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ORIGINAL PAPER

Sexual segregation in the foraging distribution, behaviour, and trophic niche of the endemic Boyd's shearwater (*Puffinus lherminieri boydi*)

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Abstract

Studies on sex-specific segregation in foraging behaviour and trophic niche have been focussed on large and dimorphic seabirds, with less information on small monomorphic species. Here, we used mini-GPS loggers, habitat suitability models, and stable isotopes to assess sex differences in the foraging movements, spatial distribution, and trophic ecology of Boyd's shearwaters *Puffinus lherminieri boydi* in Raso Islet (16°36' N, 24°35' W), Cabo Verde, during the chick-rearing periods of 2018–2019. The existence of sexual foraging segregation was tested in short (<1 day) and in long trips (≥ 1 day). Females engaged in slightly longer and more distant foraging trips, reaching northerly regions when compared to males, although sex differences were more pronounced during short trips. Spatial overlap within and between sexes was low, indicating a sex-specific pattern, albeit slight, in the foraging behaviour and spatial distribution of adult breeders. Habitat suitability models revealed a higher contribution of sea surface temperature and height for short and long trips, respectively, and regardless of sex. Stable isotope analysis revealed that both sexes occupied similar isotopic niches and the mixing model revealed no diet differences. In the absence of sexual size dimorphism, these findings may indicate that differential energetic demands may not manifest in strong differences in foraging behaviour or prey preferences, however, may be perceptible in differences in provisioning behaviour. Thus, it is possible that other factors involving distinct parental investment in chick-provisioning, such as the sensitivity to chick begging, could help explain the occurrence of sexual segregation in Boyd's shearwater.

Keywords Energetic constraints · Little shearwater · Monomorphic species · Spatial segregation · Species distribution modelling · Stable isotope mixing model

Introduction

Seabirds, as marine apex predators, are sensitive to changes at lower trophic levels, e.g. oscillations in prey availability caused by shifts in oceanographic conditions (Becker et al. 2007; Chimienti et al. 2017), and many are seen as optimal sentinel organisms for monitoring environmental and trophic changes in marine ecosystems worldwide (Furness and Camphuysen 1997; Scopel et al. 2017). In their foraging choices, seabirds are driven by extrinsic factors (i.e. environmental conditions) and also by intrinsic traits, such as sex,

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breeding stage or age (Votier et al. 2017; Sztukowski et al. 2018; Cerveira et al. 2020). The combined effect of such factors may explain the inter- and intra-species partitioning of food resources (Schoener 1974; Paiva et al. 2017), which is particularly meaningful when resources are more unpredictable and patchily distributed, as happens in tropical regions (Weimerskirch 2007).

Sexual segregation is one of the most studied subjects in seabird ecology, especially during the breeding season, when adult breeders adopt a 'central-place' foraging strategy, becoming spatially constrained by their breeding duties (e.g. Weimerskirch et al. 1994; Magalhães et al. 2008; Wojczulanis-Jakubas et al. 2018), resulting in segregation of foraging patterns in some species. Sexual segregation can be explained by three main intrinsic drivers. First, divergent parental roles should shape nest attendance and/or provisioning rates. The sex contributing more to chick provisioning would be less engaged in brooding or nest-site defence, i.e. 'reproductive role specialization' hypothesis (Paredes et al. 2006; Thaxter et al. 2009; Burke et al. 2015). For instance, in common guillemots *Uria aalge*, females were reported to invest more on chick provisioning while males invested more on self-feeding in order to prepare for the male-only parental care period during the post-fledging, when males become single parents and females are independent (Thaxter et al. 2009). Second, sexual segregation may emerge as a consequence of sex-specific nutritional requirements due to the differential parental investment during previous breeding stages, i.e. 'energetic constraint' hypothesis (Elliott et al. 2010; Pinet et al. 2012), such as the costs incurred by egg production and laying (Monaghan et al. 1998), unequal contribution to incubation (Pinet et al. 2012) or a sex-biased provisioning of chicks (Gray and Hamer 2001; Welcker et al. 2009). Third, sexual segregation may arise due to competitive exclusion as a consequence of differential competitive ability, flight or foraging efficiency, often driven by anatomic differences between males and females, i.e. sexual size dimorphism (SSD) (González-Solís et al. 2000; Phillips et al. 2004; Weimerskirch et al. 2006; Paiva et al. 2018). Here, the smaller sex, or the less efficient forager could then be outcompeted by the larger sex, or the more efficient forager, and forced to forage in less profitable waters or in remoter areas, as a way to avoid competition within foraging grounds, i.e. 'inter-sexual competition' hypothesis (González-Solís et al. 2000; Paiva et al. 2018; Almeida et al. 2021). Yet, size-mediated competitive exclusion is not the only mechanism behind sexual segregation in SSD species. In albatrosses, sexual dimorphism found in wing loading and wing area corresponded to distinct habitat preferences of males and females regarding the wind strength, suggesting a functional role of flight performance that influences at-sea distribution and mediates niche divergence/specialisation (Shaffer et al. 2001; Phillips et al. 2004; Clay et al. 2020). In another study, it was found a clear sexual segregation in foraging during years of 'poor' environmental conditions, likely years of lower food availability (Paiva et al. 2017). Female Cory's shearwaters *Calonectris borealis* undertook longer trips, enlarged their isotopic niche (i.e. an area (in δ-space) with isotopic values of different elements of a given organism's tissue (δ-values) as coordinates (Newsome et al. 2007)), fed on prey of lower trophic level, and presented lower body condition when compared to males (Paiva et al. 2017). This was in line with the hypothesis of competitive exclusion by the dominant sex (in this case males over females), which may be intensified when resources are scarce. Thus, when evaluating the existence of sexual segregation in foraging, the environmental context should always be considered, because sex differences may only be perceptible under specific conditions, such as food shortage (Gladbach et al. 2009; Paiva et al. 2017; Reyes-González et al. 2021).

Sex differences in foraging strategies (González-Solís et al. 2000; Pereira et al. 2018; Zango et al. 2020), at-sea spatial distribution (Phillips et al. 2011), parental roles (Austin et al. 2019), diet specialisation (Phillips et al. 2011), and niche partitioning (Paiva et al. 2017, 2018; Almeida et al. 2021; Reyes-González et al. 2021) have been frequently described in sexually dimorphic seabirds, such as albatrosses, boobies, and shearwaters. Yet, some studies have also reported the occurrence of sex differences in foraging patterns (Lewis et al. 2002; Welcker et al. 2009), parental role partitioning (Pinet et al. 2012), and isotopic niche in sexually monomorphic seabirds (Nisbet et al. 2002; Quillfeldt et al. 2008; Clark et al. 2021), indicating that body size would not be the explanation for sexual segregation in these species. In Barau's petrel *Pterodroma baraui*, during the prelaying exodus, males foraged in more chlorophyll-enriched waters farther from the colony, and systematically took the first incubation shift, which allowed females to recover their energy budgets depleted by oviposition (Pinet et al. 2012). In two sexually monomorphic gannet species, the northern gannet *Morus bassanus* and the Australasian gannet *M. serrator*, females occupied different trophic niches than males during the breeding stage (Stauss et al. 2012; Cleasby et al. 2015; Ismar et al. 2017). A more recent study showed that sex differences in foraging of northern gannets could arise from differential energetic demands that influenced resource partitioning (Bennison et al. 2022). Specifically, females experienced higher energetic demands, primarily due to the higher investment in chick provisioning, but also fed on different prey, possibly to avoid competitive exclusion by males (Bennison et al. 2022). Therefore, it seems that in some species, sex-specific foraging and resource partitioning may emerge from a combination of differential energetic requirements and competitive exclusion, underlining the fact that these drivers are not mutually exclusive, and not necessarily linked to size dimorphism (Clark et al. 2021; Bennison et al. 2022).

