only infer consequences to organismal fitness, but also be transmitted across generations.

The mechanisms that promote individual variation in habitat use across generations likely involve a combination of genetics, maternal effects and learnt behaviours. In fact, genetic variation associated with habitat selection is relatively common (Hedrick, 1990; Jaenike & Holt, 1991; Stamps, 2006). However, habitat selection can also be driven by social transmission, which can occur both vertically (from mother/father to offspring) and horizontally (peer to peer; Davis & Stamps, 2004). In particular, vertical social transmission can confound estimates of genetic effects, as this happens primarily between first-order relatives. Nevertheless, this means of transgenerational effect is likely critical in imbuing each generation with information on which habitat to use and how to use it.

Individual variation in habitat use may be considered an evolutionary strategy that minimises resource competition and maximises individual fitness (Araújo et al., 2011; Bolnick & Ballare, 2020). As such, it may align with theories of niche partitioning (MacArthur, 1984), which would predict that intraspecific variation in ecological niches results in equal relative fitness among conspecifics. Alternatively, because conspecifics require similar resources, we might expect fitness heterogeneities arising as a result of niche variation (Costa-Pereira et al., 2019). Nevertheless, despite robust and longstanding ecological theory, empirical tests are rare. Moreover, studies on the relationship between individual variation in habitat use and fitness do not support predictions generated from theories of niche partitioning. For instance, among European eels *Anguilla anguilla* and Soay sheep *Ovis aries*, some habitat types confer greater relative fitness (Cucherousset et al., 2011; Regan et al., 2016).

Ultimately, to begin to understand how individual variation in habitat use affects evolutionary processes we must identify (a) the extent to which individuals specialise, (b) the mechanisms driving and maintaining variation and (c) how individual variation in habitat use relates to fitness. In this study, we examined the evolution and maintenance of individual variation in habitat use in a population of Indo-Pacific bottlenose dolphins *Tursiops aduncus*. Bottlenose dolphins range across tropical and subtropical waters and inhabit a variety of coastal habitats. They are highly social mammals, have long life spans, and exhibit both individual foraging specialisations (Mann et al., 2008; Sargeant et al., 2005) and variation in their social behaviour (Connor et al., 1992; Smolker et al., 1992a). They live in highly heterogeneous habitats (Heithaus & Dill, 2002; Patterson, 2012), and as apex predators, play a disproportionate role in ecosystem dynamics (Colman et al., 2014). They exhibit fission–fusion social dynamics and there is some evidence for intra-population variation in habitat use (Ansmann et al., 2015; Kiszka et al., 2012; Patterson & Mann, 2012; Tsai & Mann, 2013), although the extent to which this aligns with theories of niche partitioning and how this variation is maintained across generations is not yet known.

To investigate the maintenance of individual variation in habitat use, we first investigated the extent to which individuals differ in their patterns of habitat use. Second, we investigated whether variation in habitat use was associated with maternal effects. And third, we investigated whether there was a relationship between individual variation in habitat use and calving success.

2 | MATERIALS AND METHODS

2.1 | Data collection

Data were collected as part of an ongoing study of a resident, coastal population of bottlenose dolphins in the eastern gulf of Shark Bay, Western Australia. Since 1984, over 1,700 individuals inhabiting an area of approximately 500 km^2 have been continuously monitored and regularly surveyed (via boat-based opportunistic and transect surveys). During the surveys, scan sampling of individuals in groups was used in the first 5 min to determine group composition, behavioural activity (i.e. forage/rest/travel/social/other; Karniski et al., 2015), demographic information (age, sex, weaning date) and reproductive state (lactating, pregnant). Individuals were identified using standard dorsal fin identification techniques and other distinctive features (Bichell et al., 2018; Würsig & Würsig, 1977). Sex was determined by views of the genital area, presence of a dependent calf (Mann et al., 2000; Smolker et al., 1992b), and/or genetics (see Foroughirad et al., 2019). Ages were known for most dolphins born since 1982, but were also estimated using size and ventral speckling information (Krzyszczyk & Mann, 2012). Mother–offspring relationships were determined through observations of offspring nursing or swimming in the nursing access position (infant position, under the mother in contact with her abdomen; Mann et al., 2000) or, rarely, through genetics (Foroughirad et al., 2019). Weaning was determined by a dramatic drop in mother–calf association and cessation of swimming in infant position (Mann et al., 2000). If individuals were sighted more than once in a day, the last survey in which they were sighted was used to reduce spatial and temporal autocorrelation (Tsai & Mann, 2013). Both male and female dolphins are philopatric in Shark Bay, and most of the individuals in the data used have home ranges that are almost entirely within the study area (Strickland et al., 2017). All sightings of dependent calves, as well as any individual under 4 years of age (average weaning age; Mann et al., 2000) were omitted from analyses. Data collected between 1988 and 2017 were used in this study.

2.2 | Habitat classification

Habitat use was defined for each sighting of each individual using recorded spatial locations, and was based on the classification of different microhabitats through the eastern gulf of Shark Bay previously identified by (Wallen et al., 2016). Habitat in this region was characterised into one of three types: (a) deep channels, (b) deep open water and (c) shallow habitats. Deep channels have a depth of between 7 and 13 m, strong currents and rocky substrate (made of rock, shell and coral debris). Deep open waters have similar depths (5–13 m) but with weaker currents and a mix of sand, silt and clay substrate. Shallow habitats consist of both sand flats and seagrass beds, both of which have similarly shallow water (both range 0.5–4 m) and little current. Generally, prey abundance is higher in vegetated habitats (i.e. shallow habitat) than in unvegetated habitats (i.e. channel and deep open habitat; Heithaus, 2004) and some prey species in channel habitats often lack swim bladders and burrow in the rubble-littered substrate, reducing prey detection via echolocation (Foote, 1980; Haslett, 1962; Patterson & Mann, 2011; Turl et al., 1991). This means that the accessibility of some prey is decreased in channel habitats without specializing in foraging tactics (Mann et al., 2008; Patterson & Mann, 2011). Furthermore, acoustic signals propagate further in deeper waters because there is less energy loss (i.e. sound absorption) than in shallow waters (Marsh & Schulkin, 1962; Quintana-Rizzo et al., 2006). Consequently, dolphins are likely to detect competitors more readily in deep open habitat than in other habitats. Finally, predation pressure by sharks is known to be most severe in shallow waters (Heithaus & Dill, 2002). Previous research has found that the use of shallow habitats (i.e. seagrass and sand) are strongly correlated with each other, and sightings of dolphins using the sand flats are rare (Patterson & Mann, 2012). Therefore, we combined these two habitat types to classify them as one shallow habitat. Deep open habitat is the largest habitat present in this area whereas the channel habitat is the smallest (Figure 1). Survey effort reflected the distribution of habitats at the study type, where channels were surveyed less often than deep open of shallows, reflecting their relative size; deep open = 2,476/2,997 survey days, shallow = 2,977/2,977 days, channel = 1,565/2,977 days.

