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Personality influences foraging of a seabird under contrasting environmental conditions

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ABSTRACT

Personality is relevant in shaping the way animals respond to environmental conditions. Some personality traits may be disadvantageous under non-optimal environmental conditions, reducing foraging success and breeding performance in the long term. In this study we tested whether individual personality plays a role in determining shifts in seabirds' foraging behaviour and habitat use when environmental conditions are poor. We used GPS-tracking information from chick-rearing Cory's Shearwaters (*Calonectris borealis*) during eight consecutive years. Boldness was measured by the response of the tracked individuals to a novel object presented at their nest. Foraging habitat was identified as the environment within geographic points where birds were flying at low speed with high turning rates. We found that bold individuals displayed more foraging habitat consistency and boldness influenced foraging habitat during years of poor environmental conditions. Bold individuals tended to remain closer to the colony under poor environmental conditions, while shy individuals dispersed considerably farther from the colony. However, there was no influence of the personality on breeding success, and the whole population tended to have a lower probability of breeding success during years of poor conditions. During adverse environmental conditions, shy birds shifted habitat, probably as consequence of exploitative competition with the bold birds, but this has no effect on the birds' ability to successfully raise a chick.

1. Introduction

Personality, or temperament, is considered a characteristic shared by all members of an animal population, which varies among animals but tends to be individually consistent (Dingemanse et al., 2010; Réale et al., 2007; Sih, 2013). Different personality traits are correlated, resulting in a behavioural syndrome (Adriaenssens and Johnsson, 2013; Sih et al., 2012; Sih et al., 2004) where individuals may respond in a similar manner to different situations. Personality is widely recognised as important in shaping the way individuals respond to environmental conditions (Chapman et al., 2011; Kurvers et al., 2012; Kurvers et al., 2010; Sih et al., 2004).

Some personality traits may be disadvantageous under non-optimal environmental conditions, reducing foraging success (Biro and Stamps, 2008; Réale et al., 2007). For instance, shy animals may be less "exploratory" than bold individuals (Van Oers et al., 2005; van Overveld and Matthysen, 2010), and consequently shy animals may have a reduced food intake during periods of resource scarcity (Biro and Stamps, 2008). However, individuals may be able to compensate for their intrinsic personality constraints to optimize their foraging and breeding

performance (Couchoux and Cresswell, 2011; Kazama et al., 2012; Sinn et al., 2008). Because there is evidence that personality is heritable (Dochtermann et al., 2014; Winney et al., 2018), and natural selection acts at the level of the individual (Dall et al., 2004; Williams, 1966), it is important to understand how individuals cope with increasing changes in the ocean environment (Burrows et al., 2011; Halpern et al., 2015; Nash et al., 2017).

Therefore, understanding which phenotypes are more affected by environmental change is important for predicting population and species-level changes in the future. Several studies have shown that when individuals are exposed to environmental change, there can be consequences at the population level, i.e. lower breeding success and lower recruitment (Crespin et al., 2006; Paiva et al., 2013a). As "central place foragers," seabirds are constrained to return to their colony during the breeding period to incubate eggs and provision chicks (Orians and Pearson, 1979). Near the colony food is depleted faster due to higher exploitation of food resources (Lewis et al., 2001) and this effect will be stronger during seasons of food shortage, forcing individuals to disperse farther from the colony (Burke and Montevecchi, 2009; Paiva et al., 2013a, 2013b; Cecere et al., 2014). Therefore, individuals must be

Table 1

Behaviours displayed by Cory's Shearwaters (*Calonectris borealis*) when exposed to a strange object in the nest during 1 min, summary of the behaviours, frequency per individual and on the population, and Permutational Multivariate Analysis of Variance (Permanova) coefficients. Coefficients are the difference between the mean value for birds placed in the negative and in the positive values of the non-metric multidimensional scaling axis1 scores. Using zero as a cut value proved to produce different groups (Permanova $F_{1,193} = 21.96$, $P = .001$). Behaviours associated to less corporal movement (see Fig. 2b and sup V1) were assumed to characterize shy individuals (italic coefficients), and behaviours associated to more corporal movements were assumed to characterize bold individuals (bold coefficients).