The ongoing miniaturisation of global positioning system (GPS) tags in the last few years, permitted the tracking of small-sized seabirds (Soanes et al. 2015; Surman et al. 2017; Zhang et al. 2019; Bolton 2021; Rotger et al. 2021), improving our knowledge on the detailed foraging movements, behaviour, and fine-scale spatial segregation, especially in tropical regions (e.g. Soanes et al. 2015; Surman et al. 2017). Boyd's shearwater *Puffinus lherminieri boydi* is a small-sized monomorphic procellariiform (Flood and van der Vliet 2019), with a current lack of information about its foraging behaviour, spatial distribution, and trophic ecology during the breeding season. To the best of our knowledge, only two studies tracked the movements of Boyd's shearwater using light-sensing geolocators (Zajková et al. 2017; Ramos et al. 2020). In addition, the trophic ecology of Boyd's shearwater during the breeding season is less known when compared to its closest-related counterpart, the Macaronesian shearwater *P. lherminieri baroli* (Neves et al. 2012; Ramos et al. 2015), and other larger breeding seabirds of Cabo Verde (Cerveira et al. 2020; Almeida et al. 2021). Here, we tracked the foraging movements of Boyd's shearwater using high-precision mini-GPS loggers and studied its trophic ecology during the chick-rearing period at Raso islet, Cabo Verde. We aimed to assess whether sexes differed in at-sea foraging behaviour, spatial segregation, and foraging habitat choices during short and long trips. During chick-rearing, pelagic seabirds usually adopt a dual-foraging strategy, involving repeated alternation of several short trips used mainly to find food for the offspring, with long trips used for adult self-provisioning to replenish the nutritional reserves depleted during successive chick-provisioning trips, e.g. Cory's shearwater, Cape Verde shearwater *C. edwardsii* (Magalhães et al. 2008; Cerveira et al. 2020). For species breeding at low profitable areas, long foraging trips often extend to areas of enhanced productivity, associated with shelf slopes, continental shelves, or frontal zones (Magalhães et al. 2008; Pereira et al. 2022). Given the lack of SSD, and an apparent equal investment of both sexes in breeding duties, we do not expect a strong sex-specific segregation in the foraging behaviour or spatial distribution within short and long trips. Simultaneously, we also aimed at assessing the isotopic niche occupied by each sex through stable isotope analysis (SIA) of carbon and nitrogen ratios (δ^{13}C and δ^{15}N, respectively), and the diet composition through isotopic mixing models. We do not expect sex-specific segregation in isotopic niche nor in diet composition, as it was already reported for its close-related counterpart the Macaronesian shearwater (Neves et al. 2012; Ramos et al. 2015).

Materials and methods

Study area and study species

Our study was carried out at Raso Islet (16°36' N, 24°35' W), Cabo Verde, an uninhabited islet integrated in the Integral Natural Reserve of Santa Luzia (Vasconcelos et al. 2015). Boyd's shearwater is a subspecies of little shearwater (c. 5,000 pairs), belonging to the *lherminieri* complex, breeding in the archipelago of Cabo Verde (BirdLife International 2020; Semedo et al. 2021). It is currently classified as "Least Concern" in the IUCN Red List; however, there are some signs of decline owing to the impacts caused by invasive species such as the black rat, *Rattus rattus* (BirdLife International 2020). This small-sized pelagic seabird (~ 160 g) is an endemic subspecies of Cabo Verde, and it is the nearest counterpart of the Macaronesian shearwater, which breeds in Azores, Madeira, Selvagens and Canary Islands (BirdLife International 2020). It is a winter breeder, and like other Procellariiformes, lays a single egg each breeding season. Briefly, adults arrive at the colony in August–September to prospect and defend their breeding burrow, females lay the egg in January–February, which hatches about 50 days later (mid-March) and the chick is fed approximately for 60 days, leaving the nest between the last half of May and the first half of June (Zajková et al. 2017).

GPS deployment and sample collection

From March to April 2018 and 2019, mini-GPS loggers (nanoFixTMGeo & Geo +, PathTrack Ltd., UK) were attached to the four central tail feathers of breeding adults, using TESA© tape (Wilson et al. 1997). Each logger together with the tape did not exceed 4 g weight, representing ~ 2.5% (2.0–2.9%) of adults' body mass (162.3 ± 18.3 g; range: 136–198 g). Although we acknowledge the potential deleterious effects of biologging on birds (Barron et al. 2010; Bodey et al. 2018; Gillies et al. 2020; Sun et al. 2020), the body mass of birds returning from a long trip, i.e. self-provisioning trip (Weimerskirch et al. 1994; Congdon et al. 2005), increased significantly from logger deployment (169.1 ± 26.0 g) to logger retrieval sessions (183.1 ± 29.4 g; paired t-test, $t_7 = 3.76$, $P = 0.007$). GPS deployment did not last more than 5 min, and adults were returned to the respective nests. Each logger was programmed to record each geographical position every 10 min (~ 140 locations per day). During deployment sessions, some breast feathers were collected for molecular sexing (see Table S1 for more details), while during logger retrieval, a blood sample (~ 0.8 ml) was collected from the brachial vein, centrifuged to separate plasma from red blood cells (RBC), and both blood partitions were kept in ethanol (70%) until preparation for SIA. Four tags were successfully retrieved in 2018 (3 males and 1 female) and 24 devices (12 males and 12 females) in 2019. Concurrently, putative prey samples were collected at local fish markets or occasionally captured during boat travelling to the islet, within the Natural Reserve of Santa Luzia, for subsequent SIA and diet modelling.

Sample preparation and stable isotope analysis

Plasma was selected for carbon and nitrogen isotopic analysis ($n = 16$), because its turnover rate corresponds approximately to the tracking period duration, i.e. around 5–7 days (Inger and Bearhop 2008), while RBC would reflect a larger timeframe of about 3–4 weeks (Bearhop et al. 2002; Cherel et al. 2005a). Nitrogen ($\delta^{15}N$; $^{15}N/^{14}N$) isotopic values are commonly used as a proxy of predator's trophic level, increasing about 2–5 ‰ at each trophic level (Minagawa and Wada 1986), while carbon ($\delta^{13}C$; $^{13}C/^{12}C$) values are used as a habitat indicator, because it only suffers a slight increase (*ca*. 0–1 ‰) at each trophic level (Kelly 2000). Seabird plasma and prey muscle were dried during 24 and 48 h, respectively, at 60 °C. Next, the samples were rinsed with a 2:1 chloroform:methanol solution to remove the overload of lipids that can deplete ^{13}C values (Cherel et al. 2005b; Post et al. 2007). All samples were ground to a powder, weighed (~ 0.35 mg) in tin capsules, and analysed through an elemental analyser/isotope ratio mass spectrometry (EA/IRMS) at MAREFOZ laboratory, in Figueira da Foz, Portugal. The results were expressed using the standard δ notation, following the equation: $\delta X = \left[\left(R_{\text{sample}}/R_{\text{standard}}\right) - 1\right] \times 1000$, where X is ^{13}C or ^{15}N, and R is the ratio ^{13}C:^{12}C or ^{15}N:^{14}N, respectively. R_{standard} values correspond to the Vienna Pee-Dee Belemnite (V-PDB) and atmospheric N_2, for ^{13}C and ^{15}N, respectively (Bond and Jones 2009). Replicate measurements of internal laboratory standards (acetanilide) indicate a precision of ± 0.2 ‰ for both carbon and nitrogen isotopic ratios. The C/N ratio was examined to verify if lipid removal was effective in all plasma and muscle samples.