Using the RASTER package (Hijmans & Etten, 2016) in R (R Development Core Team, 2013) and previously generated habitat maps (Figure 1; Patterson & Mann, 2011), we identified which of these three habitat types individuals were occupying at each of their observations. Shark Bay dolphins have a coercive mating system in which males sometimes escort females into areas or habitats they do not typically occupy (Wallen et al., 2016). Therefore, in order to best characterize habitat selection, we removed sightings of females when they were potentially being consorted by adult males. This removed observations of females that did not reflect active habitat selection, but rather habitat use emerging as a result of being consorted by males (Wallen et al., 2016). These were defined as sightings of females which were potentially cycling (i.e. not known to be pregnant or in the early stages of lactation) and seen with two or more adult males. Any sighting that included direct observation of behavioural interactions indicating possible consortship (e.g. displays, aggression) were excluded regardless of other parameters. Although behavioural activity was recorded for all individuals' observations (e.g. foraging, socialising, resting, travel) we selected to retain all observations without making a priori assumptions about the importance of using habitat for different activities. This allowed us to retain a broader perspective on each individuals' total niche relative to the populations, encompassing the habitat used for a wide variety of behaviours. Dolphins' locations between observations are unlikely to be auto-correlated because (a) our data structure reflected only one observation per dolphin per day, (b) dolphins are able to move vast distances across the study site (e.g. from one side to another) in a single day and (c) transitioning between two habitat types does not require a dolphin to move through the third (see Figure 1).

2.3 | Individual variation and maternal effects of habitat use

Our first main objective was to determine the extent to which dolphins partition their niche, and the extent to which this variation is maintained through a maternal effect. To do this, we first ran two multinomial mixed models that differed in their random effect structure. In both models, the dependent variable consisted of a categorical variable describing which habitat the individual was observed in at that observation. We included 15,062 observations of 331 individuals for which we knew the identity of their mothers. Usually, when using data to summarise behaviours, a minimum number of sightings is often required (see below). However, for these analyses we did not subset the data for a minimum number of sightings per dolphin. This was because when analysing individual variation and maternal effects on habitat use, we used all observations of dolphins as repeated measures of habitat choice and it has been found that, in such circumstances, removing individuals with a small number of observations does not considerably alter variance parameter estimates, and can sometimes bias them due to reduced statistical power (Martin et al., 2011; Van de Pol, 2012). As such, we selected to retain all individuals in our dataset. Nevertheless, we did fit number of sightings as a fixed effect in all models to account for any effect of this on our results.

The first model assessed the repeatability of individuals' habitat use and contained dolphin identity as a random effect. We calculated repeatability (i.e. proportion of phenotypic variance attributed to between-individual variation) for habitat use following methods developed to measure repeatability from logistic regressions (Nakagawa & Schielzeth, 2010). Specifically, we measured repeatability of habitat use on the link scale using Equation 1, where V_{ID} is the between-individual variance, V_{ε} is the residual variance and $\pi^2/3$ is the distribution-specific variance of a logit-link model (Nakagawa & Schielzeth, 2010).

$$R = \frac{V_{\mathrm{ID}}}{V_{\mathrm{ID}} + V_{\varepsilon} + \frac{\pi^2}{3}}. \tag{1}$$

Sex was fitted as a fixed effect to account for sex differences in habitat use. Month and year of observation were included as fixed effects to account for temporal and seasonal effects on individuals' habitat use.