| Behaviour	Abbreviation	Description	Mean ± sd number of times birds displayed each behaviour	Maximum number of times a bird displayed the behaviour	Number of birds that displayed the behaviour	Permanova Coefficients (Shy-Bold)
Pecking/lunging	Peck/Lung	Bird charged against the object and bitted, touching the object (pecking) or not touching the object (lunging).	0.25 ± 0.1	10	19	**−0.15**
Vocalization	Vocal	Bird vocalised	0.02 ± 0.14	1	4	0.003
Snapping	Snap	Bird made a sudden bite but without charging in the direction of the object	0.19 ± 0.77	8	22	0.14
Standing	Stand	Bird stood on its feet but did not move from its position	0.21 ± 0.59	4	28	**−0.18**
Gulping	Gulp	Bird seemed to gulp or swallow	0.17 ± 1.31	6	112	0.35
Move Head	Head	Bird moved the head	0.64 ± 0.91	5	79	*0.71*
Blinking	Blink	Bird blinked the eyes	0.50 ± 5.24	46	92	*1.57*
Twitching	Twitch	Bird gave a short and sudden jerking or convulsive-like movement	0.06 ± 2.23	14	68	*0.88*
Open wings	Wing	The bird opened its wings	0.11 ± 0.41	3	15	−0.03
Turn around	Turn	Bird turned around	0.18 ± 0.53	4	26	−0.025
Shake head	Shake	Bird shook its head	0.46 ± 1.03	7	49	**0.32**
Move away	Move	Bird moved in the opposite direction of the object	0.13 ± 0.37	2	24	−0.01
Open the bill	Bill	Bird hold the bill open for a few seconds, but without moving the head.	0.09 ± 0.38	3	12	0.05
