Low spatial overlap between foraging shearwaters during the breeding season and industrial fisheries off the west coast of Portugal

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ABSTRACT: Fisheries have impacted seabird populations worldwide, either via bycatch mortality or resource depletion. Understanding the overlap between seabird distributions and fisheries is an important element for bycatch risk assessment, though the drivers of variation in seabird–fishery overlap are not well understood for some seabird populations. Here, we quantified the spatial overlap between foraging Cory's shearwaters *Calonectris borealis* during the breeding season and commercial fisheries operating within the Portuguese Exclusive Economic Zone. In addition, we evaluated whether overlap varied as a function of an individual's boldness, sex or breeding stage. For this, we GPS tracked 361 foraging trips by 72 Cory's shearwaters nesting at Berlenga Island, Portugal, over 5 consecutive breeding seasons (2012–2016). Simultaneously, we used fishing effort data from Global Fishing Watch detailing the distribution of industrial fisheries within the temporal and spatial range of Cory's shearwater tracks. Although fishing vessels were present during 88.1% of foraging trips, Cory's shearwaters spent only on average 13.3% of the time foraging in the same areas as fisheries. Such low spatial overlap is likely driven by high prey availability near the colony and suggests low direct competition for resources. We also found variation in overlap with fisheries across the breeding period, with Cory's shearwaters spending approximately 11% more time foraging in the same areas as fixed gear and purse seine vessels during pre-laying than during chick-rearing. Surprisingly, no sex or boldness-related differences were found in the overlap with any fishing gear. Our findings have implications for understanding within population variation in the overlap between fisheries and seabirds and, in turn, bycatch risk.

KEY WORDS: Boldness · Bycatch risk · Cory's shearwater · *Calonectris borealis* · Global Fishing Watch · Fixed gear · Purse seine · Seabird

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1. INTRODUCTION

Seabirds and fisheries have coexisted for centuries (Coleridge 1895). Long before industrial fisheries, seabirds provided fishermen with visual cues of fish aggregation (Coleridge 1895, Le Bot et al. 2018) and also fed on food subsidies generated during fishing operations (Garthe et al. 1996, Votier et al. 2004, Bicknell et al. 2013, Sherley et al. 2020). Such interactions make seabirds susceptible to becoming bycatch (Furness 2003, Anderson et al. 2011), although risk varies both among and within species (Torres et al. 2011, Votier et al. 2013, Granadeiro et al. 2014, Patrick et al. 2015, Collet et al. 2017, Genovart et al. 2018).

Studies of seabird–fishery overlap reveal much intrapopulation variation, such as by sex and age (reviewed in Gianuca et al. 2017), but this overlap may also vary depending on other life history traits for which we lack a mechanistic understanding, such as individual boldness (Votier et al. 2010, Patrick et al. 2015). Boldness is an important individual behavioural trait, measured by whether and how individuals consistently respond to stimuli, which has important evolutionary and ecological consequences (Wolf & Weissing 2012). Boldness has previously been shown to be consistent within individuals (Dingemanse et al. 2002, Bell et al. 2009) and heritable in a variety of taxa (Sinn et al. 2006, Dochtermann et al. 2015, Winney et al. 2018), including pelagic seabird species (Patrick et al. 2013). Recent research shows that a significant amount of variation in seabird distribution and foraging behaviour can be explained by individual boldness (Patrick & Weimerskirch 2014, Krüger et al. 2019, Harris et al. 2020). For instance, shy seabirds may be more 'explorative', dispersing farther from the colony to forage after being displaced by bold individuals which remain close to the colony (Patrick & Weimerskirch 2014).

To our knowledge, only one study has addressed the influence of seabird individual boldness on overlap with fisheries, reporting no effect of boldness on overlap with longline fisheries operating in the Indian Southern Ocean in black-browed albatrosses *Thalassarche melanophris* (Patrick & Weimerskirch 2014). However, the authors suggest boldness may impact overlap in populations where fishing activity and seabirds co-occur in the colony surroundings, which was not the case in their study. Thus, we may expect that overlap with fisheries should increase with increasing boldness, because competition for food resources may be particularly intense near fishing vessels or in areas of high fishing activity (Arcos et al. 2001). Understanding whether bolder individuals are more likely to be exposed to bycatch risk could be important in the context of quantifying the impacts of fisheries on demography and reproductive measures. This is particularly relevant if increasing boldness is associated with higher parental investment and offspring survival, which has been shown for a variety of species (Smith & Blumstein 2008, Patrick & Weimerskirch 2015).

Procellariiformes may be particularly threatened by fisheries (Tasker et al. 2000, Croxall et al. 2012). In the western Mediterranean, shearwaters are at high risk of becoming bycatch on longline fishing vessels (Cortés et al. 2017), especially Scopoli's shearwaters *Calonectris diomedea* (Belda & Sánchez 2001, Barcelona et al. 2010, Báez et al. 2014). In fact, this species is known to follow fishing vessels (Soriano-Redondo et al. 2016) and to attend trawlers and longline fishing vessels in higher numbers than expected by chance (Louzao et al. 2011), particularly adult males during the breeding period (Laneri et al. 2010, Genovart et al. 2017, Cortés et al. 2018). However, in contrast to the western Mediterranean, this species was recently shown to exhibit limited interaction with fishing vessels in the central Mediterranean (Cianchetti-Benedetti et al. 2018). Furthermore, our understanding of the overlap between *Calonectris* populations breeding outside the Mediterranean and fisheries is limited, including for the abundant Cory's shearwater *Calonectris borealis* populations in the Atlantic Ocean. Previous studies have demonstrated that few Cory's shearwaters attend fishing vessels or are caught in fishing gear during breeding off the west Iberian Peninsula (Valeiras 2003, Oliveira et al. 2015, Calado et al. 2020), or the non-breeding period in the southwest Atlantic (Bugoni et al. 2008, 2010). However, these studies relied almost exclusively on onboard observations from artisanal fishing vessels operating in nearshore waters (up to 20 km off the coast), and little is known about at-sea overlap of Cory's shearwaters with industrial fishing fleets.