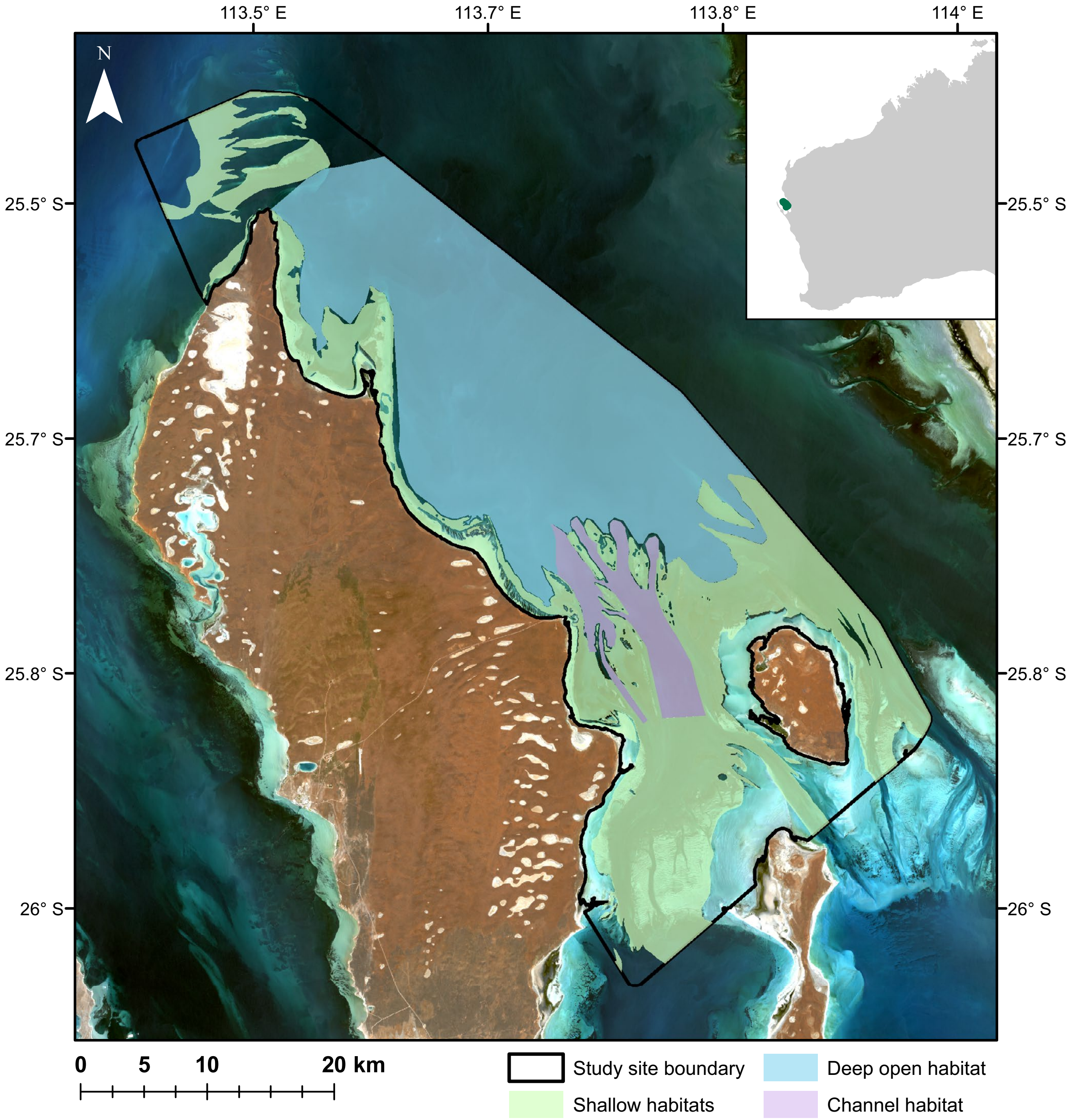

FIGURE 1 Distribution of different habitat types in Shark Bay, Australia

Age of the individual at each observation was included as a fixed effect to account for ontogenetic effects in habitat use. Finally, we included the total number of observations of each dolphin as a fixed effect. We also sought to include the length of time each dolphin was tracked (in years) as a further covariate. However, this measure was highly correlated with the total number of observations ($r^2 = 0.7$), and as a result we selected to include total number of observations alone in our models.

The second model was identical to the first but included both maternal identity and dolphin identity as random effects in order to partition variance in habitat use into maternal effects and permanent environment effects (McAdam et al., 2002; Räsänen & Kruuk, 2007; Wilson et al., 2005). Fitting a random intercept for maternal identity in this way is a common method to parse the maternal effect from other effects on the trait of interest (McAdam et al., 2002). For instance, it is possible to further fit either a relatedness matrix or an observed pedigree to the model in order to further partition genetic from non-genetic maternal effects. However, quantitative genetics models such as this require substantial statistical power and in particular a high number of replicates at the individual level. Through a power analysis, we found that the number of individuals in the genomic relatedness matrix for these data ($n = 352$) provided statistical power to detect high heritability ($h^2 = 0.4$, power = 0.97), but did not yield sufficient power to detect lower heritability ($h^2 = 0.2$, power = 0.48). As such, we opted to fit the maternal effect, but did not attempt to separate genetic from non-genetic maternal effects. Importantly, variance associated with the random effect for dolphin identity (which fits the repeated observations of individuals) therefore includes both permanent environment and non-maternal genetic effects.

Both models were fit with a multinomial distribution and a logit link using the MCMCglmm package in R (Hadfield, 2010). Fixed effects were given weakly informative flat priors, and random effects were given parameter expanded priors following (de Villemereuil et al., 2016). Residual variance was fixed at 1 (Hadfield, 2012) and each model was run for a total of 1,300,000 iterations with a burn-in of 30,000 iterations and thinning of 500 iterations, which resulted in low autocorrelation. Convergence of models was assessed by examining traceplots to visualise sampling mixing and by assessing effective sample sizes and autocorrelation. We plotted predicted random effect values to visually check for normality.

In both models, we constrained the variance–covariance matrix to a single variance parameter for habitat use (instead of estimating a 3 × 3 matrix). This was because fitting the full variance–covariance matrix would provide variance estimates for the use of two habitats in comparison to a 'reference' category (e.g. by calculating the log-odds probability of using habitat A in comparison to habitat B) resulting in parameters that are not easily interpreted biologically. However, it may be that the extent of individual variation or the strength of the maternal effect varies between habitats. In order to investigate this, we ran further analyses for each habitat separately to identify the repeatability and maternal effect for each habitat type independently. To do this, we ran two models for each habitat type that differed in their random effect structure (as above). The dependent variable in these models consisted of a binary variable describing whether or not the individual was sighted in a habitat type. As in the multinomial models, sex, year, month, age and number of observations were all fit as fixed effects in all models. In this way, a repeatability and a maternal effects model was fit independently for each habitat type (totalling six models). These models were fit with a threshold distribution and a logit link in the MCMCglmm package in R (Hadfield, 2010). We used the same priors as detailed above, and residual variance was fixed at 1. Model convergence and fit was assessed as explained above.

2.4 | Calving success

Our second objective was to assess whether individual variation in habitat use supported theories of ecological niche partitioning. We predicted that if individual variation in habitat use reflected ecological niche partitioning, there would be no statistical relationship between calving success and habitat use. This is because ecological niche partitioning expects individuals to maximise their own fitness by using a different niche to conspecifics. However, if all individuals do this in parallel, the result would be that all individuals have equal relative fitness to each other (i.e. each individual maximises their fitness, resulting in no single niche performing better than another). To test this, we investigated whether there was a relationship between habitat use and female calving success (a component of individual fitness). We investigated this for females only due to more comprehensive data for maternities than paternities, and we used females for which we had sufficient data to estimate both habitat use and calving success. We filtered the data to include females with at least 14 sightings, as this has been found to generate accurate summary measures of individual behaviours in this population (Mann et al., 2012; Sargeant et al., 2007) resulting in the inclusion of 203 females.

2.4.1 | Habitat use

To investigate the relationship between calving success and habitat use, we summarised the habitat use of individuals to remove the repeated measures in the data, facilitating the analysis of the relationship of habitat use with calving success (which is a single measure per individual, see below). We measured habitat use in three ways, each of which measured either the habitat use tactic, or the degree of individual specialisation in habitat use.

First, for each of the females, we summarised their habitat use by measuring the proportion of times they were sighted in each habitat. To do this, we used females that had at least 14 observations. As a result of the covariance structure of using different habitats (see results section), we then used a principal components analysis with the proportion of time spent in each habitat to remove multi-collinearity in the data prior to running analyses. We then used the principal components scores as variables in subsequent analysis, which reflect an individuals' tendency to use one habitat over another.

Our second approach was similar to the first, but this time we corrected for differences in proportional availability in habitats in the study site (Figure 1) by measuring selection ratios for each habitat. Selection ratios measure an individual's proportional use of each habitat relative to the proportional availability of that habitat in the population (Manly's type II design). A value of one signifies habitat use equal to availability, while values greater or less than one indicate positive or negative selection respectively. As such, this metric measures the extent to which the individual is selecting or avoiding certain habitats. We then ran selection ratios per individual through a principal component analysis in the same way as explained above.

Our third approach was to measure individuals' habitat breadth relative to the population, thereby measuring the extent to which individuals exhibit specialisation. To do this for each individual, we measured the PSi index, which reflects the proportional similarity between an individual's niche and the populations, such that a value of one means an individual's habitat use is the same as the population's, whereas a value of zero would mean an individual's habitat use is completely different to the population (Bolnick et al., 2002).