Inspecting object	Inspect	Bird moved its head in the direction of the object, without opening the bill nor biting, nor touching the camera.	0.16 ± 0.51	4	23	−0.01
Gardening	Garden	Bird accommodated the nest, excavating the soil with the feet	0.01 ± 0.10	2	1	−0.01
Touching object	Touch	Bird touched the camera with the bill, without opening the bill.	0.04 ± 0.26	3	5	−0.03
Accomodate egg	Egg	Bird accommodated the egg with the bill	0.02 ± 0.14	1	4	−0.02
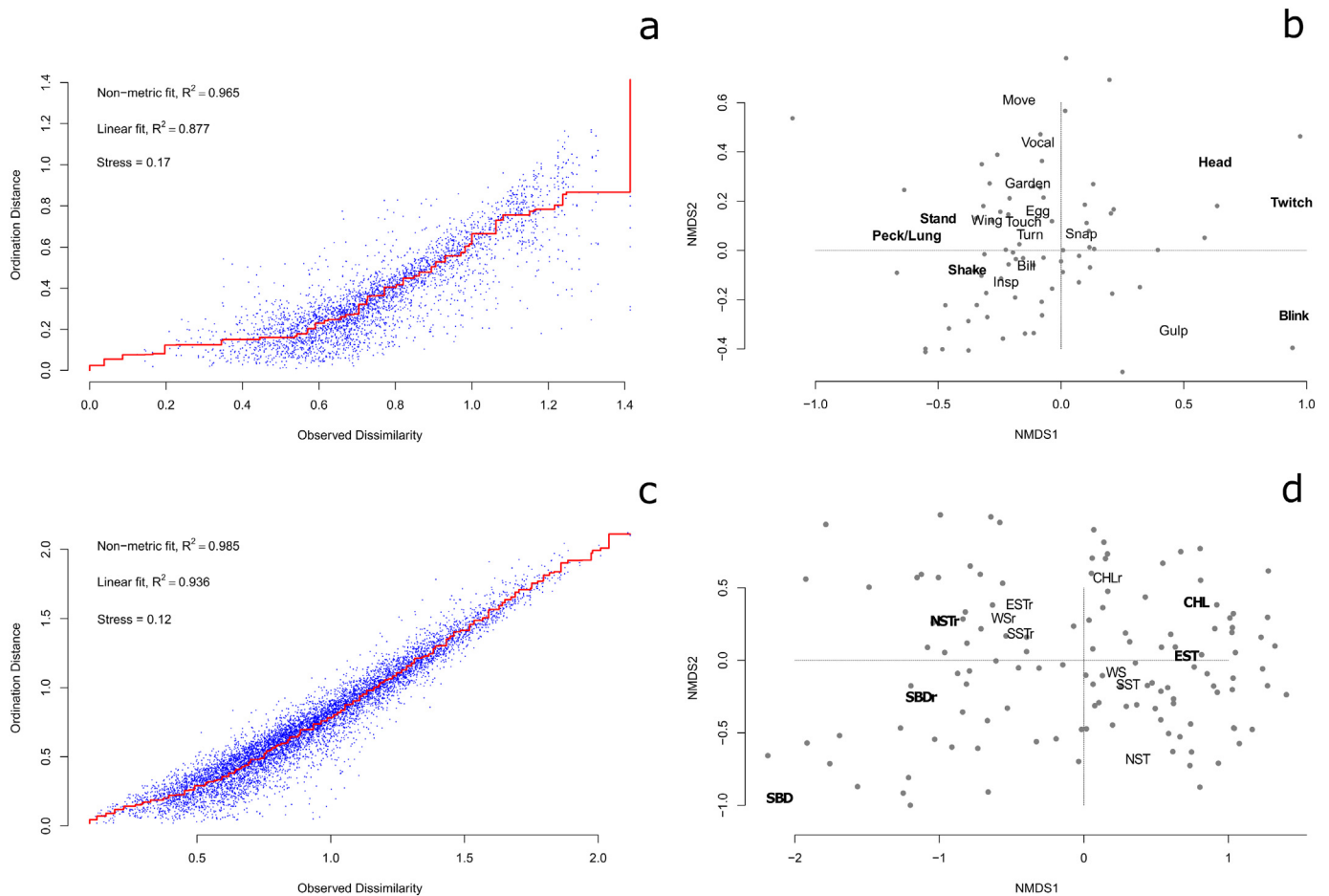
Fig. 1. Non-metric multi-dimensional scaling (NMDS) for the Cory's Shearwaters (*Calonectris borealis*) personality (a,b) sampled at nest using the 'response to a novel object' method, and foraging habitat (c,d) tracked during incubation with GPS technology. Each word in a and b is a different variable and points represent individuals (NMDS ordination distance from both analyses presented a high non-metric and linear fit (R^2) to the observed dissimilarity, and a fair stress level, indicating the analyses were accurate (a,c)). For personality variable abbreviations see Table 1. Chlorophyll-a concentration (CHL), Sea Surface Temperature (SST), Surface Wind Speed (WS), Northward Wind Stress (NST), Eastward Wind Stress (EST) and Sea Bed Depth (SBD). Lower 'r' at the environmental variables (d) indicates that those are variables ranges (minimum-maximum) used by the birds.
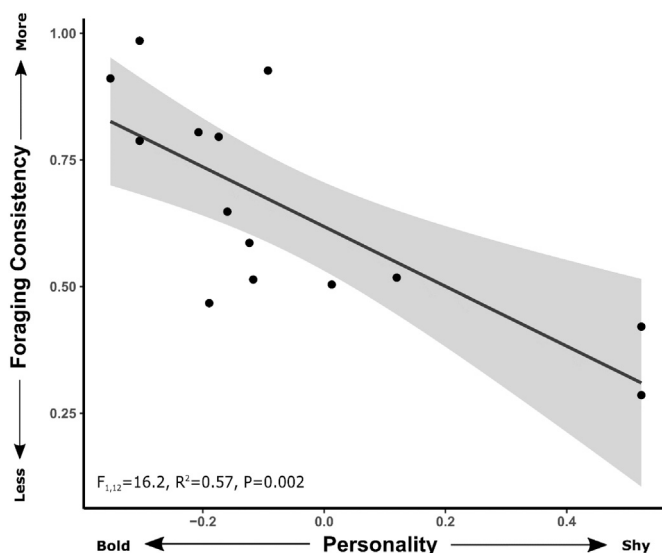