Here, by combining fine-scale data from bird-borne GPS trackers with data on the spatial distribution of gear-specific fishing effort, we were able to quantify the extent to which Cory's shearwaters overlap with fisheries of different gear types during the pre-laying and chick-rearing periods over 5 breeding seasons (2012−2016). Spatial overlap does not necessarily imply interaction, but it is commonly used as a proxy for potential exposure to fishing gear and increasing bycatch risk (Le Bot et al. 2018). In addition, we also explored the extent to which such spatial overlap is influenced by boldness, breeding stage and sex. We made the following predictions: (1) because Cory's shearwaters exhibit shorter foraging trips during chick-rearing (Paiva et al. 2010c, Ceia et al. 2014), we expected higher overlap with coastal fisheries during this stage than during pre-laying, when the species usually has a more pelagic range (Paiva et al. 2013); and (2) because fishing activity and breeding seabirds co-occur close to the colony in our study area, we expect males and bolder individuals to overlap more with coastal fisheries independent of breeding stage, as they may be able to outcompete females and shy individuals for fishery-related resources (Paiva et al. 2017, Krüger et al. 2019).

2. MATERIALS AND METHODS

2.1. GPS tracking and data preparation

We used Global Positioning System (GPS) loggers (IgotU GT-120, Mobile Action Technology) to track foraging trips of Cory's shearwaters breeding on Berlenga Island, Portugal (39° 23′ N, 9° 36′ W) during pre-laying (April–May) and mid chick-rearing (August–September) periods from 2012 to 2016. The period of deployment was similar across years: between 5 May and 7 June for pre-laying and between 31 August and 21 September for chick-rearing. Each device was sealed with heat-shrink tubing to make it waterproof and programmed to record locations at 5 min intervals. GPS devices with heat-shrink tubing weighed approximately 17 g, which was 2.9% of the body mass of the lightest bird tagged. Previous studies found no effects of similar GPS devices on foraging behaviour, body mass change or fledging success in breeding Cory's shearwaters (Paiva et al. 2010a,c, Passos et al. 2010, Villard et al. 2011). GPS loggers were attached using TESA® tape to the bird's back feathers following Wilson et al. (1997). Birds were captured on their nests at night and individually identified by their ring numbers. Each bird was sexed according to bill measurements and vocalisations (Granadeiro 1993). The handling process did not exceed 10 min and birds were released back into the breeding burrow to minimise stress. Details of sample sizes and tracking period for each stage of breeding and study year are given in Table 1.

Tracking data were first filtered to remove locations within a 1 km radius of the colony. This buffer was used to reduce the influence of rafting behaviour close to the colony, which often occurs at sunset before the birds return to their nests at night (Weimerskirch et al. 2020b). In addition, by using this buffer we were able to identify individual foraging trips and calculate the following metrics: (1) trip duration, (2) cumulative distance travelled between all position (hereafter trip length), (3) maximum distance from colony and (4) percentage of short trips vs. percentage of long trips. Short and long trips were distinguished based on histograms of frequency of occurrence of (1) trip duration (d) and (2) maximum distance from colony on each foraging trip (km). During both pre-laying and chick-rearing, short trips were defined as ≤1 d and ≤100 km and long trips as >1 d and >100 km (see Fig. 2).

2.2. Behavioural classification

To characterise the foraging behaviour for each individual trip, we classified each GPS position as one of 4 behavioural states using the expectation maximisation binary clustering method implemented in the R package EMbC (Garriga et al. 2016). The 4 states were as follows: (1) travelling (high velocity, low turning angles), (2) relocating (high velocity, high turning angles), (3) intensive foraging (low velocity, high turning angles) and (4) resting (low velocity, low turning angles) (Louzao et al. 2014). This technique has previously been used to interpret ecologically meaningful behaviours from movement data in a variety of procellariforms (de Grissac et al. 2017, Clay et al. 2019a, De Pascalis et al. 2020), including exploring behavioural differences between different populations of shearwaters (Pereira et al.