Prey assemblage

Prey assemblage was established according to prey taxa (squid or fish), life-stage (larval or adult), and distribution in the water column (epipelagic or mesopelagic). In this sense, four main prey groups were initially set: epipelagic fish, mesopelagic fish, squid, and fish larvae. Epipelagic fish was comprised of three fish species which inhabit the epipelagic layer of the ocean (i.e. the upper 200 m of the water column): *Tylosurus acus*, *Sardinella maderensis*, *Selar crumenophthalmus*; mesopelagic fish was comprised of *Myctophum affine* and *Hygophum* sp.; squid included individuals of two different species: *Hyaloteuthis pelagica* and *Callimachus rancureli*; finally, fish larvae included fingerlings captured near surface during pelagic tours, identified as *Ophioblennius* sp. and *Synodus saurus*. All potential prey were identified to the lowest possible taxonomic level, weighed, and measured the body-length (for fish) or mantle-length (for squid). Preys were initially identified using local guides or catalogues and, specifically, squid were identified using their beaks (Xavier and Cherel 2009). In addition, a small piece of muscle tissue of each species was collected to create a DNA reference collection (see Table S1), either to confirm the previous identification or to achieve a lower taxonomic level. These species are among the most abundant of each group within Cabo Verde archipelago and are generally ingested by local breeding seabirds (Carreiro, personal observation).

GPS data analysis: behavioural classification and kernel estimation

To estimate missing locations and standardise sampling effort, GPS tracks were resampled by linear interpolation to exactly 10 min interval. Individual foraging trips were divided in short (< 1 day) and long (≥ 1 day), after inspecting trip duration frequency using a histogram (Fig. S1). To avoid potential disturbance caused by social interaction and flying movements while landing at the colony, a distance to colony filter of 1 km radii was applied (Pereira et al. 2021), to discard those locations. Maximum distance to colony, total distance travelled, latitude and longitude at the distal point of each foraging trip were computed using several functions within *trip* R package (Sumner et al. 2020). Behavioural classification was computed through the expectation–maximisation binary clustering (*EMbC* R package) algorithm coupled to a post-processing smoothing to account for a possible incorrect labelling of positions (Garriga et al. 2016; Cecere et al. 2020). This algorithm uses flight speed and turning angle values between consecutive locations to attribute a behavioural state: (1) low speed/low turning angle (LL; resting behaviour), (2) low speed/high turning angle (LH; intensive search or foraging behaviour), (3) high speed/high turning angle (HH; extensive search or relocating behaviour), or (4) high speed/low turning angle (HL; travelling behaviour).

Extensive (HH) and intensive search (LH) states were used together to represent the positions where adults were foraging. Extensive search characterises high speed movements when individuals are foraging in a large area in order to locate prey patches, while intensive search characterises the low speed and high turning movements when individuals adopt an area restricted search (ARS) behaviour after prey location (Weimerskirch 2007; Louzao et al. 2014;

Ravache et al. 2020). Following the methods and R scripts described by (Lascelles et al. 2016), we calculated mean ARS zones radii for short and long trips, and used those values as smoothing parameters (*h*) in the computation of Kernel Utilization Distribution (Kernel UD). A smoothing parameter of 4 km was used for short trips, and a smoothing parameter of 8 km for long trips. Kernel UD contours (95% and 50%), and its areas, were calculated using the 'kernelUD' and 'kernel.area' functions, respectively, within the *adehabitatHR* R package (Calenge 2006). The 50% and the 95% UD contours were computed to represent adults' foraging areas (FA) and home range areas (HR), respectively. The overlap of UD contours, with land omitted, was calculated between sexes within short and long trips using the 'kerneloverlap' function, using the Bhattacharyya's affinity (BA), under the *adehabitatHR* R package (Calenge 2006).

Environmental predictors and habitat suitability models

Monthly values of ocean (1) bathymetry (BAT, blended ETOPO1 product, 0.01° spatial resolution, m), (2) chlorophyll *a* concentration (CHL, 0.04° spatial resolution, mg m^{-3}), (3) ocean mixed layer thickness (OMLT, 0.08° spatial resolution, m), (4) sea surface height above geoid (SSH, 0.08° spatial resolution, cm), and (5) sea surface temperature (SST, 0.08° spatial resolution, °C) were extracted within the foraging range of Boyd's shearwater for March 2018–2019 and April 2019, and the mean raster was calculated for each environmental predictor. Variable 1 was downloaded from https://www.ngdc.noaa while variables 2–5 were downloaded from http://marine.copernicus.eu. Spatial gradients were calculated by estimating rates of change by moving a window function (3 × 3 grid cells; function = [(max. value − min. value) × 100]/(max. value)) (Louzao et al. 2009). Bathymetry gradient (BATG) identifies the presence of oceanic topographic features, such as seamounts or shelf-breaks (i.e. slope areas); the gradient of CHL (CHLG) and SST (SSTG) can be used as a proxy of oceanic fronts, while OMLT gradient (OMLTG) indicate the change level on the mixed layer thickness, and consequently, the depth of the thermocline which drives the abundance and distribution of marine prey; the gradient of SSH (SSHG) could help identify the occurrence of mesoscale eddies. All environmental predictors were rescaled to the coarsest spatial resolution (i.e. 0.08°) and extracted for each GPS location, before running habitat suitability models. All computations were conducted under several functions within *raster* R package (Hijmans et al. 2020).

Habitat suitability models were computed separately for males and females for long and short trips, i.e. four modelling exercises. Tracking data from 2018 and 2019 was jointly analysed given the low sample size of tags retrieved in 2018 and similar foraging range and distribution between years (Fig. S2). Prior to habitat modelling, all environmental predictors (BAT, CHL, OMLT, SSH, SST), and respective gradients (BATG, CHLG, OMLTG, SSHG, SSTG), were inspected for multicollinearity issues, using the variation inflation factor (VIF > 2.5), while correlation among environmental predictors was examined using Pearson correlation coefficients (r > 0.6) (Table S2), under the *usdm* R package (Naimi 2017). Testing for collinearity issues enables to account only with non-redundant variables, avoiding model overfitting and inflated errors (Zurell et al. 2020). Ensemble Species Distribution Models (ESDM; Marmion et al. 2009) were computed using the 'ensemble_modelling' function within the *SSDM* R package (Schmitt et al. 2017) using all GPS locations (presence data; Fig. S3), and with modelling, 10,000 pseudo-absences were randomly generated (Barbet-Massin et al. 2012) within the foraging range of adult Boyd's shearwaters as previously computed for little shearwaters (Ramos et al. 2020) and Cape Verde shearwater (Cerveira et al. 2020). For modelling exercises, we tested 7 algorithms that are commonly used in ensemble model exercises: Artificial Neural Network (ANN), Classification Tree Analysis (CTA), Generalised Additive Models (GAM), Generalised Linear Models (GLM), Multiple Adaptive Regression Splines (MARS), Random Forest (RF), and Support Vector Machine (SVM). Each model algorithm was computed ten times using a tenfold cross-validation procedure, using 70% of all data set for model calibration and the remaining 30% grid squares as random test for model validation (Araujo et al. 2005; Marmion et al. 2009; Zurell et al. 2020). This conservative approach avoids model overfitting and minimises effects of spatial autocorrelation in both seabird presence and environmental predictors. Model goodness of fit was examined using the area under the receiver-operating characteristic (ROC) curve (AUC). Models were classified excellent when AUC > 0.90, good when 0.80 < AUC < 0.90, reasonable when 0.70 > AUC < 0.80, and not acceptable when AUC < 0.70 (Araujo et al. 2005). The relative contribution of environmental predictors to the probability of occurrence of each sex within short or long trips was given by the average contribution calculated from all models.