Fig. 2. Foraging consistency of Cory's Shearwaters (*Calonectris borealis*) during chick-rearing as a function of the personality (see Fig. 1). Bold birds are more time-consistent in their foraging behaviour.

flexible to adjust and compensate for environmental constraints (Haug et al., 2015; Paiva et al., 2013a, 2013b) in order to successfully raise a chick.

To the best of our knowledge, only one previous study attempted to relate individual seabird personality with foraging habitat (Patrick et al., 2014). Patrick et al. (2014) found that bolder Black-browed Albatrosses (*Thalassarche melanophris*) forage closer to the coast than shy individuals, and this affected breeding success and was influenced by individual sex. However, they evaluated only two years, therefore it is not possible to precisely infer long-term consequences of habitat changes based on their results. In this study we use Cory's Shearwater (*Calonectris borealis*) as a model species to test whether personality plays a role in determining shifts in at-sea behaviour and foraging habitat in relation with contrasting environmental conditions. Based on the findings of Patrick et al. (2014) we hypothesize that under adverse environmental conditions, shy Cory's Shearwaters may be displaced by more competitive bold individuals to forage far from the colony. As observed by Paiva et al. (2013a, 2013b), such displacements may result in differences in breeding success. Given current trends in climate change, poor environmental conditions are likely to increase for many pelagic seabirds. Therefore, understanding how personality will influence the decisions made by individuals is important to help understand how populations will cope with environmental changes.
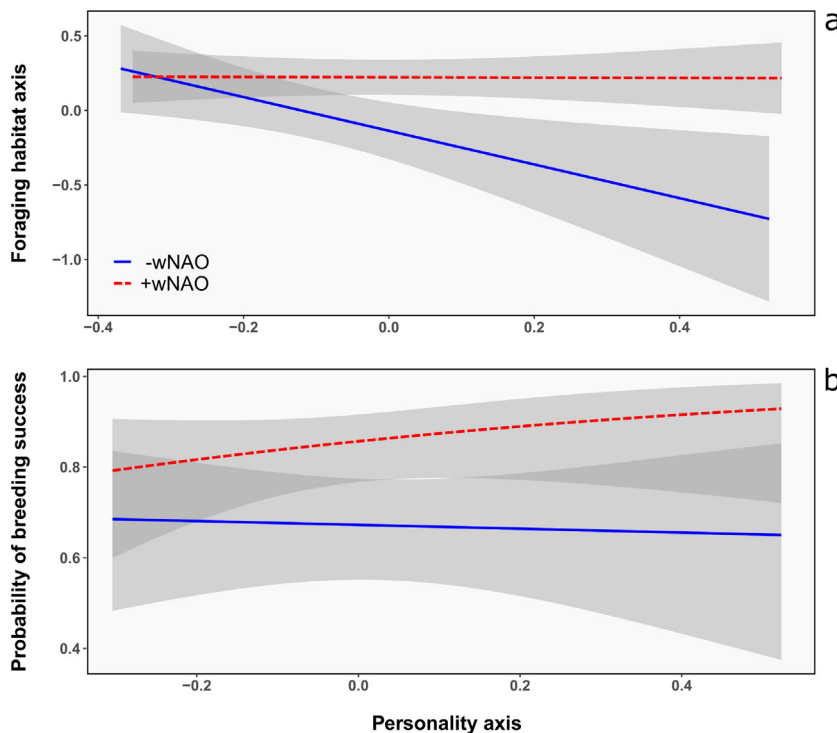
Fig. 3. Predicted foraging habitat (a) and probability of breeding success (b) of chick-rearing Cory's Shearwaters (*Calonectris borealis*) estimated through a Generalised Additive Model as a function of Personality and values of the winter North Atlantic Oscillation (wNAO). Lines are tendencies and grey area represent the standard deviation.

2. Material and methods

2.1. Study area and study species

This study was conducted in Berlenga Island, Portugal (39°24′N; 9°30′W) from 2010 to 2017. Berlenga is a coastal island within a large continental shelf where the bathymetry and shallow waters cause a strong upwelling (Sousa et al., 2008). Cory's Shearwaters are burrowing breeders, at Berlenga they breed in natural crevices on the rocks, excavated burrows or in artificial nests (i.e. Granadeiro, 1991; Lecoq et al., 2010).

2.2. Personality

Personality was quantified by use of the "response to a novel object" method (i.e Grace and Anderson, 2014b; Patrick and Weimerskirch, 2014b). We used a camera (Rollei action cam S-30) within its protective case, coupled to a head-lamp by plastic belts, as the novel object (Supplementary Fig. S1). We took advantage of the presence of the birds within their burrows during the incubation period. Response to the novel object by breeding birds at their nest was recorded in May 2015, 2016 and 2017. The camera was attached to a 1.5 m fibre pipe with plastic belts and inserted within the nest to record the bird response over 1.5 min (Supplementary Fig. S1). After recording, birds were carefully taken from the nest to be identified by the ring number. We were able to use a total of 124 records from 83 individuals; 47 were recorded in 2015 and 24 in 2016. We recorded 24 birds more than once; from those, 12 were recorded twice and 12 individuals were recorded three or four times; 58 individuals were recorded only once. Of the 24 birds recorded more than once, 20 were recorded the second time during the same year, 10 were recorded in the consecutive year, and only seven individuals were recorded again in both the same and consecutive years. We excluded the first 30 s of the videos and only used the subsequent 1 min to classify and quantify different behaviours.

To characterize each individual in terms of personality we applied a non-metric multi-dimensional scaling NMDS (euclidian distance, 20 minimum and 200 maximum random starts, Wisconsin standardization and 'monoMDS' engine) over individuals' displayed behaviours using the 'vegan' R-package (Oksanen et al., 2013). NMDS is a robust non-parametric factorial analysis which is adequate to non-normal variables (Kruskal, 1964a, 1964b; Kenkel and Orloci, 1986), like the ones in our multivariate data. The scores resulting from the first NMDS axes were used to characterize each individual for personality. We classified each individual (see results) as "Bold" and "Shy" based on the behaviours displayed (Table 1, Supplementary video 1). We also used a permutational multivariate analysis of variance PERMANOVA (Euclidian distance and 999 permutations) in order to test if classifying groups using zero as a threshold produces different groups. We used records as the sampling unit for the NMDS, as several individuals were recorded more than once (see below). We tested influence of sex on personality using a linear mixed model ('lmerTest' Kuznetsova et al., 2018) to compare personality between males ($n = 72$) and females ($n = 54$). A total of 69 birds could not be sexed.