Table 1. Tracking period and number of tracked Cory's shearwaters *Calonectris borealis* (number of foraging trips) during pre-laying and chick-rearing for each year of the study (2012–2016)

	2012	2013	2014	2015	2016	Total
Pre-laying						
Tracking period	9–28 May	10–25 May	5–22 May	12 May–1 Jun	24 May–7 Jun	–
N tracked Cory's shearwaters	12	8	9	7	10	46
N tracked Cory's shearwaters of known sex and boldness (N trips)	6 (25)	4 (21)	1 (2)	5 (25)	8 (22)	24 (95)
N males (N trips)	6 (25)	3 (20)	1 (2)	4 (24)	6 (16)	20 (87)
N females (N trips)	0	1 (1)	0	1 (1)	2 (6)	4 (8)
Chick-rearing						
Tracking period	4–19 Sep	8–21 Sep	3–15 Sep	2–12 Sep	31 Aug–12 Sep	–
N tracked Cory's shearwaters	9	9	8	18	16	60
N tracked Cory's shearwaters of known sex and boldness (N trips)	6 (51)	8 (43)	6 (35)	15 (75)	13 (62)	48 (266)
N males (N trips)	5 (41)	6 (36)	5 (29)	8 (43)	6 (30)	30 (179)
N females (N trips)	1 (10)	2 (7)	1 (6)	7 (32)	7 (32)	18 (87)

2020, Weimerskirch et al. 2020b). We further calculated the percentage of time individuals spent in each behavioural state during each foraging trip.

2.3. Boldness tests and analysis

Boldness of individual Cory's shearwaters was measured as the degree of response and/or aggression of individuals towards a novel object (2015–2018). This methodology has been used effectively in other seabirds (Grace & Anderson 2014, Patrick & Weimerskirch 2014, Harris et al. 2020), including Cory's shearwaters (Krüger et al. 2019). The novel object (an LED headlamp, 6.2 × 4.0 × 3.5 cm, ~70 g; Lighting EVER®) attached to a Campark Action HD waterproof camera (6.0 × 2.5 × 4.0 cm, ~77 g; Campark®) was placed in the nest entrance for approximately 2 min and the bird's response filmed (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m657p209_supp.pdf). Because boldness can be influenced by the presence of another bird, tests were conducted when only one adult was present. After the test was complete, birds were taken from the nest to be identified by ring number.

Repeated tests were conducted on different days whenever possible, for a total of 314 videos of 124 individuals: 49 individuals were tested once, 22 were tested twice, 33 were tested 3 times, 7 were tested 4 times, 7 were tested 5 times, 4 were tested 6 times and 2 were tested 8 times. The full field protocol for boldness tests and video analysis is described in detail by Krüger et al. (2019). We applied non-metric multidimensional scaling (NMDS) to assign the recorded behaviours (see Table S1 in the Supplement) along a boldness/shyness gradient using the R package vegan (Oksanen et al. 2013). To obtain a single estimate of boldness per individual we used scores from the first NMDS axis (see Table S2 in the Supplement). Individuals were characterised as bold (lower values on first NMDS axis) or shy (higher values on first NMDS axis) based on the behaviours displayed (see Fig. S2 in the Supplement). Fewer movements or non-agressive behaviour to the object (e.g. twitching, moving head or blinking eyes) indicated shyer individuals, whereas agitated behaviours and more interactions with the object (e.g. pecking, protecting the egg or the chick, moving towards the object) indicated bolder individuals. Boldness was previously shown to be consistent within individuals and not influenced by sex in our study population of Cory's shearwaters (Krüger et al. 2019).

2.4. Overlap of foraging shearwaters and fisheries

Raster files detailing the daily distribution of fishing effort (in h) were downloaded from Global Fishing Watch (http://globalfishingwatch.org/) at a 0.01° grid cell resolution (approx. 1 km) for every day during 2012–2016. Global Fishing Watch is an open access global database that uses remote sensing and convolutional neural networks to classify the activity of vessels larger than 15 m as fishing or not fishing (Kroodsma et al. 2018). We downloaded data on 3 fishing gear types: (1) fixed gear, (2) purse seiners and (3) trawlers. Fixed gear encompasses pots and traps, set gillnets and set longlines.

To quantify spatial overlap of fisheries with tracked birds, we only included fishing effort data collected from the temporal and spatial extent of Cory's shearwater tracking data. Secondly, we grouped the subset of daily rasters as the mean fishing effort at a 10 × 10 km grid resolution within the study area. This grid cell size was chosen following the methodological considerations used in previous studies quantifying the large-scale overlap between commercial fisheries and foraging shearwaters during the breeding season (Waugh et al. 2016, Carle et al. 2019), and because this resolution allows fishing effort data to be grouped without losing much spatial detail (Genovart et al. 2018). This design also allows us to compare our results with those of studies on similar shearwater species breeding elsewhere. Next, we extracted fishing effort (if any) only for the GPS locations where Cory's shearwaters engaged in intensive foraging behaviour (i.e. each GPS location was associated with the corresponding daily fishing effort in the 10 × 10 km grid cell). GPS locations where Cory's shearwaters were classified as travelling, relocating and resting were excluded from the overlap analysis. Lastly, we quantified the relative Cory's shearwater–fishery overlap per trip by calculating: (1) percentage of time overlapping with fishing vessels and (2) fishing effort in foraging areas.

2.5. Effect of boldness, sex and breeding stage on overlap with fisheries

To investigate the effect of boldness, breeding stage and sex on the overlap with fisheries, we modelled percentage of time overlapping with fishing vessels and fishing effort in foraging areas as response variables in linear mixed models (LMMs). Response variables were inspected for normality and homogeneity before each statistical test and trans-

formed when necessary. The fishing effort in foraging areas was standardised (observation – mean / standard deviation), while percentage of time overlapping with fishing vessels was arcsin-transformed to meet parametric assumptions. We did not test for an interaction between sex and breeding stage due to an unbalanced sex ratio, especially during the pre-laying period (see Table 1). Trip identity nested within bird identity (ring) and year were fitted as random effects to account for multiple trips per individual and the effects of environmental variation and irregular sampling. LMMs were also used to test for differences in trip metrics (i.e. trip duration, trip length, maximum distance from colony and percentage of short trips) and behaviour during foraging trips (i.e. time spent in each behavioural state) between individuals of varying boldness, breeding stage and sex. LMMs were computed using the R packages lme4 (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2017). All statistical analyses were conducted in R v.3.6.2 (R Core Team 2018). All data are presented as mean ± SD. Differences were considered statistically significant when p ≤ 0.05.