Isotopic niche and mixing models

Stable Isotope Bayesian Ellipses in R, i.e. *SIBER* (Jackson et al. 2011), were used to calculate the isotopic niches of females and males. Bayesian estimation of standard ellipse area (SEA_B), encompassing 40% of all observations within each group, was calculated using Markov-chain Monte Carlo runs with 2 × 10,000 iterations; the first 1 × 1000 runs were discarded, thinned by ten and over two chains (Jackson et al. 2011). We extracted 95% credible intervals (CI) of SEA_B, and based on this Bayesian approach we calculated the probability of group 1 (e.g. females) SEA being smaller than that of group 2 (e.g. males), using the *rjags* R package (Plummer et al. 2019). Standard ellipse areas corrected for small sample size (SEA_C) were computed for visualisation purposes. Bayesian estimates of overlap between males' and females' standard ellipse areas was scaled to include 95% of data distribution, and calculated for each posterior draw (and averaged over the 1000 draws) using the 'bayesianOverlap' function within *SIBER* R package (Jackson et al. 2011). We extracted 95% CI and calculated the proportion of overlap between the two ellipses, drawn as the proportion of the non-overlapping areas (i.e. $prop_{overlap} = area_{overlap}/(area\ ellipse_2 + area\ ellipse_1 - area_{overlap})$).

The contribution of each prey group for Boyd's shearwater diet was estimated using Bayesian mixing models within the *simmr* package (Parnell and Inger 2016). Prior to running the mixing model, prey isotopic signatures ($\delta^{13}C$—$\delta^{15}N$) were visually inspected to warrant prey groups occupied different isotopic niches (Fig. S4). Thus, *C. rancureli*, *Hygophum* sp., and one specimen of *H. pelagica* were excluded from the mixing model exercise: epipelagic fish (mean ± SD: $\delta^{13}C = -16.95 \pm 0.48$ ‰, $\delta^{15}N = 9.72 \pm 0.70$ ‰, $n = 16$; $C/N = 3.59 \pm 0.06$), mesopelagic fish (mean ± SD: $\delta^{13}C = -18.78 \pm 0.40$ ‰, $\delta^{15}N = 10.26 \pm 0.45$ ‰, $n = 8$; $C/N = 3.20 \pm 0.05$), squid (mean ± SD: $\delta^{13}C = -16.17 \pm 0.51$ ‰, $\delta^{15}N = 12.98 \pm 0.65$ ‰, $n = 4$; $C/N = 2.89 \pm 0.11$), and fish larvae (mean ± SD: $\delta^{13}C = -18.68 \pm 0.24$ ‰, $\delta^{15}N = 8.38 \pm 0.43$ ‰, $n = 10$; $C/N = 3.04 \pm 0.04$). Trophic discrimination factors (TDFs) are needed to accurately run the isotopic mixing model and these are often tissue-specific, species-specific and diet-specific, meaning that they may vary according to consumer's species and its diet, and the tissue analysed (Phillips et al. 2014). To our best knowledge, there are no TDF available for Boyd's shearwaters; hence, TDF values were obtained using the *SIDER* R package (Healy et al. 2018), a package that uses a phylogenetic regression model using Bayesian inference based on a compiled dataset to estimate the most accurate discrimination factors. This recent approach was already successively applied to study wild animal diets, including birds (e.g. Johnson et al. 2020; Swan et al. 2020; Morgenthaler et al. 2021; Navarro et al. 2021). We performed a prior selection of the discrimination factors provided by *SIDER* dataset, based on the type of tissue (blood), habitat (marine), and diet type (carnivore). Therefore, we used a TDF of 0.39 ± 1.11 ‰ (-1.80—2.61, 95% CI) and $+2.62 \pm 1.21$ ‰ (0.26—4.99, 95% CI) for carbon and nitrogen, respectively. Before running the model, a simulation method proposed by Smith et al. (2013) was used to inspect the feasibility of the isotopic mixing polygons. The sensitivity analysis (using 1500 iterations) applied to mixing polygons indicated that none of adult isotopic signatures felt outside the 95% source mixing regions (probability ranges: 0.07 to 0.37 for males, 0.13 to 0.49 for females), validating our model (Fig. S5). A final mixing model with sex as covariate was computed using the function 'simmr_mcmc' from the *simmr* R package (Parnell and Inger 2016). Comparisons of dietary proportions between males and females were calculated for each prey group (i.e. source), as the probability of the proportion of a given source (e.g. squid) in group 1 (e.g. females) being higher than in group 2 (e.g. males), using the function 'compare_groups' within the *simmr* R package (Parnell and Inger 2016).

Statistical analysis

Generalised linear mixed models (GLMMs) were used to test the effect of sex on adult trip parameters, at-sea foraging behaviour, and at-sea spatial use, separately for short and long trips: (1) trip duration, (2) maximum distance to colony, (3) total distance travelled, (4) percentage of time spent foraging, (5) latitude and (6) longitude coordinates at the maximum distance to colony, (7) kernel area of foraging areas (FA; 50% UD) and (8) kernel area of home range areas (HR; 95% UD). All models were run using sex as a fixed factor, while the bird identity (i.e. individual) was included as a random factor to avoid pseudo-replication. Years were pooled together due to the lower sample size recorded in 2018 (3 males and 1 female). Spearman correlation coefficients revealed a positive and strong correlation ($r_s > 0.7$) among trip duration, maximum distance to colony, and total distance travelled, thus the mixed model was only run for trip duration. Mixed models were conducted with the *lme4* R package (Bates et al. 2015). All response variables were tested for normality, transformed to follow a Gaussian distribution if necessary or by specifying the family (and respective link function) within the model. Specifically, kernel areas of FA and HR were log transformed, while for trip duration a GLMM with a Gamma distribution (inverse link function) was used. The values are expressed as mean ± SD throughout the results. All analyses and modelling computations were performed using the R software ver. 4.0.2 (R Core Team 2020) and the significance level was set at $P \leq 0.05$.

Results

Foraging behaviour and foraging areas during short and long trips

Over the two chick-rearing periods, each logger recorded an average of 5.1 ± 1.7 days in a total of 98 trips made by 28 adult Boyd's shearwaters (M: $n = 15$; F: $n = 13$). Of these, 59 trips were classified as short trips (M: $n = 34$; F: $n = 25$), while 39 trips were classified as long trips (M: $n = 20$; F: $n = 19$). Overall, both sexes foraged in waters