2.3. Personality repeatability

In order to assume a behavioural syndrome, individual traits must be consistent along time, therefore repeatable. Moreover, boldness was shown to be consistent for other seabird species that are taxonomically (Patrick and Weimerskirch, 2014a) and ecologically (Grace and Anderson, 2014a, 2014b; Kazama et al., 2012) similar to Cory's Shearwater. Personality repeatability was tested using a contingency table with χ^2 test and fisher's exact test. We tested if the position of individuals recorded more than once changed their position in the NMDS first axis (positive and negative) in consecutive years. For the few individuals (see Results) who changed the signal in different records, we used the stronger value to identify their personality.

2.4. Foraging habitat

Birds were tracked with Geographical Position System (GPS) loggers between 2010 and 2017 during the mid-chick rearing period (late August – mid September). We used iGot-U and CatTraqTravel GPS-Loggers (Perthold Engineering LCC) encapsulated on a thermal plastic case (Supplementary Fig. S2). GPS-Loggers were attached with TESA tape (Wilson et al., 1997) to the back feathers (Supplementary Fig. S2,
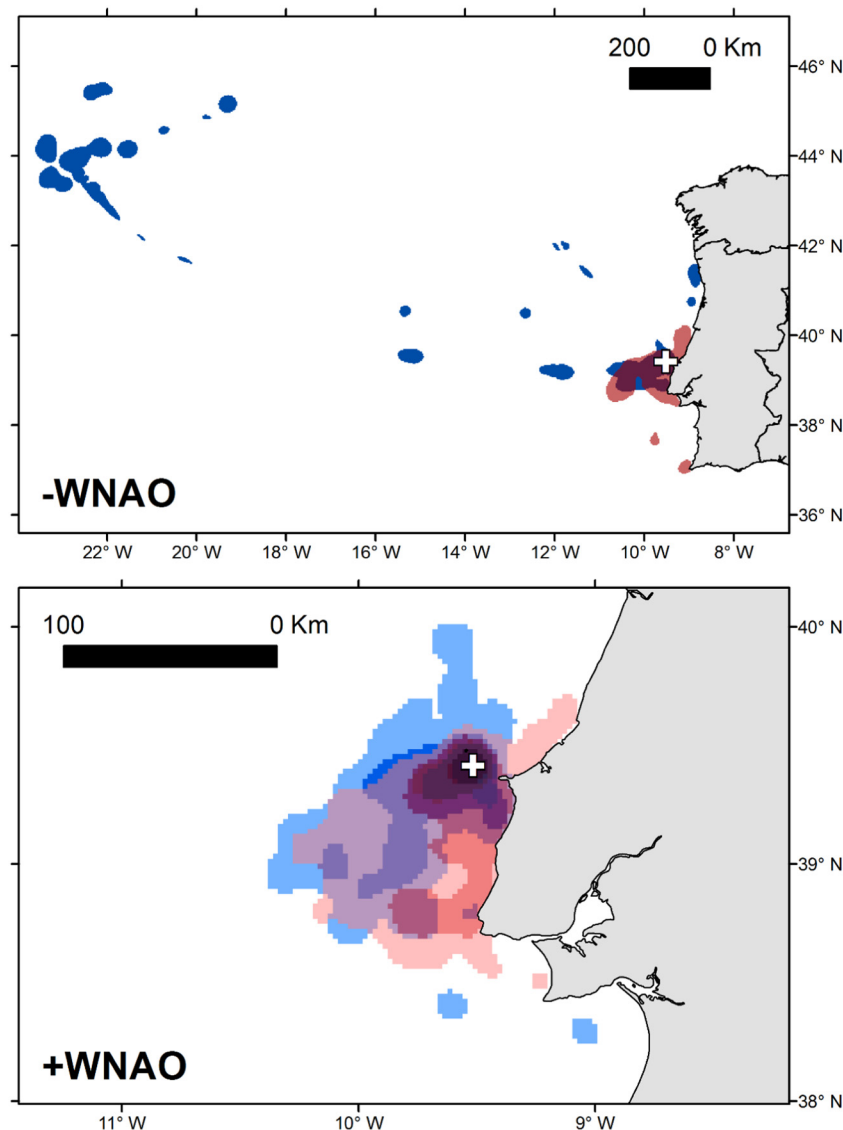
Fig. 4. Kernel Usage Density (KUD) for Bold (red) and Shy (blue) chick-rearing Cory's Shearwaters (*Calonectris borealis*) during years of different winter North Atlantic Oscillation (wNAO) values. At the top panel (-wNAO) only the 95% KUD was presented, and at the bottom panel (+ wNAO) 25%, 50%, 75% and 95% KUDs are presented, from the darker to the lighter colours. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Supplementary video 2). Devices weight broadly 17 g, representing from 1.6% to 2.6% of the birds' body weight, which is assumed to have no deleterious effects on seabirds' foraging behaviour in general (Phillips et al., 2003), and particularly on Cory's Shearwaters (Passos et al., 2010; Paiva et al., 2010b; Villard et al., 2011). GPS-loggers were set to collect data every 5 min, and the total handling time never exceeded ten minutes. Birds were immediately returned to their nests once the GPS-Loggers were successfully attached. A total of 124 tracks were recorded from 88 individuals. Sixty-seven individuals were tracked only during one chick-rearing period, 12 were tracked during two chick-rearing periods and eight in three or four chick-rearing periods. A single individual was tracked during five chick-rearing periods.