3. RESULTS

3.1. Foraging trip characteristics

Overall, we recorded 361 foraging trips made by 72 adult Cory's shearwaters of known sex over 5 breeding seasons (Fig. 1): 24 Cory's shearwaters were tracked during pre-laying (95 trips) and 48 during chick-rearing (266 trips). We collected tracking data from 22 females and 50 males over both breeding stages combined (Table 1). Sex ratio was more skewed towards males during pre-laying (20 males vs. 4 females) than during chick-rearing (30 males vs. 18 females). Foraging trips differed between breeding stages (Fig. 1), with trip duration (mean ± SD: 2.2 ± 3.4 vs. 1.6 ± 1.1 d; $F_{4,356}$ = 3.82, p = 0.05), trip length (61.0 ± 135.0 vs. 31.1 ± 45.0 km; $F_{4,356}$ = 7.71, p = 0.001), maximum distance from colony (112.7 ± 241.9 vs. 58.2 ± 71.5 km; $F_{4,356}$ = 10.69, p = 0.001), percentage of time spent in intensive foraging (31.0 ± 15.8 vs. 22.5 ± 8.8%; $F_{4,356}$ = 18.88, p = 0.001) and percentage of time spent resting (29.6 ± 11.2 vs. 23.2 ± 10.9%; $F_{4,356}$ = 12.72, p = 0.001) all higher during pre-laying than chick-rearing. Although Cory's shearwaters made significantly higher foraging effort during the pre-laying period, individuals made mainly short trips in both breeding stages (pre-laying: 78.9% short trips vs. chick-rearing: 64.3%) (Fig. 2). Trip

metrics and behaviour during foraging trips were not influenced by sex (all models: p > 0.07) or by boldness (all models: p > 0.15).

3.2. Drivers of variation in overlap with fisheries: effect of boldness, breeding stage and sex

We found that foraging Cory's shearwaters overlapped with fisheries at least once in 318 of the 361 trips (88.1%): 256 trips (70.9%) with fixed gear, 285 trips (78.9%) with purse seiners and 236 trips (65.4%) with trawlers. Overall, more trips where Cory's shearwaters and fisheries overlapped occurred during chick-rearing (78.3%) than during pre-laying (21.7%) (Fig. 3). Moreover, all the trips where overlap occurred were within the Portuguese Exclusive Economic Zone (EEZ); 93.1% of trips were within a radius of 100 km of the colony and 84.3% of trips were within a radius of 50 km (Fig. 3).

Although fishing vessels were present on most foraging trips, Cory's shearwaters only spent on average 13.3% of their foraging time in the same area as fishing vessels within the Portuguese EEZ. The percentage of time overlapping with fishing vessels was relatively similar for all gear types: 17.9% of their time was spent in the same area as fixed gear, 14.1% in the same area as purse seine vessels and 7.3% in the same area as trawlers. Similarly, the fishing effort in foraging areas was also relatively similar for all gear types: fixed gear spent 0.70 h in Cory's shearwater foraging areas, purse seine vessels spent 0.65 h and trawlers spent 0.76 h. Percentage of time Cory's shearwaters spent foraging in the same areas as fixed gear and purse seine vessels differed between breeding stages, with relatively higher overlap occurring during pre-laying (27.2 and 22.5%, respectively) than during chick-rearing (16.0 and 11.5%, respectively) (Table 2). This represent a variation in overlap of approximately 11% for both fishing gears. Neither the percentage of time overlapping with fishing vessels nor the fishing effort in foraging areas were influenced by boldness, sex or the interaction of these factors with gear type (Table 2).