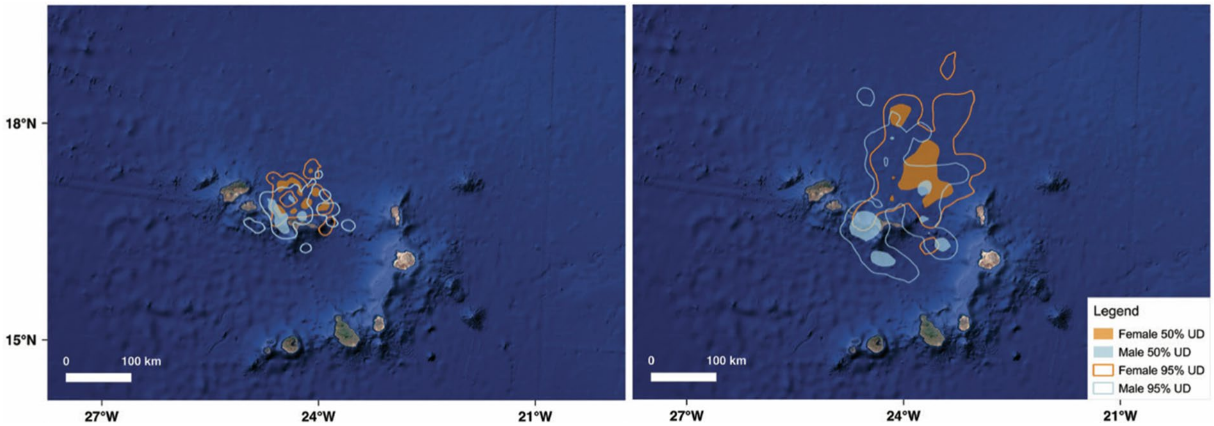

Fig. 1 Main core foraging areas (FA; 50% UD, filled polygons) and home range areas (HR; 95% Kernel UD, solid lines) used by male (blue) and female (orange) Boyd's shearwaters during short (< 1 day trips; left panel) and long (≥ 1 day trips; right panel) foraging trips during the chick-rearing periods of 2018–2019. Bathymetric relief in the background

Table 1 Trip characteristics, foraging behaviour, and spatial ecology parameters of male and female Boyd's shearwaters during the chick-rearing periods of 2018–2019 at Raso islet (joint data for both years), Cabo Verde. Individual trips were separated by its duration as short (< 1 day) or long (≥ 1 day) foraging trips. The overlap of foraging areas (FA) was measured within each sex and trip type and between sexes (within trip type) using the Bhattacharyya's affinity index (BA). Values are mean ± SD

	Short trips		Long trips	
	Males	Females	Males	Females
Trip parameters				
Number of trips [*n* birds]	34 [13]	25 [12]	20 [13]	19 [11]
Trip duration (days)	0.60 ± 0.05	0.63 ± 0.06	1.65 ± 0.80	2.59 ± 1.57
Maximum distance to colony (km)	52.17 ± 28.82	75.65 ± 20.68	107.93 ± 50.47	150.46 ± 57.34
Total distance travelled (km)	117.98 ± 51.87	143.11 ± 54.10	221.37 ± 97.49	309.51 ± 114.83
Latitude coordinates (at maximum distance, ºN)	16.77 ± 0.22	17.06 ± 0.27	17.01 ± 0.64	17.56 ± 0.56
Longitude coordinates (at maximum distance, ºW)	−24.29 ± 0.38	−24.18 ± 0.27	−23.92 ± 0.44	−23.69 ± 0.38
Time spent foraging (%)	28.19 ± 11.46	19.96 ± 10.54	22.62 ± 9.48	16.46 ± 4.86
Time spent relocating (%)	12.17 ± 6.11	9.02 ± 4.61	6.61 ± 4.19	2.00 ± 0.82
Time spent resting (%)	12.42 ± 9.71	13.65 ± 11.48	36.39 ± 13.11	36.24 ± 2.00
Time spent travelling (%)	47.06 ± 13.92	57.09 ± 11.59	34.39 ± 10.20	45.10 ± 5.07
Spatial ecology parameters				
Foraging areas (FA): 50% UD area (km^2)	143.87 ± 46.10	150.76 ± 56.30	652.38 ± 322.12	755.56 ± 502.10
Home range areas (HR): 95% UD area (km^2)	626.45 ± 192.93	679.45 ± 251.08	3500.05 ± 2519.25	3647.71 ± 2395.50
FA overlap within sex and trip type (BA index)	0.02 ± 0.02	0.01 ± 0.01	0.02 ± 0.04	0.01 ± 0.01
FA overlap among sex, within trip type (BA index)	0.01 ± 0.01		0.01 ± 0.01	

close to the colony, travelling for short distances and for short periods of time (Fig. 1, Table 1). Adults were more likely to be foraging at sea during the day but also exhibited two peaks of foraging activity during crepuscular hours (Fig. S6). During short trips, males carried out slightly shorter trips (in duration), kept closer to the colony, over waters further south, and spent more time foraging than females. Size of foraging (FA, 50% UD) and home range areas (HR, 95% UD), calculated for each foraging trip, were consistently larger for females than for males (Table 2). During long trips, males carried out slightly shorter trips (both in duration and distance), kept slightly closer to the colony over waters further south, and showed slightly smaller HR than females (Table 2). The overlap within and between sexes and trip type was low, evidencing spatial segregation at the foraging trip and sex levels (Fig. 1, Table 1).

Table 2 Summary of (generalised) linear mixed models used to test the effect of sex on trip metrics, at-sea foraging behaviour, and at-sea spatial use parameters of adult Boyd's shearwaters during short and long foraging trips. All models included bird identity (i.e. individual) as a random factor to avoid pseudo-replication issues. Parametric coefficients ($\beta \pm$ SE), *t*, and *P* values are also shown. Significant values ($P \leq 0.05$) are shown in bold

Models	Short trips				Long trips			
	$\beta \pm$ SE	*t* value	*P* value	Effect	$\beta \pm$ SE	*t* value	*P* value	Effect
Trip duration	−0.04 ± 0.02	−2.09	**0.05**	M < F	−0.45 ± 0.22	−2.09	**0.04**	M < F
Latitude at maximum distance	−0.33 ± 0.08	−4.16	**< 0.001**	M < F	−0.54 ± 0.23	−2.35	**0.03**	M < F
Longitude at maximum distance	−0.12 ± 0.11	−1.12	0.27		−0.23 ± 0.13	−1.71	0.11	
Time spent foraging	8.05 ± 3.49	2.31	**0.03**	M > F	0.17 ± 0.09	1.84	0.07	
50% Kernel UD (FA)	−0.28 ± 0.07	−3.74	**< 0.01**	M < F	−0.28 ± 0.15	−1.93	0.07	
95% Kernel UD (HR)	−10.20 ± 2.67	−3.82	**< 0.001**	M < F	−16.75 ± 7.35	−2.28	**0.03**	M < F

Habitat modelling

Multicollinearity examinations detected that only two of the ten tested environmental variables showed collinearity issues, i.e. BAT and CHLG, and consequently were not used for habitat modelling exercises. The ESDMs computed separately for short and long trips for male and female adults (four ensemble models in total), exhibited good to excellent predictive performance (0.88 < AUC < 0.94, Table S3), which indicates that models were quite efficient in separating the suitable from the unsuitable marine habitats for adult Boyd's shearwaters. Variable relative contribution was quite similar between sexes in explaining adults' distribution during both short and long trips (Fig. 2, Table S3); SST was the variable that best explained the distribution of Boyd's shearwaters during short trips, while SSH was the variable that best explained their distribution during long trips. Despite its reduced relative contribution, CHL was the variable that differed the most between sexes during long trips (Fig. 2, Table S3). Interestingly, females preferred regions with