To assess foraging habitat, we classified the positioning of tracks with different behaviours based on estimated speed and turning rate using the Expectation-Maximization Binary Clustering (*EmBC*) R package (Garriga et al., 2016), and defined foraging locations as the areas where birds were at Low Speed ($< 1.0\,\mathrm{ms}^{-1}$) and High Turning Rate ($> 0.48\,\mathrm{rad}$). We extracted values of chlorophyll *a* concentration ($\mathrm{mg/m}^3$), sea depth (km), sea surface temperature (°C), sea surface wind speed (m/s), eastward wind stress ($\mathrm{N/m}^2$) and northward wind

stress ($\mathrm{N/m}^2$) within those points (Supplementary Fig. S3). All variables were downloaded from the browser Giovanni (https://giovanni.sci.gsfc.nasa.gov/giovanni/). Dynamic variables (except depth) were obtained as monthly averages for August and September of each year, and then averaged yearly for the two months. A mean value of those variables was extracted for the foraging locations of each individual per year. Given the spatial and temporal scale of the study, the resolution for averaging the variables was sufficient to reflect conditions experienced by the birds (Lambert et al., 2017; Wakefield et al., 2009).

To characterize the foraging habitat of each individual we applied a non-metric multi-dimensional scaling (NMDS) using the 'vegan' R-package (Oksanen et al., 2013). The scores resulting from the first NMDS axes were used to characterize each individual foraging habitat. Again, we used individual tracking for each season as sampling unit in order to detect when individuals changed their foraging habitat over multiple years. We tested the influence of sex (23 females and 38 males) on foraging habitat in contrasting wNAO conditions using a mixed model with bird unique ID as a random factor on the 'lmerTest' R package (Kuznetsova et al., 2018).

2.5. Environmental conditions

The North Atlantic Ocean is strongly driven by a climate system characterised by extreme swings of air pressure between 40°N and 60°S, depicted by the North Atlantic Oscillation (NAO) index (Hurrell and Van Loon, 1997). Shifting states of the NAO index are related to shifts in local climate variables that influence ecological processes of the North Atlantic (Stenseth et al., 2003). The winter shifts are particularly strong, therefore shifts in the winter NAO (wNAO) are usually followed by drastic changes in North Atlantic food webs (Stenseth et al., 2003) with particularly intense cumulative effects on seabirds (Descamps et al., 2010; Genovart et al., 2013; Ramos et al., 2015; Sandvik and Einar Erikstad, 2008). Paiva et al. (2013b) has shown that a negative wNAO is indicative of poor years for Cory's Shearwater breeding in Berlenga Island. Negative wNAO correlates with severe storms at sea and strong upwelling carries away fish eggs, which will not recruit in the next warm season. Therefore, in a summer following such a cold season, there will be less food for seabirds in Berlenga (Paiva et al., 2013b). We classified each year of tracking as good years (positive wNAO) or poor years (negative wNAO).

2.6. Personality and foraging habitat

We were able to record personality for 34 out of the 88 tracked birds. Of those 34, 14 were tracked in multiple years. We calculated a measure of foraging consistency for those 14 birds as $1 - \sigma^2 FH$, where $\sigma^2 FH$ is the standard deviation of the foraging habitat NMDS value of each individual for multiple years. This measure of consistency varied from 0 (no consistency) to 1 (complete consistency). We tested if this foraging consistency is associated with personality using a linear regression.