4. DISCUSSION

In this study, we investigated whether foraging Cory's shearwaters spatially overlapped with fisheries over 5 consecutive breeding seasons, and whether overlap varied as a function of boldness, sex and breeding stage. Our findings suggest that
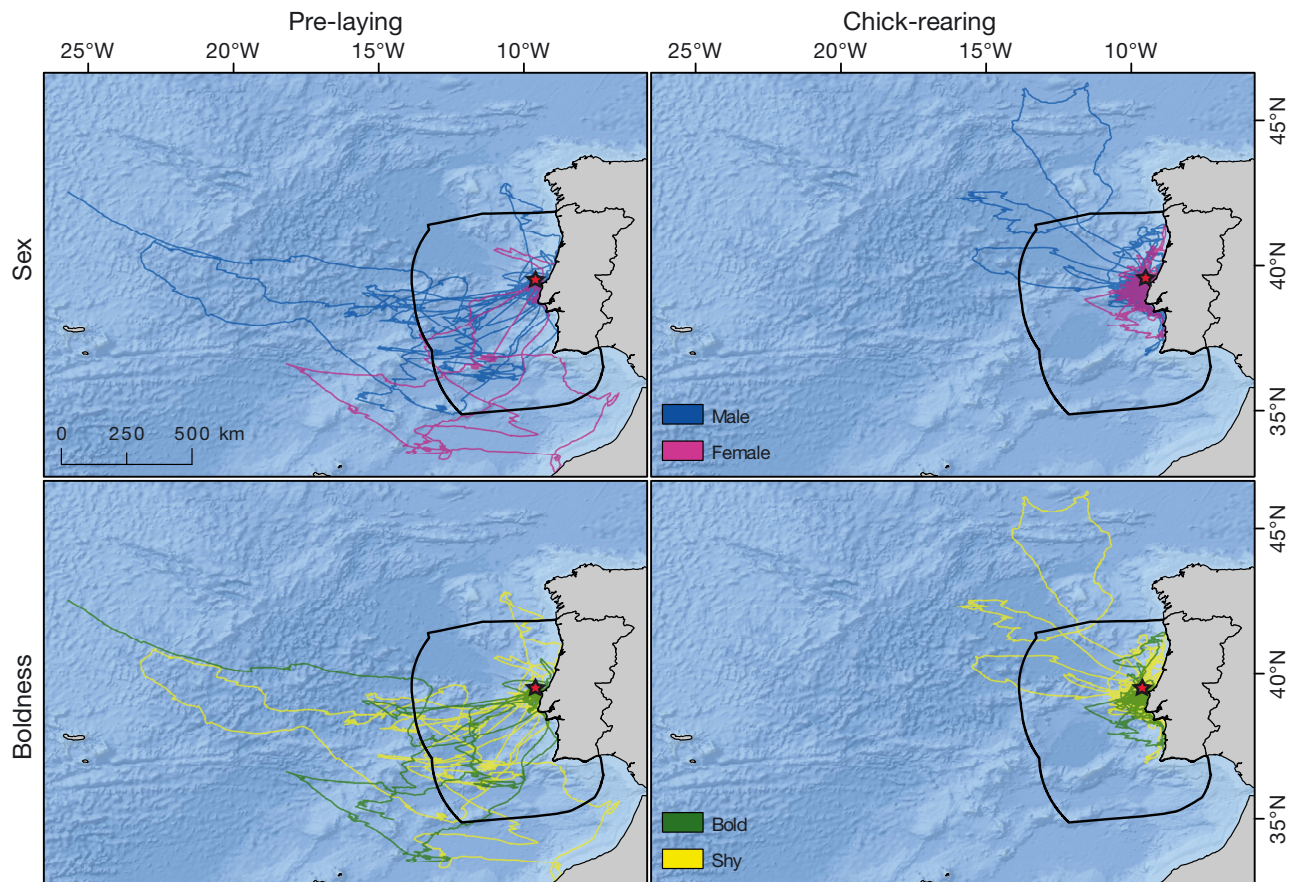
Fig. 1. Foraging range for Cory's shearwaters breeding on Berlenga Island, Portugal (red star) in relation to breeding stage (pre-laying vs. chick-rearing), sex (males vs. females) and boldness (bold vs. shy) over 5 consecutive breeding seasons (2012–2016), overlaid on bathymetry of the region (where darker blue indicates increasing depth). Black solid line represents the Portuguese Exclusive Economic Zone (EEZ)
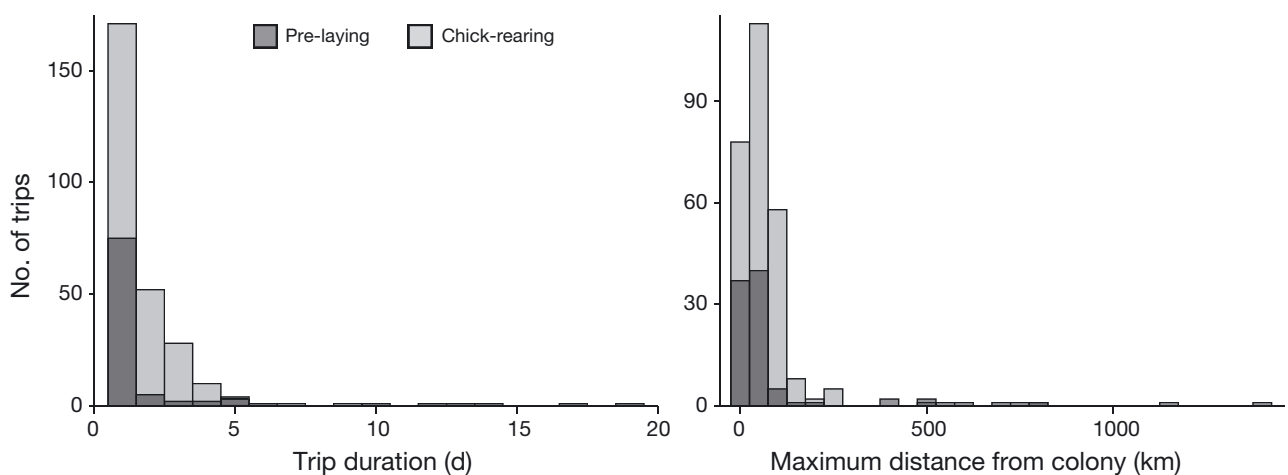