This was measured per individual using Equation 2 where p_{ij} is the frequency that individual *i* uses habitat *j*, and q_j is the frequency that the population uses habitat *j* as a whole.

$$\mathrm{PS}_i = 1 - 0.5 \sum_j (p_{ij} - q_j). \tag{2}$$

Using this measure, we also investigated the extent to which individuals exhibited greater specialisation in their habitat use than expected. This was done by comparing the observed PSi values with those generated from a Monte Carlo simulation. This was done in the RINSP package in R (Zaccarelli et al., 2013).

2.4.2 | Measuring calving success

Calving success in female dolphins can be understood as a component of individual fitness, and we define it here as the number of calves surviving to age 3 (approximate minimum weaning age) divided by the number of years where the female's reproductive state was known. For example, a female that had three surviving calves in a 15-year period would have a calving success rate of 0.20. As such, this measure reflects long-term reproductive success (i.e. average yearly weaning rate across reproductive lifetime), as opposed to short-term reproductive success which could be measured in a binary way (i.e. whether or not a calf was weaned). A female's reproductive years start at age 11, the minimum age of a female's first birth observed in our dataset, with one exception (Mann, 2019). If a female's age was not known (e.g. if the female was already an adult at the start of the study), then her reproductive years started with her first year of observation. If the female was first observed with a calf, then her reproductive years started with the estimated year that the calf was born. If the survival status of a calf was not known, then those reproductive years, from when the calf was born until we could again determine her reproductive status based on sighting records, were not included for that female. If there was a gap in the female's sighting record, such that she could have had a calf survive to age 3 in that period, those years were not included for that female. Females had to have at least 4 adult years of observation (i.e. reproductive years) to be included. The average number of reproductive years was calculated as 15 (range = 4–39). Although temporal variation in resource availability may affect calf survival in the short-term (Mann et al., 2021), calving success is a long-term measure (i.e. averaged through a females lifetime). As such, we did not explicitly account for temporal effects, although we acknowledge it may affect calving success in a particular year. Eighty percent of individuals had 10 or more reproductive years included in the analyses ($n = 203$).

2.4.3 | Analysis

For each of the three habitat use measures we calculated, we ran a model which tested whether there was a relationship between individuals' habitat use and calving success. These models fitted calving success as the dependent variable and habitat use as fixed effects, and we fit three models, one for each of the measures of habitat use. The first two models fit calving success as a function of principal component scores (one for raw habitat use, and the second for selection ratios). The third model fit calving success as a function of PSi. In all three models we fit the number of years we tracked each dolphin as a fixed effect to account for the effect of differences in tracking effort on calving success. We also sought to fit age of the dolphin as a further fixed effect to account for reproductive senescence (Karniski et al., 2018). However, age was highly correlated with the number of years of observation, and as such, we selected to include only the latter variable in all models investigating the relationship between habitat use and calving success. These models were all fit with a binomial distribution in STAN using the BRMS interface in R and were run for 3,500 iterations across four chains with a warm-up period of 1,000 iterations (total = 14,000 iterations) which resulted in low autocorrelation. Fixed effects were given weakly informative priors (normal (0, 10)), and convergence of models was assessed by examining traceplots to visualise sampling mixing and by assessing effective sample sizes as well as Rhat diagnostic (Rhat = 1).

3 | RESULTS

The average number of observations per individual was 45 (range = 1–465, Figure S1), and on average dolphins were tracked for 16.4 years (range = 1 day–28.9 years). Dolphins were most commonly sighted in the deep open habitat (42% observations), while channel and shallow habitats had similar rates of use (channel = 27.9%, shallow = 29.9%). Importantly, these overall differences in habitat use in the population did not reflect relative differences in survey effort (see methods), suggesting that survey effort did not bias habitat use estimates in this dataset. These patterns did not differ between males and females (males; deep = 39.6%, channel = 29.8%, shallow = 30.6%: females; deep = 43.5%, channel = 26.9%, shallow = 29.6%). Females were observed in possible consortships with males in 4% of observations, which were removed prior to any subsequent analysis.

3.1 | Individual variation and maternal effects of habitat use

We included 15,062 observations of 331 individuals in analyses of individual variation in habitat use. These individuals were the offspring of 185 mothers (i.e. number of levels in maternal effect analyses); mothers averaged 2 offspring in this dataset (min = 1, max = 6). We did not find an effect of age or number of observations on habitat use (Tables 1 and 2). We found that the probability that dolphins used deep open habitat decreased with years, potentially due to changes in survey effort (Tables 1 and

TABLE 1 Parameter estimates from model used to estimate between-individual variation in habitat use