We tested the influence of personality on foraging habitat according to the value of the wNAO using 61 tracks from the 34 birds with both personality and tracking data recorded. Because some individuals were repeated over time, we used a Generalised Additive Mixed Model (GAMM) ('mgcv' R package) and entered bird ID as a random term to control for the lack of independence on repeated birds [gamm(FH~ wNAO + s(Personality, by = wNAO), random = list(bird ID = ~ 1), family = "gaussian")].

Finally, we applied Kernel Usage Density (KUD) with the 'kernelUD' function of the 'adehabitatHR' R package (Calenge, 2011) to visually inspect the distribution of bold and shy individuals in contrasting wNAO values. We first generated the KUD for each individual in each year separately, and then calculated a mean KUD for each group. This procedure allows for the calculation of unbiased KUD, preventing individuals with more tracking points from being more influential on the final KUD estimation. We used a smoothing term (h) of 0.1° and an epanechnikov kernel function (Kerm, 2003; Scaillet, 2004).

2.7. Breeding success

Birds were monitored in all years for breeding success. We considered success when a bird was able to successfully fledge a chick (1) or not (0). We tested the influence of personality and wNAO over the breeding success using a binomial GAMM with bird ID as a random term [gamm(BS ~ wNAO + s(Personality, by = wNAO), random = list (ID = ~ 1), family = "binomial")].

3. Results

3.1. Personality

We recorded 17 different behaviours (Table 1). While personality was treated as a continuous variable, birds could be classified in two distinct groups based on a small number of behaviours displayed (Permanova $F_{1,193} = 21.96$, $p = .001$): Pecking or Lunging and Standing for one group and Blinking, Moving Head and Twitching for the other (Table 1). Given the nature of the behaviours characterising the differences between groups (Table 1, Supplementary video 1), we identified which birds can be seen as Shy (behaviours associated with less movements or response towards the object, positive side of the NMDS axis) or Bold (behaviours associated with more body mobility and actions towards the camera, negative side of the NMDS axis). Personality was consistent, i.e., when recorded again, birds had a high chance of repeating similar response to the novel object ($\chi^2 = 15.95$, Fisher's $p < .0001$). Personality was not influenced by sex ($F_{1,124} = 2.16$, $t = 1.47$, $p = .146$; Supplementary Fig. S4).

3.2. Personality, foraging habitat and breeding success

Foraging Habitat was related to increased chlorophyll *a* concentration, eastward wind stress and shallow waters (Fig. 1cd). It is logical to assume that negative values of this axis are associated with the opposite trend for these variables. There was no difference in foraging habitat between sexes ($F_{1,59} = 0.15$, $t = -0.04$, $p = .972$; Supplementary Fig. S5). Foraging consistency was related to personality ($F_{1,12} = 16.2$, $R^2 = 0.57$, $p = .002$). The bolder an individual, the more consistent it was for foraging habitat (Fig. 2). Foraging habitat was different between years of –wNAO and + wNAO (GAMM $t = 2.94$, $\beta = 0.32$, $p = .005$), and the foraging habitat was related to the smoothed personality in years of –wNAO (GAMM $t = -2.56$, $\beta = -0.32$, $p = .017$) but not during + wNAO (GAMM $t = -0.05$, $\beta = -0.02$, $P = .957$). During + wNAO years both bold and shy individuals shared similar habitats, but segregated habitat considerably during –wNAO years (Fig. 3a).

Breeding success was different between years of contrasting wNAO (GAMM $t = 2.7$, $\beta = 1.12$, $p = .007$), but it was not significantly related to the personality during + wNAO (GAMM $t = -0.18$, $\beta = -0.05$, $p = .856$) nor during –wNAO (GAMM $t = 1.07$, $\beta = 0.37$, $p = .288$) years. Breeding success was higher during + wNAO years (Fig. 3b).

During + wNAO years, both bold and shy individuals remained closer to the breeding colony, overlapping most of their home ranges (95% KUD), but segregated in foraging areas (both 75% and 50% KUD); bold individuals remained closer to the coast when compared to shy individuals (Fig. 4). During –wNAO years both bold and shy individuals travelled greater distances from the colony, particularly the shy individuals (Fig. 4).

4. Discussion

We found, as expected, that boldness influenced foraging distribution. Bold birds were more consistent in their foraging habitat between years, and shy birds were more prone to change their foraging habitat. The influence of boldness was more evident during negative wNAO, assumedly poor years for seabirds breeding in Berlenga (Paiva et al., 2013b), when shy birds foraged considerably farther from the colony than the bold birds. However, probability of successful breeding was lower in –wNAO for the population as a whole.