Fig. 2. Frequency of occurrence (number of trips) by trip duration (d) and maximum distance from colony (km) during pre-laying and chick-rearing periods. For both breeding stages, short trips were defined as ≤1 d and ≤100 km and long trips as >1 d and >100 km

despite the high density of fishing vessels within the Portuguese EEZ, Cory's shearwaters spent little time foraging in the same areas as fisheries during the breeding season. In contrast to our predictions, Cory's shearwaters spent more time foraging in the same areas as fixed gear and purse seine vessels during
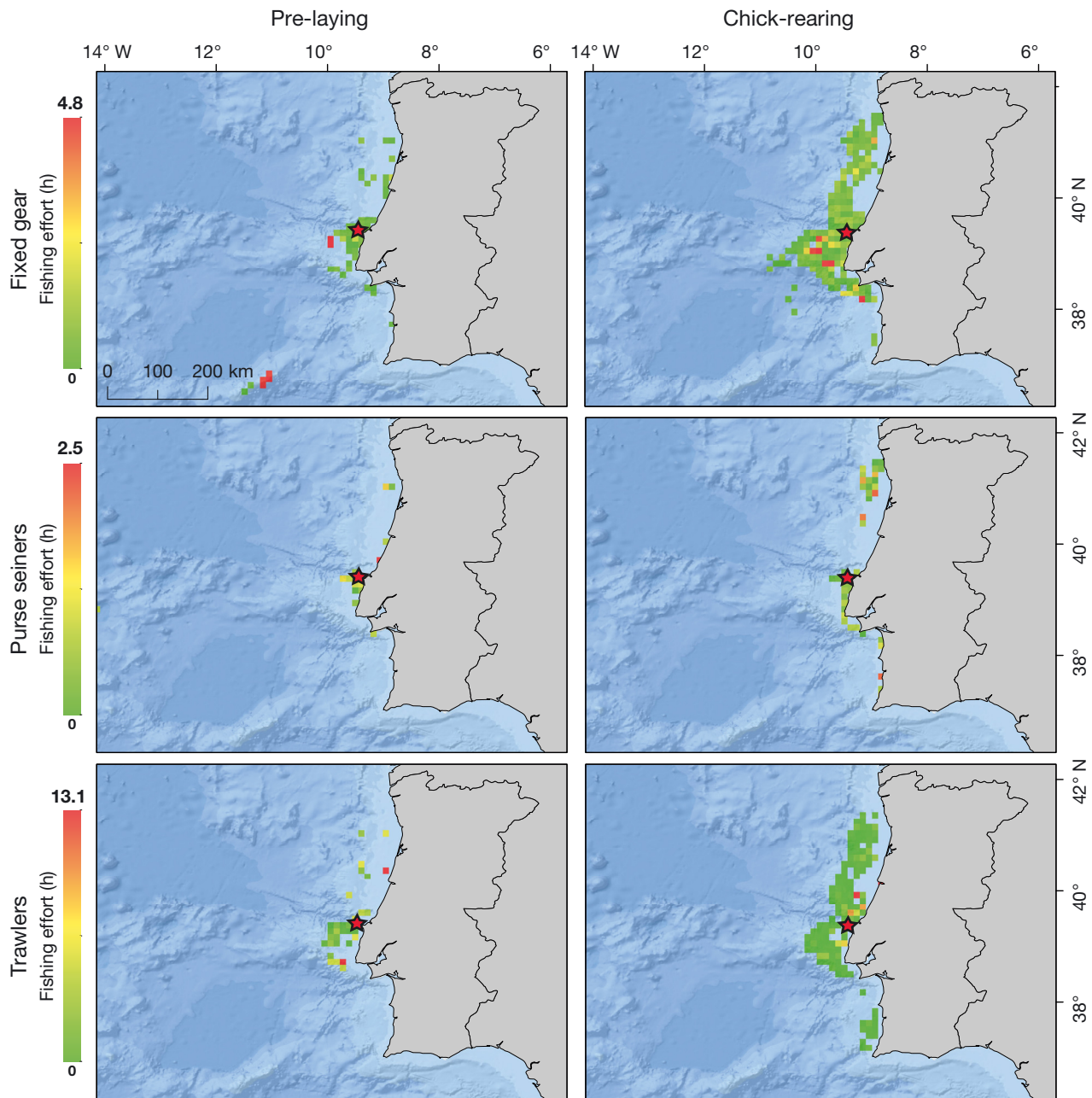
Fig. 3. Extent of overlap between foraging Cory's shearwaters breeding on Berlenga Island (red star) and industrial fishing vessels along the Portuguese coast during the pre-laying and chick-rearing periods. Values are calculated as the average number of fishing hours fixed gear vessels, purse seiners and trawlers spent in the same area as foraging shearwaters at a resolution of 10 × 10 km grid cells. Fishing effort is overlaid on bathymetry of the region (where darker blue indicates increasing depth. Fixed gear includes pots and traps, set gillnets and set longlines

pre-laying than during chick-rearing. Moreover, we found no evidence of boldness or sex differences in the overlap with fishing vessels. Below we discuss the potential reasons that foraging Cory's shearwaters show little overlap with fishing vessels within Portuguese national waters and explain the drivers of variation in overlap with fisheries.