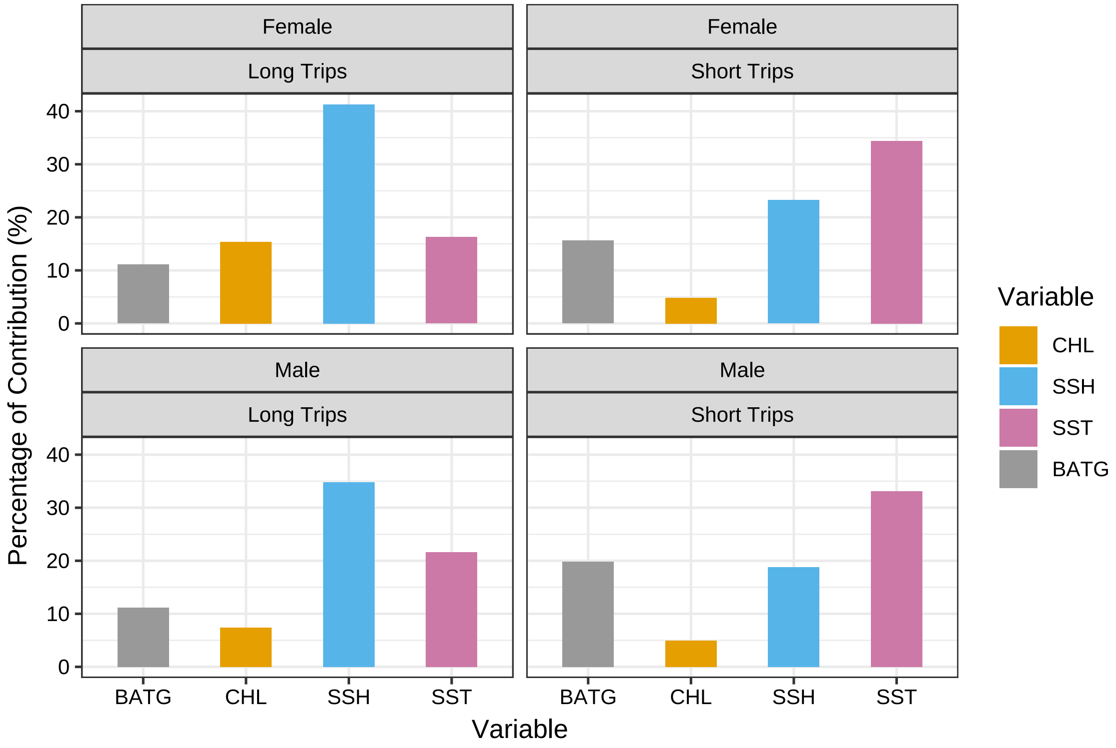

Fig. 2 Percentage contribution of gradient of bathymetry (BATG), chlorophyll a concentration (CHL), sea surface height (SSH), and sea surface temperature (SST) in explaining the at-sea distribution of adult male and female Boyd's shearwater during short and long foraging trips, recorded during the chick-rearing periods of 2018–2019 (more details in Table S3)

Table 3 Males and females isotopic niche measurements of Boyd's shearwaters, using plasma signatures collected chick-rearing period of 2019. Carbon and nitrogen isotopic values (mean ± SD) are expressed in ‰. SEA_C represents the area of the standard ellipse (explaining 40% of the total data) corrected for small samples sizes; SEA_B (CI) represents the Bayesian estimation of standard ellipses and the respective 95% credible intervals; SEA_B (P=) assesses niche size probability differences between sexes; C/N represents the average ratio between carbon and nitrogen percentage values

Sex	$\delta^{13}C$	$\delta^{15}N$	SEA_C	SEA_B (CI)	SEA_B (P=)	C/N
Males (n=8)	− 18.47 ± 0.55	11.11 ± 0.57	0.92	0.96 (0.36–1.75)	0.19	3.78
Females (n=8)	− 18.31 ± 0.40	11.36 ± 0.44	0.63	0.61 (0.22–1.09)		3.79

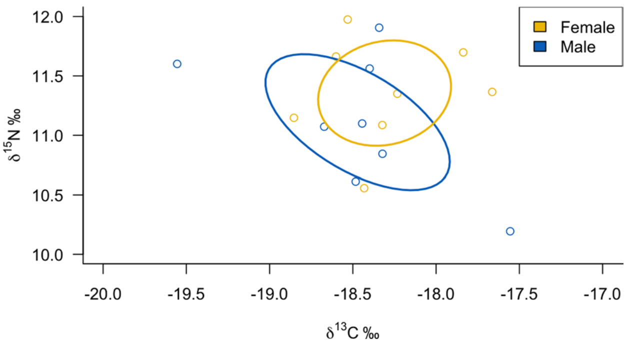

Fig. 3 Isotopic niches of male (blue) and female (orange) Boyd's shearwaters plasma at Raso islet, Cabo Verde. The standard ellipse area corrected for small sample sizes (SEA_C) is presented in solid bold lines

slightly higher SSH during short and long trips, while during long trips females distributed along regions with slightly lower CHL than males (Fig. S7).

Isotopic niche and diet composition

Overall, there was no evidence that male and female occupy different isotopic niches according to plasma isotopic signatures (MANOVA, Wilks's λ, $F_{1,14} = 0.95$, $P = 0.41$, $n = 16$; Table 3, Fig. 3). A separate analysis for each stable isotope revealed that neither $\delta^{13}C$ ($F_{1,14} = 0.46$, $P = 0.51$) and $\delta^{15}N$ ($F_{1,14} = 0.93$, $P = 0.35$) values showed evidence of sex differences. The Bayesian estimation of standard ellipse area (SEA_B) revealed no evidence of sex differences on the isotopic niche ($SEA_{B\ (MALES)} = 0.96$ (0.36–1.75, 95% CI), $SEA_{B\ (FEMALES)} = 0.61$ (0.23–1.09, 95% CI), Table 3), nor on isotopic niche size (probability that $SEA_{B\ (FEMALES)} > SEA_{B\ (MALES)} = 0.19$, Table 3). The overlap of isotopic niches, here represented by the overlap of Bayesian estimates of standard ellipse area indicated that approximately 34% (10 − 59%, 95% CI) of males' isotopic niche overlapped with that of females (Fig. 3). The isotopic mixing model showed no apparent diet differences between sexes, indicating a major reliance on fish larvae (M: 69.1 ± 12.3%; F: 62.2 ± 11.8%), followed by mesopelagic fish (M: 16.1 ± 11.7%; F: 19.8 ± 11.8%), while epipelagic fish (M: 9.5 ± 6.6%; F: 12.1 ± 7.6%) and squid had a minor importance in the diet of Boyd's shearwaters (M: 5.3 ± 3.5%; F: 6.0 ± 3.6%) (Fig. 4).

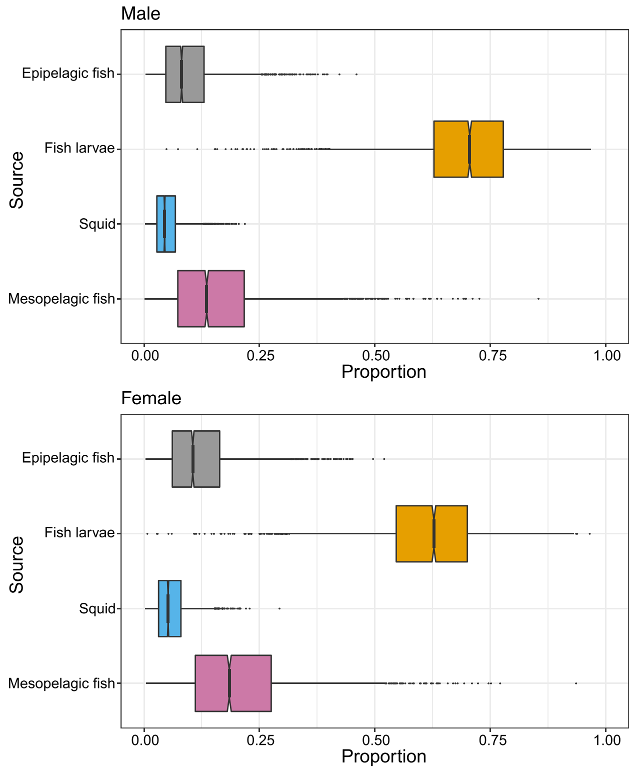

Fig. 4 Stable isotope Bayesian mixing model graphical outputs exhibiting the prey contributions in the diet of Boyd's shearwaters. Boxplots display the range between 25 and 75% quantiles, error bars extend to a maximum (97.5%) and minimal values (2.5%), and the mean is represented by the solid black line. The top panel corresponds to diet outputs obtained for males, and the bottom panel for females. For clarification of prey species belonging to each group, please consult "Prey assemblage" and "Isotopic niche and mixing models" in Methods