	Parameter	Habitat use	Channel	Deep	Shallow
$\beta_{(95\%\ \mathrm{CI})}$	Intercept	$66.48_{(-45.07\text{ to }166.77)}$	$-45.57_{(-92.14\text{ to }-0.12)}$	$66.79_{(11.77\text{ to }127.7)}$	$-37.63_{(-69.65\text{ to }-6.41)}$
	$\mathrm{Sex}_{\mathrm{Female}}$	$-1.66_{(-2.98\text{ to }-0.59)}$	$0.86_{(0.16\text{ to }1.50)}$	$-0.36_{(-1.08\text{ to }0.35)}$	$-0.41_{(-0.82\text{ to }0.03)}$
	$\mathrm{Sex}_{\mathrm{Male}}$	$-1.54_{(-2.71\text{ to }-0.37)}$	$0.78_{(0.11\text{ to }1.44)}$	$-0.001_{(-0.74\text{ to }0.69)}$	$-0.53_{(-0.96\text{ to }-0.09)}$
	Age	$-0.01_{(-0.07,\ 0.04)}$	$-0.0004_{(-0.03\text{ to }0.02)}$	$0.02_{(-0.001\text{ to }0.05)}$	$-0.02_{(-0.04\text{ to }-0.01)}$
	Sightings	$0.002_{(-0.002\text{ to }0.005)}$	$0.0008_{(-0.001\text{ to }0.002)}$	$-0.001_{(-0.003\text{ to }0.002)}$	$0.002\ _{(0.0006\text{ to }0.003)}$
	Year	$-0.03_{(-0.08\text{ to }0.02)}$	$0.02_{(-0.0004\text{ to }0.05)}$	$-0.003_{(-0.01\text{ to }-0.006)}$	$0.02_{(0.003\text{ to }0.03)}$
	$\mathrm{Month}_{\mathrm{JAN}}$	$-1.12_{(-1.72\text{ to }-0.56)}$	$0.58_{(0.27\text{ to }0.89)}$	$-0.42_{(-0.70\text{ to }-0.14)}$	$0.02_{(-0.27\text{ to }0.31)}$
	$\mathrm{Month}_{\mathrm{FEB}}$	$0.78_{(0.12\text{ to }1.42)}$	$-0.39_{(-0.74\text{ to }-0.08)}$	$0.25_{(0.03\text{ to }0.52)}$	$-0.02_{(-0.26\text{ to }0.23)}$
	$\mathrm{Month}_{\mathrm{MAR}}$	$-0.45_{(-0.80\text{ to }-0.08)}$	$0.24_{(0.06\text{ to }0.43)}$	$-0.13_{(-0.29\text{ to }0.33)}$	$-0.05_{(-0.22\text{ to }0.13)}$
	$\mathrm{Month}_{\mathrm{MAY}}$	$0.08_{(-0.17\text{ to }0.35)}$	$-0.04_{(-0.17\text{ to }0.09)}$	$-0.09_{(-0.20\text{ to }0.05)}$	$0.09_{(-0.03\text{ to }0.23)}$
	$\mathrm{Month}_{\mathrm{JUN}}$	$0.50_{(0.26\text{ to }0.76)}$	$-0.26_{(-0.38\text{ to }-0.13)}$	$-0.14_{(-0.27\text{ to }-0.02)}$	$0.36_{(0.24\text{ to }0.48)}$
	$\mathrm{Month}_{\mathrm{JUL}}$	$0.41_{(0.17\text{ to }0.66)}$	$-0.22_{(-0.34\text{ to }-0.09)}$	$-0.12_{(-0.22\text{ to }-0.0007)}$	$0.29_{(0.18\text{ to }0.41)}$
	$\mathrm{Month}_{\mathrm{AUG}}$	$1.07_{(0.83\text{ to }1.35)}$	$-0.55_{(-0.67\text{ to }-0.42)}$	$0.08_{(-0.03\text{ to }0.19)}$	$0.33_{(0.21\text{ to }0.45)}$
	$\mathrm{Month}_{\mathrm{SEP}}$	$0.27_{(0.01\text{ to }0.52)}$	$-0.13_{(-0.26\text{ to }0.001)}$	$-0.10_{(-0.22\text{ to }0.01)}$	$0.21_{(0.09\text{ to }0.33)}$
	$\mathrm{Month}_{\mathrm{OCT}}$	$-0.04_{(-0.29\text{ to }0.31)}$	$0.03_{(-0.10\text{ to }0.15)}$	$-0.36_{(-0.48\text{ to }-0.24)}$	$0.37_{(0.22\text{ to }0.45)}$
	$\mathrm{Month}_{\mathrm{NOV}}$	$0.05_{(-0.24\text{ to }0.31)}$	$-0.01_{(-0.16\text{ to }0.12)}$	$-0.36\ _{(-0.50\text{ to }-0.24)}$	$0.39_{(0.26\text{ to }0.51)}$
	$\mathrm{Month}_{\mathrm{DEC}}$	$-1.03_{(-1.36\text{ to }0.72)}$	$0.54_{(0.38\text{ to }0.70)}$	$-0.65_{(-0.83\text{ to }-0.50)}$	$0.19_{(0.03\text{ to }0.35)}$
$\sigma^2_{(95\%\ \mathrm{CI})}$	Dolphin ID	$5.98_{(5.05\text{ to }7.06)}$	$1.23_{(0.95\text{ to }1.52)}$	$2.07_{(1.64\text{ to }2.57)}$	$0.55_{(0.41\text{ to }0.68)}$
R		$0.58_{(0.55\text{ to }0.62)}$	$0.22_{(0.19\text{ to }0.26)}$	$0.32_{(0.28\text{ to }0.37)}$	$0.11_{(0.09\text{ to }0.14)}$
R^2	Marginal	$0.06_{(0.03\text{ to }0.09)}$	$0.05_{(0.03\text{ to }0.08)}$	$0.04_{(0.01\text{ to }0.07)}$	$0.05_{(0.01\text{ to }0.08)}$
	Conditional	$0.86_{(0.84\text{ to }0.88)}$	$0.57_{(0.52\text{ to }0.63)}$	$0.69_{(0.64\text{ to }0.74)}$	$0.38_{(0.32\text{ to }0.44)}$

β = fixed effect estimates; σ^2 = random effect variance; R = repeatability, defined as proportion of variance attributed to parameter; 95% credible intervals in subscript parentheses. All months are compared to reference month, which is set at April. Parameter estimates for 'Habitat Use' are derived from a multinomial model with a response variable of either channel, deep or shallow habitats, whereas the 'Channel', 'Deep' and 'Shallow' estimates are derived from three separate models with binary response variables denoting presence/absence in each habitat type at each observation. Marginal R^2 describes the proportion of variance explained by the fixed effects, and the conditional R^2 describes variance explained when including random effects. Both were calculated according to (Nakagawa & Schielzeth, 2013).

2). Furthermore, there was evidence for monthly differences in habitat use (see Tables 1 and 2 for details). However, the marginal R^2 (providing an estimate of how much variance was explained by fixed effects) was low (marginal $R^2 = 0.02–0.06$) in all our models (see Tables 1 and 2).

The variance in habitat use among-individuals was high (dolphin ID: $\sigma^2 = 5.98$, $95\%_{\mathrm{CI}} = 5.05–7.06$, Table 1), and the repeatability (i.e. proportion of variation attributed to among-individual variation) of habitat use was also high ($R = 0.58$, $95\%_{\mathrm{CI}} = 0.55–0.62$, Table 1). This suggests that there was considerable variation in individuals' habitat use after accounting for temporal and tracking effects, which was also reflected in a very high conditional R^2 for our model (conditional $R^2 = 0.86$). Variance among-individuals was also high for all three habitat types when investigating them separately, although considerably higher for the deep open habitat than either channel or shallow habitats (Table 1). Repeatability was highest for deep open habitat, and lowest for shallow habitats (channel: $R = 0.22$, $95\%_{\mathrm{CI}} = 0.19–0.26$; deep open: $R = 0.32$, $95\%_{\mathrm{CI}} = 0.28–0.37$; shallow: $R = 0.11$, $95\%_{\mathrm{CI}} = 0.09–0.14$, Table 1). This suggests that there was variation among-individuals in the probability of using any of the habitats, but that there was more variation among-individuals in the probability of using deep open habitat than for either channel or shallow habitats.

