

Foraging plasticity in a pelagic seabird species along a marine productivity gradient

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ABSTRACT: The foraging plasticity in a pelagic seabird species, Cory's shearwater *Calonectris diomedea*, was compared during incubation and chick-rearing among 7 different breeding sites in the North Atlantic. These sites, with contrasting ecological conditions, were situated in the Azores (Corvo, Faial, Graciosa and Sta. Maria), Berlengas (Berlenga), Madeira (Desertas) and Selvagens (Selvagem Grande) archipelagos. Behavioural data were obtained by intensively deploying compass-temperature and temperature-depth data loggers, monitoring 302 and 22 foraging excursions, respectively. A principal component analysis revealed 2 main groups, one foraging along a neritic shelf (Berlengas population) and the other foraging in pelagic oceanic areas (populations from Azores, Madeira and Selvagens). There was a significant positive correlation ($r_s = 0.55$) between the percentage of short foraging trips in the different breeding sites and the concentration of chlorophyll-*a* in the waters surrounding those sites. Birds exploiting neritic areas used shallower depths (4.9 ± 2.3 m) and shorter dives (17.0 ± 2.2 s) than birds feeding in oceanic waters (9.8 ± 2.4 m and 32.0 ± 5.8 s respectively). This indicates that birds adapted their modes of predation to cope with the diverse distribution of their prey items. Overall, the behavioural response of the different populations was mainly dictated by the heterogeneity of their habitat, which was driven by 2 productivity gradients present in the north Atlantic. (1) Productivity is expected to increase from the subtropical warmer waters close to Selvagens to northern colder waters north of the Azores archipelago. (2) Oceanic environments are expected to be less profitable than coastal areas (upwelling areas), such as the Portuguese and African coasts.

KEY WORDS: Data loggers · Ecological plasticity · Environmental heterogeneity · Foraging behaviour · Seabird

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INTRODUCTION

Animals allocate a large proportion of their time to foraging (Drent & Daan 1980), which is constrained by the distribution, abundance, mobility and predictability of food resources (Bell 1991). To overcome these constraints, many animals show a certain degree of plasticity, i.e. a variation in behaviour in response to varying environments. At sea, prey abundance and availability vary considerably on temporal and spatial scales influenced by a variety of biotic and abiotic parameters (Hunt & Schneider 1987). Temporal variation in prey patch location or richness is experienced at

annual, seasonal, diurnal or even smaller time scales (Fauchald et al. 2000). For seabird species that generally access only the upper few meters of the water column, the occurrence of oceanographic phenomena and physical features that concentrate prey and enhance food availability are of major importance (Hunt 1997, Tew Kai et al. 2009). For example, these characteristics include oceanic frontal regions (Rodhouse et al. 1996) and bathymetric features, such as continental shelves, seamounts or canyons (Yen et al. 2004, Mann & Lazier 2005). In the oceanic areas of the north Atlantic, all these features are patchily distributed (Morato et al. 2008a), which, in conjunction with

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fish schooling behaviour, creates spots of productivity exploited by seabirds and other marine predators (Yen et al. 2004, Palacios et al. 2006).

The plasticity of seabird at-sea behaviour is characterised by significant changes in terms of diving effort (Lewis et al. 2004), diving pattern (Kato et al. 1996), diel rhythms of feeding events (Garthe et al. 2003), proportion of the foraging trip spent travelling (Monaghan et al. 1994) and trip duration (Congdon et al. 2005). These are responses to environmental heterogeneity or to changes in the energetic needs of the seabirds in relation to the different stages of their annual cycle (reproduction, migration, moult). Such plasticity needs to be investigated for a better understanding of the ecological and evolutionary role played by foraging behaviour in explaining the use of different marine areas by seabirds.