Discussion

Our study documented a partial sex-specific segregation in foraging by adult Boyd's shearwaters during the chick-rearing period. We found a sex-specific pattern on adult foraging distribution, with females consistently reaching further and northerly areas and exhibiting enlarged foraging and home range areas, although the evidence of sex differences were stronger in short than in long trips. The foraging distribution was largely explained by sea surface temperature (SST) and sea surface height (SSH) during short and long trips, respectively, and regardless of sex. There was no strong evidence of sex differences in the isotopic niche, although the overlap was not complete, and the mixing model revealed similar diets between sexes, mostly comprised of fish larvae.

Overall, Boyd's shearwaters foraged mostly near the colony (up to 300 km), in the pelagic waters located northwards of the archipelago of Cabo Verde. This is in line with the prevalence of an oceanic foraging distribution in the colony surroundings, reported in previous studies using light-sensing geolocators (Zajková et al. 2017; Ramos et al. 2020), and in other close-related *Puffinus* spp. during the breeding season (Neves et al. 2012; Ramos et al. 2015). Alternation between short and long trips is a common strategy adopted by Procellariiformes during the chick-rearing period, where adults use several short trips to provision food to their offspring, to cope with the nutritional needs of their growing chick and ensure breeding success, with one or two long trips for self-provisioning to replenish body reserves depleted during short trips (Weimerskirch et al. 1994; Congdon et al. 2005). We must underline, however, that our low sample size and the short period of tracking might have limited the power to detect a more pronounced dual-foraging in Boyd's shearwaters, thus, we opted to discuss the results with caution and aside from the dual-foraging.

In monomorphic biparental care species, sex differences in nest attendance, chick provisioning, and overall foraging strategy were traditionally pointed out as a consequence of distinct parental roles, competitive exclusion or differential energetic constraints (Peck and Congdon 2006; Thaxter et al. 2009; Welcker et al. 2009). In thick-billed murres *U. lomvia* and razorbills *Alca torda*, females were found to provide more food to their offspring, while males spent more time brooding the nestlings. Parental role differences were related to the male-biased capability of defending the nest, and not necessarily to the female-biased provisioning effort (Paredes et al. 2006). However, our results do not support this hypothesis because males and females presented only slight differences in foraging trip duration, and we have no concrete evidence that can attest the occurrence of parental role specialisation in Boyd's shearwater.

Sex-specific foraging behaviour could, on the other hand, evolve from competitive exclusion at the foraging grounds, often attributed to size-related differences in SSD species that may be indicative of differential foraging and flight performance (González-Solís et al. 2000; Phillips et al. 2004; Weimerskirch et al. 2006; Almeida et al. 2021). The incidence of competitive exclusion was already suggested for sexually monomorphic species, although the proximate mechanism by which this could have emerged may not be so obvious as for sexually dimorphic species (Peck and Congdon 2006). Resource partitioning is expected to be greater when resources are scarcer or when larger individuals outcompete the smaller co-specifics from using the same resources (Young et al. 2010; Phillips et al. 2011; Almeida et al. 2021). In fact, tropical marine regions are often described as oligotrophic environments where food resources are more limited (Jaquemet et al. 2005; Mann and Lazier 2013). The seasonal and localised upwelling felt during winter within and around the archipelago of Cabo Verde (Meunier et al. 2012; Peña-Izquierdo et al. 2012; Cardoso 2017) may, however, provide sufficient resources for Boyd's shearwaters when exploring colony surroundings during short trips and more pelagic and northerly waters during long trips. Our results do not greatly support a competitive exclusion scenario at the foraging grounds, since there is no obvious foraging segregation between sexes, neither evidence of higher aggressiveness of male shearwaters, as previously observed for gannets (Nelson 1965), and suggested as a potential driver of female displacement to more distant foraging grounds (Lewis et al. 2002; Stauss et al. 2012). In addition, in a recent study, female northern gannets exhibited greater proportions of vessel-associated foraging, although males have shown a higher consumption of fishery discards (Giménez et al. 2021). Despite females being slightly heavier than males, the higher aggressiveness of male gannets was underlined as a possible explanation for this sexual mismatch between vessel-associated foraging and discard consumption (Giménez et al. 2021). Thus, competitive exclusion may also occur in sexually monomorphic or slight dimorphic species, however, might be more context-dependent and related to localised competition for food resources, such as fishery discards.

Despite the biparental care, adult breeders may invest slightly different in breeding duties, according to disparate energetic constraints (e.g. Pinet et al. 2012). Once both parents share the incubation of the egg, it can be claimed that females might be energetically more depleted and in poorer body condition at the onset of the rearing period, due to carry-over costs incurred at the time of egg production and laying (Monaghan et al. 1998). In this regard, males may attempt to compensate the greater nutritional requirements of females by investing more during incubation or during the chick-provisioning (Lewis et al. 2002; Pinet et al. 2012). The slight longer foraging trips carried out by female Boyd's shearwaters may suggest sex-specific energetic constraints in foraging behaviour, however, the high overlap of isotopic niches and diet composition indicates there is no resource partitioning between sexes, which may suggest that nutritional requirements did not drive segregation in foraging. Actually, there are some studies that reported sex-related differences in the isotopic niche of sexually monomorphic species, such as the common tern *Sterna hirundo* (Nisbet et al. 2002), thin-billed prion *Pachyptila belcheri* (Quillfeldt et al. 2008), and the northern (Cleasby et al. 2015; Clark et al. 2021) and Australasian gannets (Ismar et al. 2017), although sex differences in foraging behaviour were only observed in gannets. A long-term study revealed that female northern gannets travelled further and consistently exhibited lower δ^{13}C and δ^{15}N values than males (Clark et al. 2021). Isotopic niche partitioning was related to differential prey preferences of each sex potentially driven by different parental investment, i.e. males invest more in nest defence, that consequently impact sex-specific nutritional requirements. Moreover, males were found to spent more time at the nest during the day and more likely to be at sea overnight, which may also drive the feeding on different prey, since prey accessibility varies according to diel vertical migrations (Garthe et al. 2007; Davoren et al. 2010). In the absence of clear sexual dimorphism, other drivers, usually related to energetic constraints of each sex, may be depicted, and interpreted under each context, e.g. reliance on fishery discards, environmental conditions, habitat or niche specialisation (Lewis et al. 2002; Cleasby et al. 2015; Clark et al. 2021). At the first sight, our results seem to be contradictory, however, it is likely that sexual segregation in Boyd's shearwaters may arise when analysing other parameters, rather than foraging behaviour. For instance, chick begging intensity gives information about chick condition, acting as a honest signal for parents to adjust the provisioning rates, and thus, avoid under or overfeeding (Granadeiro et al. 2000; Quillfeldt et al. 2004; Tyson et al. 2017). However, parents should adjust provisioning rates according to chick energetic requirements but without compromising their own needs, which may be performed differently if sexes are under different energetic constraints (Shoji et al. 2015; Tyson et al. 2017). Female Manx shearwaters *P. puffinus* were observed to be more responsive to chick begging behaviour than males, adjusting the timing of trips and the meal size more carefully in response to chick energetic state (Quillfeldt et al. 2004; Hamer et al. 2006). Conversely to the scenario of competitive exclusion proposed by Gray and Hamer (2001), the different energetic constraints manifested in a better adjustment of provisioning effort by female shearwaters (Quillfeldt et al. 2004; Shoji et al. 2015; Tyson et al. 2017), which may be experiencing a deficit of energy during the chick-rearing period due to the higher energetic costs of egg production and laying. Thus, sex-specific energetic requirements in shearwaters can manifest in differences in provisioning behaviour, rather than in foraging parameters. To empirically ascertain whether this hypothesis lies behind the partial sexual segregation observed in Boyd's shearwater, further studies on monitoring nest attendance, meal mass delivered, and the estimation of energy expenditure, through accelerometery data, should be performed, as it was for northern gannets (Bennison et al. 2022), great cormorants *Phalacrocorax carbo* (Wilson et al. 2006), imperial cormorants *P. atriceps*, or Magellanic penguins *Spheniscus magellanicus* (Wilson et al. 2017).