In the second model, we further partitioned individual variation in habitat use in order to estimate maternal effects. The variance in habitat use that was attributed to a maternal effect was high (maternal ID: $\sigma^2 = 3.45$, $95\%_{\mathrm{CI}} = 2.24–4.68$, Table 2) and the proportion of variance in habitat use associated with the maternal effect was also high ($R_{\mathrm{maternalID}} = 0.32$, $95\%_{\mathrm{CI}} = 0.26–0.39$, Table 2). The variance in habitat use associated with dolphin identity was slightly lower than the maternal effect (dolphin ID: $\sigma^2 = 2.94$, $95\%_{\mathrm{CI}} = 2.35–3.52$; $R_{\mathrm{dolphinID}} = 0.28$, $95\%_{\mathrm{CI}} = 0.23–0.32$, Table 2). Notably, maternal effect variance was higher for the deep open habitat than either channel or shallow habitats when investigating them separately (see Table 2), which corresponded with a greater proportion of variation attributed to the maternal effect for deep open than either channel or shallow habitats (channel: $R_{\mathrm{maternalID}} = 0.19$, $95\%_{\mathrm{CI}} = 0.15–0.24$; deep open: $R_{\mathrm{maternalID}} = 0.30$, $95\%_{\mathrm{CI}} = 0.25–0.35$; shallow: $R_{\mathrm{maternalID}} = 0.11$, $95\%_{\mathrm{CI}} = 0.08–0.14$, Table 2). We found that the variance in the probability of using each habitat that was attributed to dolphin identity was very low for all habitats (see Table 2). This suggests that individual variation in the probability of using each habitat was

TABLE 2 Parameter estimates from model used to estimate maternal and permanent environment effects associated with between-individual variation in habitat use

	Parameter	Habitat Use	Channel	Deep	Shallow
$\beta_{(95\%\ \text{CI})}$	Intercept	$77.62_{(-31.03\text{ to }184.64)}$	$-48.50_{(-81.45\text{ to }-19.45)}$	$40.18_{(9.17\text{ to }71.56)}$	$-2.04_{(-24.64\text{ to }21.76)}$
	$\text{Sex}_{\text{Female}}$	$1.95_{(-31.13\text{ to }-0.62)}$	$0.92_{(0.41\text{ to }1.47)}$	$0.07_{(-0.47\text{ to }0.65)}$	$-0.59_{(-0.99\text{ to }-0.23)}$
	Sex_{Male}	$-1.72_{(-2.97\text{ to }-0.57)}$	$0.74_{(0.33\text{ to }1.38)}$	$0.27_{(-0.25\text{ to }0.85)}$	$-0.35_{(-1.04\text{ to }-0.28)}$
	Age	$-0.003_{(-0.06\text{ to }0.05)}$	$-0.002_{(-0.02\text{ to }0.01)}$	$0.007_{(-0.008\text{ to }0.02)}$	$-0.004_{(-0.02\text{ to }0.008)}$
	Sightings	$-0.001_{(-0.01\text{ to }0.003)}$	$0.0006_{(-0.0007\text{ to }0.002)}$	$0.00008_{(-0.001\text{ to }0.001)}$	$0.0002_{(-0.0008\text{ to }0.001)}$
	Year	$-0.04_{(-0.09\text{ to }0.01)}$	$0.02_{(0.008\text{ to }0.04)}$	$-0.02_{(-0.04\text{ to }-0.004)}$	$0.0008_{(-0.01\text{ to }0.01)}$
	$\text{Month}_{\text{JAN}}$	$-1.14_{(-1.72\text{ to }-0.55)}$	$0.58_{(0.28\text{ to }0.88)}$	$-0.43_{(-0.72\text{ to }-0.14)}$	$0.03_{(-0.26\text{ to }0.33)}$
	$\text{Month}_{\text{FEB}}$	$0.78_{(0.10\text{ to }1.43)}$	$-0.39_{(-0.72\text{ to }-0.07)}$	$0.25_{(-0.003\text{ to }0.48)}$	$-0.02_{(-0.25\text{ to }0.25)}$
	$\text{Month}_{\text{MAR}}$	$-0.44_{(-0.77\text{ to }-0.09)}$	$0.24_{(0.05\text{ to }0.42)}$	$0.14_{(-0.30\text{ to }0.03)}$	$-0.03_{(-0.22\text{ to }0.13)}$
	$\text{Month}_{\text{MAY}}$	$0.08_{(-0.18\text{ to }0.35)}$	$-0.04_{(-0.17\text{ to }0.10)}$	$-0.09_{(-0.22\text{ to }0.04)}$	$0.10_{(-0.02\text{ to }0.23)}$
	$\text{Month}_{\text{JUN}}$	$0.52_{(0.30\text{ to }0.81)}$	$-0.27_{(-0.40\text{ to }-0.19)}$	$-0.14_{(-0.27\text{ to }-0.03)}$	$0.35_{(0.23\text{ to }0.47)}$
	$\text{Month}_{\text{JUL}}$	$0.43_{(0.18\text{ to }0.67)}$	$0.22_{(-0.35\text{ to }-0.09)}$	$-0.12_{(-0.23\text{ to }-0.004)}$	$0.28_{(0.18\text{ to }0.41)}$
	$\text{Month}_{\text{AUG}}$	$1.09_{(0.83\text{ to }1.34)}$	$-0.55_{(-0.67\text{ to }-0.40)}$	$0.08_{(-0.04\text{ to }0.19)}$	$0.32_{(0.21\text{ to }0.45)}$
	$\text{Month}_{\text{SEP}}$	$0.26_{(0.02\text{ to }0.53)}$	$-0.13_{(-0.25\text{ to }0.005)}$	$-0.10_{(-0.22\text{ to }0.007)}$	$0.21_{(0.09\text{ to }0.33)}$
	$\text{Month}_{\text{OCT}}$	$-0.06_{(-0.31\text{ to }0.19)}$	$0.03_{(-0.10\text{ to }0.15)}$	$-0.36_{(-0.47\text{ to }-0.24)}$	$0.33_{(0.21\text{ to }0.45)}$
	$\text{Month}_{\text{NOV}}$	$0.03_{(-0.24\text{ to }0.30)}$	$-0.004_{(-0.15\text{ to }0.13)}$	$-0.36_{(-0.49\text{ to }-0.23)}$	$0.74_{(0.25\text{ to }0.51)}$
	$\text{Month}_{\text{DEC}}$	$-1.07_{(-1.41\text{ to }-0.76)}$	$0.55_{(0.37\text{ to }0.69)}$	$-0.65_{(-0.81\text{ to }-0.48)}$	$0.18_{(0.002\text{ to }0.33)}$
$\sigma^2_{(95\%\ \text{CI})}$	$V_{\text{maternalID}}$	$3.45_{(2.24\text{ to }4.68)}$	$1.06_{(0.74\text{ to }1.39)}$	$1.89_{(1.39\text{ to }2.52)}$	$0.54_{(0.38\text{ to }0.72)}$
	$V_{\text{dolphinID}}$	$2.94_{(2.35\text{ to }3.52)}$	$0.15_{(0.09\text{ to }0.22)}$	$0.14_{(0.08\text{ to }0.22)}$	$0.09_{(0.04\text{ to }0.13)}$
R	Maternal ID	$0.32_{(0.26\text{ to }0.39)}$	$0.19_{(0.15\text{ to }0.24)}$	$0.30_{(0.25\text{ to }0.35)}$	$0.11_{(0.08\text{ to }0.14)}$
	Dolphin ID	$0.28_{(0.23\text{ to }0.32)}$	$0.03_{(0.02\text{ to }0.04)}$	$0.02_{(0.01\text{ to }0.03)}$	$0.02_{(0.01\text{ to }0.03)}$
R^2	Marginal	$0.06_{(0.03\text{ to }0.08)}$	$0.04_{(0.03\text{ to }0.06)}$	$0.02_{(0.01\text{ to }0.04)}$	$0.02_{(0.01\text{ to }0.02)}$
	Conditional	$0.87_{(0.85\text{ to }0.89)}$	$0.57_{(0.50\text{ to }0.63)}$	$0.68_{(0.62\text{ to }0.73)}$	$0.39_{(0.33\text{ to }0.46)}$