4.1. Foraging and boldness

Several seabird species show long-term consistency in their foraging behaviour and strategy (like Black-browed Albatrosses, Patrick and Weimerskirch, 2014a, 2014b) or foraging location (like Northern Gannets *Morus bassanus* Patrick et al., 2014 or Desertas Petrel *Pterodroma deserta* Ramírez et al., 2016). However, Cory's shearwaters have been seen as a plastic species, more able to adjust their behaviour in response to environmental stochasticity (this study, Granadeiro et al., 1998; Paiva et al., 2010a). Cory's shearwaters short-term foraging consistency is well known (Ceia et al., 2014a) but long term consistency is controversial. There is more support for flexible behaviour across multiple years (Catry et al., 2013; Granadeiro et al., 1998). This is also

supported by our results showing shy individuals as less consistent in their foraging habitat between years. It is important to consider that consistency in foraging behaviour may vary among different populations (Paiva et al., 2010b; Alonso et al., 2012). Therefore, Cory's shearwaters from other populations may respond differently to environmental variability, particularly because Berlenga is a coastal island and is exposed to different conditions compared to pelagic islands.

We found that during poor environmental conditions (negative wNAO and low prey availability, Paiva et al., 2013b) shy individuals that foraged close to the colony tended to shift away from the colony, indicating flexibility in this population. Therefore, our results show that bold individuals demonstrate a less exploratory personality (or explore less) in Cory's shearwaters. This contradicts previous findings for other groups of animals including geese (Kurvers et al., 2012), tits (Van Oers et al., 2005), baboons (Carter et al., 2013), deer (Bergvall et al., 2011) and lemurs (Dammhahn and Almeling, 2012) and fish. For example, bold freshwater fish are more likely to migrate (Chapman et al., 2011) or disperse (Cote et al., 2010) than shy individuals and bold animals are quicker to make foraging decisions under experimental (Carter et al., 2013; Kurvers et al., 2012; Van Oers et al., 2005) or free-ranging conditions (Bergvall et al., 2011; Dammhahn and Almeling, 2012). Bold animals should be more prone to "take risks" under unknown or adverse environmental situations (Carter et al., 2013; Dammhahn and Almeling, 2012). However, under a central place forager perspective, it seems that competition is more important in determining spatial segregation, as the more aggressive (presumably bold) individuals may occupy foraging areas near the colony while shy individuals forage in more distant areas (Patrick and Weimerskirch, 2014b, this study), probably by consequence of indirect (exploitative) competition.

Sex differences in spatial distribution are largely known for this species. Usually females are more dispersive and engage in longer trips than males (Quintana et al., 2011; Ceia et al., 2012; Patrick and Weimerskirch, 2014a; Patrick et al., 2014; Ceia et al., 2014b), but our results showed that this is not reflected in the oceanographic conditions explored by each sex. Patrick and Weimerskirch (2014a, 2014b) showed that females who are more flexible in their foraging range and habitat have a higher breeding success in poor years. But our results showed that both sexes changed their foraging habitat during –wNAO.

4.2. Breeding success

Our results confirmed the hypothesis that shy individuals are more prone to change their foraging characteristics under adverse environmental conditions. This is probably because bold individuals are more competitive, and may cause shy individuals to disperse (through exploitative competition) in order to find food. Bold animals have been shown to be more efficient in searching for food resources than shy individuals (i.e Kurvers et al., 2012; Carter et al., 2013). During good years both the bold and shy individuals tended to forage closer to the colony, with slight spatial segregation. However, in poor years bold individuals tended to maintain this trend, while shy individuals shifted habitat. This might be explained by: a) intra-population competition - when food is scarce shy individuals reduce spatial overlap with bold individuals (evidence for this in Wolf and Weissing, 2010 and Cole and Quinn, 2011), and b) bold birds are more able to cope with the environmental constraints closer to the colony than shy birds. However, we did not find any evidence to support that personality affects the breeding success in contrasting years. Under adverse conditions the overall population breeding success tended to decrease. We conclude that individuals displaced to forage farther from the colony during years of poor environmental conditions will have lower breeding success (Paiva et al., 2010b, 2010c; Paiva et al., 2013a), and ultimately this cost is borne not just by shy individuals, but the population as a whole. Future research should evaluate whether increased environmental variability driven by climate change influences the frequency of shy or bold individuals in a population and how shifts in the proportions of

each personality might impact population dynamics.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2019.04.003.

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