4.1. Overlap of breeding Cory's shearwaters and fisheries in the Portuguese EEZ

Overlap analysis revealed that although fishing vessels were present in most foraging trips occurring within the Portuguese EEZ, Cory's shearwaters rarely foraged in the same areas as fisheries, re-

Table 2. Results of linear mixed models (LMMs) testing the effects of boldness (bold vs. shy), breeding stage (pre-laying [PL] vs. chick-rearing [CR]) and sex (male vs. female) on the percentage of time shearwaters spent foraging in the same area as fisheries and the average number of hours fixed gear, purse seiners and trawlers spent fishing in Cory's shearwater foraging areas. Fixed gear included pots and traps, set gillnets and set longlines. Each model included trip identity nested within individual ID and study year (2012–2016) as a random term. Differences were considered statistically significant when p ≤ 0.05 (in **bold**)

| Fishing gear | Percentage of time overlapping with fishing vessels | | | | Fishing effort in foraging areas | | | |
	Fixed effects	LMM	p	Effect	Fixed effects	LMM	p	Effect
Fixed gear	Boldness	$F_{4,251} = 0.11$	0.74		Boldness	$F_{4,251} = 0.35$	0.56	
	Breeding stage	$F_{4,251} = 11.70$	**<0.001**	PL > CR	Breeding stage	$F_{4,251} = 1.43$	0.23	
	Sex	$F_{4,251} = 4.07$	0.06		Sex	$F_{4,251} = 1.37$	0.25	
	Boldness × Sex	$F_{4,251} = 0.01$	0.96		Boldness × Sex	$F_{4,251} = 0.51$	0.51	
Purse seiners	Boldness	$F_{4,280} = 0.02$	0.90		Boldness	$F_{4,280} = 0.01$	0.99	
	Breeding stage	$F_{4,280} = 15.62$	**<0.001**	PL > CR	Breeding stage	$F_{4,280} = 2.49$	0.12	
	Sex	$F_{4,280} = 2.59$	0.11		Sex	$F_{4,280} = 2.80$	0.11	
	Boldness × Sex	$F_{4,280} = 0.01$	0.99		Boldness × Sex	$F_{4,280} = 0.20$	0.65	
Trawlers	Boldness	$F_{4,231} = 0.91$	0.34		Boldness	$F_{4,231} = 2.86$	0.10	
	Breeding stage	$F_{4,231} = 0.08$	0.78		Breeding stage	$F_{4,231} = 0.16$	0.69	
	Sex	$F_{4,231} = 0.20$	0.66		Sex	$F_{4,231} = 0.01$	0.94	
	Boldness × Sex	$F_{4,231} = 2.20$	0.14		Boldness × Sex	$F_{4,231} = 0.54$	0.54	

gardless of gear type. Our results contrast with those reported for other species of shearwaters breeding in areas of intense fishing pressure, where competition for food resources is expected to be higher. For instance, breeding pink-footed shearwaters *Ardenna creatopus* were shown to extensively overlap with industrial purse seine fishing fleets targeting small pelagic fish off the west coast of Chile (Carle et al. 2019). Nevertheless, our findings are in line with recent studies finding low spatial overlap or few encounters between a wide range of seabird species and fishing vessels (Sztukowski et al. 2017, Cianchetti-Benedetti et al. 2018, Grémillet et al. 2019, Bonnet-Lebrun et al. 2020, Clark et al. 2020). Cianchetti-Benedetti et al. (2018) found that Scopoli's shearwaters breeding in the central Mediterranean exhibited limited interaction with fishing vessels during chick-rearing, in contrast to patterns observed in other populations of the same species in the western Mediterranean (Soriano-Redondo et al. 2016). The authors suggested that this limited overlap may indicate that Scopoli's shearwaters prefer to exploit 'natural' high quality prey during the breeding period, when food is plentiful in the area, rather than scavenge for low quality prey discarded during fishing operations. Similar results were reported for northern gannets *Morus bassanus* in Iceland, with a low overlap with fisheries and preference to forage on 'natural' prey (Clark et al. 2020) and Cape gannets *Morus capensis*, which only foraged in association with industrial fisheries when numbers of pelagic fish were low near the breeding colony (Tew Kai et al. 2013).

Despite the variation in foraging effort across breeding stages, the majority of Cory's shearwaters in our study made mainly short trips, both in duration and length. The prevalence of short trips indicates conditions of high prey availability near the breeding colony, as demonstrated in previous studies (Paiva et al. 2017). The west coast of the Iberian Peninsula is characterised by a strong April–September upwelling (matching Cory's shearwaters' breeding period), which provides optimal conditions for aggregations of large pelagic fish populations (Sousa et al. 2008), including some of the main prey of Cory's shearwaters such as European pilchard *Sardina pilchardus*, horse mackerel *Trachurus trachurus*, Atlantic mackerel *Scomber scombrus*, European anchovy *Engraulis encrasicolus* and garfish *Belone belone* (Paiva et al. 2010b, Alonso et al. 2012). Thus, we suggest that Cory's shearwaters breeding off the west coast of Portugal are likely to be influenced by the high prey availability near the colony, and can feed on 'natural' prey, rather lower quality prey discarded by fishing vessels. To some extent, this was confirmed by onboard observations from artisanal fishing vessels operating along the west coast of the Iberian Peninsula showing that few Cory's shearwaters were seen attending fishing vessels and the species was rarely recorded as bycatch during the breeding period (Valeiras 2003, Oliveira et al. 2015, Calado et al. 2020).