β = fixed effect estimates; σ^2 = random effect variance; R = repeatability, defined as proportion of variance attributed to parameter; 95% credible intervals in subscript parentheses. Parameter estimates for 'Habitat Use' are derived from a multinomial model with a response variable of either channel, deep or shallow habitats, whereas the 'Channel', 'Deep' and 'Shallow' estimates are derived from three separate models with binary response variables denoting presence/absence in each habitat type at each observation. Marginal R^2 describes the proportion of variance explained by the fixed effects, and the conditional R^2 describes variance explained when including random effects. Both were calculated according to (Nakagawa & Schielzeth, 2013).

attributed predominantly to a maternal effect, with very little variation attributed to either (non-maternal) additive genetic effects or components of the individuals' environment.

3.2 | Calving success

To investigate the relationship between habitat use and calving success, we used data from 203 females. The average number of calves weaned per year for these females was 0.10 (min = 0, max = 0.28), meaning that females successfully wean one calf on average every 10 years (max = one calf every 4 years).

Principal component analysis using proportional habitat use measures and selection ratios (which adjusts for the availability of habitats within the study site) produced similar results. Both of these analyses resulted in two principal components. The first component (PC1) described females' tendency to use deep open habitats over channel or shallow habitats, and explained 72% variance in the data. The second (PC2) described females' tendency to use channel habitat over shallow habitat, and explained 25% of variance in the data. The final principal component (PC3) explained a very small proportion of variance in the data (3%), and so was omitted from downstream analyses (Table S1). The average proportional similarity between an individual's habitat use and that of the population as a whole (Psi) was 0.61, which was greater than expected by chance ($\text{MC}_{\text{RESAMPLING}}$ p-value = 0.001), suggesting a high degree of individual specialisation in habitat use in the population. However, we found that individuals also varied substantially in the amount their habitat use reflected the population's overall habitat use (min = 0.29, max = 0.98, Figure 2c), suggesting variance in the tactic employed by individuals (e.g. specialist vs. generalist). We did not find any evidence for an effect of habitat use on calving success, which was true for all analyses we ran and for all measures of habitat use. For instance, there was no evidence to suggest that either principal components describing habitat use (i.e. PC1 = deep habitat over channel and shallow habitat, PC2 = channel over shallow habitat) predicted calving

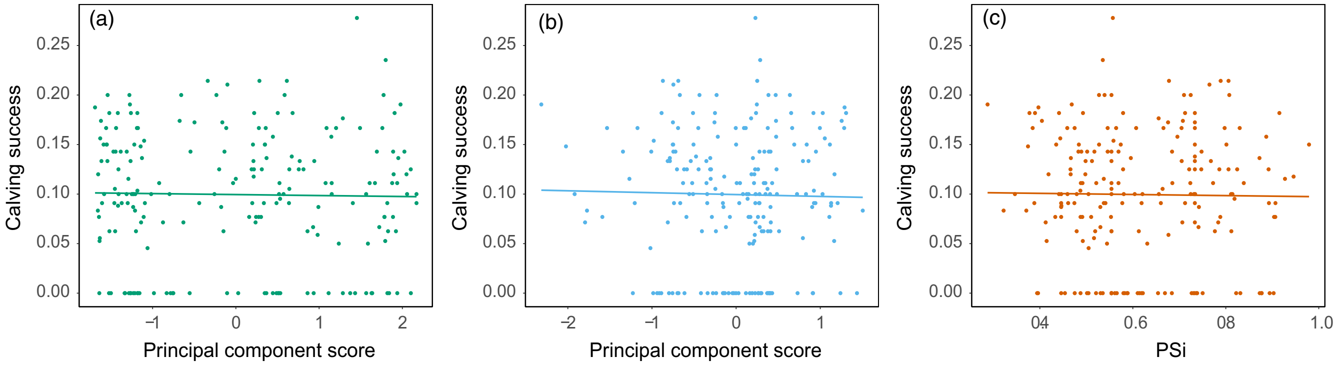

FIGURE 2 Relationship between habitat use and calving success for 203 female dolphins. Principal components in (a) and (b) were derived from selection ratio analysis. Principal component in (a) PC1: describes tendency to use deep open habitat over channel or shallow, and in (b) PC2: describes tendency to use channel over shallow habitat. (c) Psi is the proportional similarity of an individual's habitat use to the populations. Regression lines estimated from the mean of the posterior distribution in respective models

TABLE 3 Results from models used to investigate the effect of habitat use on calving success

Variable/model	Parameter	β
Habitat use	Intercept	$-2.41_{(-2.78,\ -2.06)}$
	PC1	$-0.08_{(-0.34,\ 0.18)}$
	PC2	$-0.11_{(-0.55,\ 0.34)}$
	Tracking time	$0.02_{(0,\ 0.03)}$
Selection ratio	Intercept	$-2.42_{(-2.79,\ -2.07)}$
	PC1	$-0.03_{(-0.11,\ 0.06)}$
	PC2	$-0.03_{(-0.18,\ 0.12)}$
	Tracking time	$0.02_{(0,\ 0.03)}$
Individual specialisation	Intercept	$-2.36_{(-2.94,\ -1.80)}$
	Psi	$0.07_{(-0.79,\ 0.65)}$
	Tracking time	$0.02_{(0,\ 0.03)}$

Habitat use = proportional use of each habitat; PC1 = describes tendency for individuals to use deep open habitat over channel or shallow habitat; PC2 = describes tendency for individuals to use channel over shallow habitat; Tracking time = total number of years that the female was observed; β = regression coefficient for the effect of each habitat use on calving success; 95% credible intervals in subscript parentheses.

success in females (Table 3; Figure 2a,b; Figure S2). Furthermore, there was no evidence to suggest that Psi predicted calving success in females (Table 3; Figure 2c).