Habitat suitability models revealed that, regardless of sex, the distribution of Boyd's shearwaters was mostly driven by SST and SSH during short and long trips, respectively. The relative contribution of SST in explaining the foraging distribution of shearwaters in tropical areas has already been reported (McDuie et al. 2018; Cerveira et al. 2020), while variations in SSH were reported to impact seabird foraging grounds, especially in oceanic areas (Pereira et al. 2020). Patterns in SST are closely linked to gradients of marine productivity (Catry et al. 2013; Cerveira et al. 2020; Pereira et al. 2020), which influence vertical and horizontal distribution of prey, as well as its abundance (Morato et al. 2008; Hsieh et al. 2009), while patterns in SSH can be indicators of mesoscale eddies, which play an important role on the recycling of nutrients in oceanic areas (Stramma et al. 2013; Braun et al. 2019), a recurrent phenomenon inside and outside Cabo Verde (Meunier et al. 2012; Cardoso 2017). Lower values of SSH are associated with the occurrence of cyclonic mesoscale eddies, which pump the deeper and cooler waters to the euphotic zone, promoting ephemeral and localised events of enhanced productivity (Falkowski et al. 1991; Klein and Lapeyre 2009). Male Boyd's shearwaters exhibited a slightly stronger association to lower SSH values than females, regardless of trip type, suggesting a stronger association with cyclonic eddies that might boost the aggregation of prey (Stramma et al. 2013; Braun et al. 2019). Moreover, CHL doubled its relative contribution in explaining females' foraging distribution when compared to that of males during long trips. Specifically, males selected areas of slightly higher CHL values than females, although we must bear in mind the lower relative contribution of CHL to explain foraging distribution. The CHL is often used as an indicator of upwelling events that can promote aggregations of planktivorous epipelagic fish and their aquatic predators (Ichii et al. 2004; López-Pérez et al. 2020), translating into higher foraging opportunities for seabirds (Jaquemet et al. 2005; Weimerskirch 2007). Within the archipelago of Cabo Verde, upwelling events only occur in winter, when the Intertropical Convergence Zone (ITCZ) migrates towards the south (Peña-Izquierdo et al. 2012). Together with the intense currents generated by the inter-island channels, and the subsequent formation of mesoscale eddies promoted by the convergence of currents (Meunier et al. 2012; Peña-Izquierdo et al. 2012; Cardoso 2017), the oligotrophic waters can become, albeit temporarily, nutrient-rich waters providing great foraging opportunities for seabirds. Thus, males may be taking advantage of these temporarily profitable waters, especially during long trips, however, we acknowledge that the slight differences among habitat suitability models are quite weak to depict an environmentally driven sexual segregation scenario.

Overall, we did not detect sexual segregation in the isotopic niche of Boyd's shearwaters, which was further supported by similar diet composition obtained from the mixing model. As expected, adults showed low δ^{15}N values, feeding mainly on small epipelagic fish larvae, less enriched in δ^{15}N when compared to mesopelagic fish or squid (Fig. S4). Interestingly, mesopelagic fish revealed to be the second most important prey for Boyd's shearwaters, which was quite unpredicted since there are fewer evidence of this prey in little shearwaters' diet (Catry et al. 2009; Neves et al. 2012; Ramos et al. 2015; Monteiro 2019). Despite the more intense foraging activity during the day, Boyd's shearwaters remained active during crepuscular hours, suggesting that adults may rely on mesopelagic species that perform diel vertical migrations towards the epipelagic zone, following the diel movements of zooplankton (Davoren et al. 2010). The higher abundance of mesopelagic prey at surface layers during crepuscular hours makes them available to little shearwaters when light intensity is high enough to allow the detection of prey (Ramos et al. 2020). When compared to the diet composition of its close-related counterpart the Macaronesian shearwater, our results indicate a minimal importance of squid in the diet (Neves et al. 2012; Ramos et al. 2015), not exceeding 6% on average. However, the method used to assess diet in those studies (stomach flushing) is prone to detect more squid beaks which accumulate in the stomach over time (Barrett et al. 2007). Moreover, the small number of squid species included in our model and, more importantly, the higher δ^{15}N values of squid might have caused model-biased estimates. Without previous knowledge of Boyd's shearwater diet, it is difficult to ensure correct model-biased estimates, thus, studying the diet through more detailed methods, such as DNA metabarcoding, it will improve significantly our understanding of Boyd's shearwater trophic ecology (Xavier et al. 2018; Carreiro et al. 2020).

In summary, this study provides the first detailed analysis on the foraging movements of the small and endemic Boyd's shearwater, a winter breeder of Cabo Verde archipelago. It was found a partial sex-specific foraging mostly observed during short trips, while both sexes exhibited more similar foraging metrics during long trips. Despite the low spatial overlap of FA, the sexual segregation was not explained by differences in foraging habitat conditions, nor in the isotopic niche, or even in diet composition. Further research is needed to evaluate whether provisioning rates are sex-dependent, which could lead to differential energetic demands, and ultimately, explain sexual segregation in foraging. Still, additional data are needed to evaluate the sex-related spatial and trophic consistency across several years, for a better comprehension of the effect of oceanographic conditions in driving foraging behaviour (Paiva et al. 2017; Clark et al. 2021). These data are highly valuable for future marine spatial planning and further implementation of species' conservation plans in the archipelago of Cabo Verde, as it was already proposed for other local breeding seabirds (Paiva et al. 2015; Almeida et al. 2021). Although the current legislation has banned any fishing activity in the marine area of the Natural Reserve of Santa Luzia (Vasconcelos et al. 2015), there is no efficient surveillance implemented, which may entail an unfavourable future scenario for the conservation of seabird species.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00227-022-04127-7.

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Author contributions IS, JAR, and VHP: conceptualisation and methodology. IS, FRC, IR, NA, and SA carried out the fieldwork and collected the samples. ARC and RJL undertook the molecular sexing of birds and prey identification. IS and DM carried out the stable isotope analysis. PG provided logistical and fieldwork support. IS, JAR, and VHP: investigation, writing, and visualisation. All the authors have read, reviewed, and edited the manuscript and approved its submission.

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Data availability Data will be available upon reasonable request to the authors.

Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed. All animals were handled in strict accordance with good animal practice as defined by the current European legislation. All animal work was approved by the "National Directorate of the Environment" of Cabo Verde (DNA) through licences issued annually, authorising the work carried out at Raso Islet, Desertas Islands Natural Reserve. All sampling procedures and/or experimental manipulations have been reviewed and specifically approved as part of obtaining the field license.

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