4.2. Drivers of variation in overlap with fisheries

We found some variation in the overlap between Cory's shearwaters and fisheries across the breeding period. Contrary to our predictions, Cory's shearwaters spent relatively more time foraging in the same area as fixed gear and purse seine vessels during pre-laying than during chick-rearing. While the evidence is circumstantial and supported only by the overlap results, we suggest that individuals are likely to exhibit higher behavioural plasticity in the use of foraging habitats early in the breeding season because they are less constrained by breeding duties (Paiva et al. 2010a, 2013, Quillfeldt et al. 2019). Thus, birds might follow fishing vessels or use fishing areas during pre-laying, which ultimately enhances bycatch exposure during this period. A comparably higher overlap with longline fisheries during the pre-breeding or incubation period, and likely higher reliance on fishery-related resources, was also observed for flesh-footed shearwaters *Puffinus carneipes* in New Zealand (Thalmann et al. 2009, Reid et al. 2012).

The only other study to examine the link between boldness of a seabird population and fisheries distribution found that neither sex nor boldness of black-browed albatrosses had an influence on their overlap with longline fisheries operating in the Indian Southern Ocean (Patrick & Weimerskirch 2014). However, the authors suggested that differences in overlap with fisheries may occur only in systems where fishing activity and breeding seabirds co-occur in the colony surroundings, as it is the case in our study population (Patrick & Weimerskirch 2014). Similar to Patrick & Weimerskirch (2014), we found no sex or boldness-related effects on the overlap between foraging Cory's shearwaters during the breeding season and industrial fishing vessels operating within the Portuguese EEZ. We also found no influence of sex or boldness on trip metrics or at-sea foraging behaviour. Previous tracking studies reported no sexual segregation in foraging strategies or evidence for competitive exclusion in Cory's shearwaters (Magalhães et al. 2008, Navarro & González-Solís 2009, Paiva et al. 2010b), except during periods of unfavourable environmental conditions and likely lower prey availability (Paiva et al. 2017, Krüger et al. 2019). The majority of the tracking datasets used in this study were collected in years of good environmental conditions (with likely higher prey availability; see Paiva et al. 2017); we suggest that intrapopulation differences in overlap with fisheries may be stronger during periods of food scarcity. Future stud-ies should look at the influence of varying environmental conditions on seabird–fishery overlap.

4.3. Methodological considerations

The probability of encounter between seabirds and fisheries is commonly estimated by examining the overlap between the distribution of GPS-tracked birds and that of fisheries at several spatio-temporal scales (reviewed in Le Bot et al. 2018). However, spatial overlap does not necessarily imply direct interactions with vessels, but rather suggests that seabirds and fisheries are targeting the same areas and sharing the same resources (Pichegru et al. 2009, Torres et al. 2013, Collet et al. 2015). Detailed information on seabird–fishery interactions is only possible with on-board observations (Le Bot et al. 2018), which are logistically demanding and mainly used for regular monitoring of marine biodiversity in relatively small and coastal areas (Pereira et al. 2018). Our methodological approach is not suitable for investigating fine-scale seabird–fishery interactions. Instead, it provides reliable information on general patterns and drivers of spatial overlap between GPS-tracked Cory's shearwaters and satellite detected fishing effort for a relatively large area, such as the Portuguese EEZ. The results presented here should be interpreted as a proxy for potential exposure to fishing gear or bycatch risk and are of particular importance because little is known about the overlap between industrial fishing fleets and *Calonectris* populations outside the Mediterranean Sea. The amount of time foraging seabirds overlapped with large-scale distribution of commercial fisheries was previously shown to accurately model the impact of bycatch on population dynamics (Tuck et al. 2001, Votier et al. 2010, Genovart et al. 2018), and to pinpoint high risk areas with a strong probability of encounter over vast oceanic areas (Clay et al. 2019b). This methodology is commonly used to assess bycatch risk patterns in highly mobile marine predators such as seabirds (e.g. Genovart et al. 2018), marine mammals (Cronin et al. 2012, Baylis et al. 2018) and sharks (Queiroz et al. 2016, 2019). A similar methodological approach was used to quantify spatial overlap between trawling fisheries operating on the Patagonian shelf and South American fur seals *Arctocephalus australis* breeding on the Falkland Islands (Baylis et al. 2018). By overlapping the foraging activity of GPS-tracked South American fur seals with daily resolution fishing effort, the authors mapped the areas of greatest overlap over the Argentinean EEZ at a near real time scale.

4.4. Conclusions and implications for bycatch

Our study shows that despite the high density of fishing vessels within the Portuguese EEZ, Cory's shearwaters spent little time foraging in the same areas as fisheries during the breeding period. We suggest that scavenging is likely to be limited in areas of high prey availability and that seabirds may prefer to feed on 'natural' prey during the breeding period, particularly during chick-rearing. Thus, the population studied here may have relatively low exposure to industrial fisheries at large spatial scales. However, this Cory's shearwater population seems to forage more in areas used by fixed gear vessels (e.g. longliners and gillnets) and purse seiners during the pre-laying period. The importance of this fact should not be underestimated, because longline fisheries and gillnets represent the most lethal fishing gear, particularly for procellariform species (Anderson et al. 2011, Žydelis et al. 2013). Furthermore, spatial overlap could be underestimated in this study because (1) radio-based Automatic Identification System (AIS) data used to track vessel movements are mainly limited to large industrial fishing fleets, thus do not account for the distribution of smaller artisanal fishing fleets, and (2) industrial fishing can also switch off their AIS systems (Ford et al. 2018), making these data a conservative picture of their at-sea distribution and effort. Future studies using recently developed radar detectors combined with GPS loggers may empirically detect real interactions with fishing vessels and confirm drivers of variation in overlap with fisheries (Weimerskirch et al. 2018, 2020a).

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