4 | DISCUSSION

Individual variation in niche use has been found in several species (Araújo et al., 2011), and although we know that some of this variance may be attributed to age or sex effects, how it is maintained across generations and how it shapes individual fitness remains unclear. As such, our results provide insight into the evolution and maintenance of individual variation in niche use. We first demonstrate that a resident population of bottlenose dolphins show consistent individual variation in habitat use and exhibit a range of both generalist and specialist tactics in their habitat use. We then found that these patterns were attributed to a maternal effect for all habitat types. Finally, we show that habitat use did not predict individual variation in calving success.

Our results add to growing evidence for intraspecific variation in niche use across taxa (Bolnick et al., 2003). Of course, the niche is inherently multidimensional, and habitat use constitutes a single, although central, component of an organism's niche (Ingram et al., 2018). Dolphins in Shark Bay face distinct challenges in each habitat, as they differ in prey type, abundance and availability (Heithaus, 2004; Patterson & Mann, 2012) as well as level of predation risk (Heithaus & Dill, 2002). Accordingly, some dolphins in this population specialise in foraging tactics (Sargeant & Mann, 2009). For example, in the channel habitat, dolphins use tools that enable them to access prey that are well camouflaged and difficult to detect with echolocation (Mann et al., 2008; Patterson & Mann, 2011), and dolphins using shallow sand flats along the coast use strand-foraging or beaching to catch prey (Sargeant et al., 2005). Additionally, social behaviours such as male alliance structure and consortship rate vary with space use (Connor et al., 2017; Hamilton et al., 2019). It is likely that, together, these tactics contribute to the patterns of variation in habitat use found in this study, although formal investigation into the covariance of these behaviours would be needed to confirm this hypothesis. Interestingly, we found that habitat use did not change through ontogeny, aligning with evidence to suggest that home ranges are consistent through time in this population (Mann et al., 2021). As such, it could provide interesting insight into the development of habitat use to explore at what stage in their lifetime dolphins canalise their habitat use strategy.

Variation in habitat use was driven by a maternal effect for all habitat types. Dolphin calves spend, on average, 4 years' dependent on their mother (Karniski et al., 2018; Mann et al., 2000), adopt maternal foraging tactics early in life (Mann & Sargeant, 2003; Sargeant & Mann, 2009) and overlap extensively in home-range post-weaning

(Mann et al., 2021; Tsai & Mann, 2013). This all suggests that individuals learn where to live and forage from their mother through cultural transmission. Foraging tactics have also been shown to be culturally transmitted and reinforced through association in dolphins in Shark Bay (Mann et al., 2012). Cultural transmission is increasingly accepted as an important mechanism of inheritance and has been shown to accelerate the speed at which animals respond to their environment (Bonduriansky & Day, 2018; Danchin et al., 2004; Fisher & McAdam, 2019; Mameli, 2004). Our analyses were not able to explicitly distinguish between genetic and non-genetic maternal effects. However, it is likely given the life history and behaviour of this species that vertical social transmission constitutes a significant portion of the maternal effect identified here. Variation in habitat use was also associated with a dolphin identity effect, although this effect was very low when estimated for each habitat independently. This might reflect an additive genetic effect associated with variation in habitat use, as we were not able to partition permanent environment from additive genetic effects. Social transmission between peers (i.e. horizontal transmission) may also contribute to variance, although further data would be needed to accurately estimate such effects.

We found that while habitat use differed between individuals, habitat use did not correlate with female calving success. Similarly, Mann et al. (2008) found that tool-using dolphins that forage in channel habitats did not have different fitness from other females in the population. It is important to note that calving success reflects a component of long-term reproductive fitness, and although we selected this in order to measure long-term evolutionary consequences of habitat use, an individual's habitat use may still confer fitness benefits over shorter time periods (e.g. in a single year). Nevertheless, our results could suggest that there are no fitness consequences for habitat use in this population. However, this would be somewhat surprising given the known variation in resource availability (Heithaus, 2004), predation pressure (Heithaus & Dill, 2002) and sexual coercion (Connor et al., 2017; Hamilton et al., 2019) between habitat types in this population, all of which are likely to affect fitness. Alternatively, these results might suggest that individual variation in females' habitat use represent stable evolutionary strategies used to minimise competition for resources and maximise individual fitness. While our results contrast with recent research in other species showing that using certain habitats over others can provide increased fitness (Regan et al., 2016), they do align with theories of ecological niche partitioning (MacArthur, 1984). This is because we found that that no single habitat provides increased fitness over others. This may be a result of trade-offs between resource availability and potential costs or competition within each habitat. For example, in seagrass there is high abundance of prey species, but also a greater risk of predation from tiger sharks (Heithaus, 2004). Although we do not know how our results relate to levels of resource competition experienced by individuals per se, we do provide compelling evidence that niche partitioning may play an important role within a single population.

Our results provide new evidence to show that repeatable differences in individuals' habitat use does not result in differences in their calving success, a component of their fitness, potentially aligning with ecological theories of niche partitioning. Furthermore, our results suggest that maternal effects, common in species with parental care and which are likely composed of both genetic inheritance and cultural transmission, can facilitate the emergence of intraspecific niche variation. To truly understand the evolutionary consequences of maternal effects associated with niche partitioning, one must endeavour to link these patterns to population level responses. For instance, understanding how the processes involved in niche partitioning in this population relate to absolute fitness (i.e. population growth) would enhance our understanding of population dynamics. However, the paradox of the niche concept presents certain challenges to its study. For instance, the habitat that an organism uses is important because it provides the selective pressures and regimes that it will be subject to (Clark et al., 2019; Laland et al., 2001). However, individuals do not necessarily remain in the habitat that they find themselves in. Rather, they may actively select the habitat that they are most suited to (Sultan, 2015). In reality, it is likely a complex feedback of selecting and remaining in certain habitats, making the niche concept a challenge to study. In any case, understanding the temporal nature of niche/habitat use in response to temporal heterogeneity in environments or demographic events may help us to better understand the intricacies of the niche and how intraspecific variation is maintained.

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AUTHORS' CONTRIBUTIONS

K.S., J.M. and C.H.F. conceived the study; J.M., V.F. and A.L.L. collected observational and genetic data; J.M. curated data and obtained funding; A.L.L. contributed funding for genotyping; K.S. analysed the data; C.H.F. supervised all aspects of the study and provided funding; K.S. wrote the first draft of the manuscript; all authors contributed to reviewing and editing of manuscript.

DATA AVAILABILITY STATEMENT

All data needed to replicate analyses presented in the manuscript can be found at Strickland et al. (2021) and https://github.com/kashastrickland/dolphin_niche_construction.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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