While foraging in heterogeneous environments, adult petrels and shearwaters may alternate between long and short foraging trips (Chaurand & Weimerskirch 1994, Weimerskirch et al. 1994), a strategy allowing efficient food delivery to chicks without compromising their own requirements (Baduini & Hyrenbach 2003). Cory's shearwaters *Calonectris diomedea* have been observed making use of such a dual foraging strategy (Magalhães et al. 2008), in which individual parents make both short and long foraging trips, especially under food shortage around the breeding colony (Granadeiro et al. 1998a). Moreover, it is well known that procellariiform seabirds of the southern (e.g. Einoder & Goldsworthy 2005, Xavier et al. 2004) and the northern (e.g. Shaffer et al. 2006, Magalhães et al. 2008) hemisphere travel long distances to exploit highly productive marine areas such as shelf slopes or frontal zones. However, little information is available to explain how different populations of Cory's shearwaters adapt their activity patterns to exploit spatially contrasting oceanographic conditions. Cory's shearwater is well suited to address this question because it shows plasticity in foraging techniques, as it is well adapted to sea-surface feeding, but may sometimes dive to exploit prey in deeper waters (Martin 1986). Also, the investment in a dual foraging strategy may be constant or vary among different Cory's shearwater breeding populations (Baduini & Hyrenbach 2003).

Until the late 1990s, little information on the at-sea foraging behaviour of Cory's shearwaters was available (Mougin & Jouanin 1997). Newer studies (Navarro et al. 2007, 2009, Magalhães et al. 2008, Navarro & González-Solís 2009) interpreted behaviour using proxies from positioning data and did not focus on the detailed movements and habits of birds during their forays at sea. This is possible using more accurate data proxies for bird behaviour, such as the ambient temperature collected concurrently with positioning. We

addressed these issues by deploying data loggers to measure parameters of their foraging distribution and foraging efforts, comprising (1) diving rate, (2) sea surface temperature, (3) proportion of time spent travelling (i.e. time spent flying, in contrast to time in the water), (4) trip duration, geographic position as (5) latitude and (6) longitude, (7) dive depth, (8) dive duration, and (9) dive shape. This allowed us to compare the at-sea behaviour of Cory's shearwater during incubation and chick-rearing among birds from 7 breeding sites on 4 archipelagos in the north Atlantic with contrasting environmental conditions. Overall, accessibility to highly productive habitats (considering both colony surroundings and relatively distant zones) should decrease in the following order: Berlengas, Azores, Madeira and Selvagens. Thus, we expected Cory's shearwater populations from these 4 archipelagos to exhibit a corresponding increase in their foraging effort.

MATERIALS AND METHODS

Study area. We deployed data loggers on Cory's shearwaters breeding in colonies in the North Atlantic (Fig. 1) during a 4 yr period (2005 to 2008) to track their movements, foraging behaviour and daily activity patterns. Sampling effort was spread across 7 study sites situated in 4 archipelagos: Berlenga (Berlengas); Corvo, Faial, Graciosa and Santa Maria (Azores); Desertas (Madeira) and Selvagem Grande (Selvagens; Tables 1 & 2). On Berlengas, birds breed within a neritic system, i.e. an island within a long continental shelf of ≤ 200 m depth. At the 4 sites in the Azores, the birds breed within an oceanic system, i.e. oceanic islands with a short shelf (Table 1). The last colony, Selvagem Grande, is surrounded by an oceanic environment, but is situated within 375 km of a large neritic system, the African continental shelf (Fig. 1). Ocean circulation in this region of the Atlantic is complex. Coastal upwelling, present on the northern Portuguese (Sousa et al. 2008) and African (Davenport et al. 2002) coasts, enhances the primary production of these areas (Huntsman & Barber 1977). On the other hand, Azores and Madeira, situated in the mid Atlantic, are characterised by low marine productivity, but the conjunction of equatorial and tropical waters transported by the Gulf Stream with colder northern waters creates frontal zones (Gould 1985, Pingree et al. 1999) with enhanced marine productivity (Santos et al. 1995). The ocean circulation in the north Atlantic generates a north-south productivity gradient. The lower productivity pattern towards the southern area of the north Atlantic region is occasionally interrupted by underwater features, such as seamounts (Morato et al. 2008a,b), eddies (Li &

Hansell 2008), canyons or upwelling areas, which are known to increase the abundance of marine biota (Mann & Lazier 2005). In addition, the Mid-Atlantic Ridge (MAR), with several large seamounts (1000 to 2000 m height; Morato et al. 2008a), influences local

and regional oceanic circulation patterns and enhances productivity (Sutton et al. 2008).

Methods. Between 2005 and 2008, 187 data logger deployments (both compass and pressure loggers; N = 34 devices) were made on 187 Cory's shearwaters,

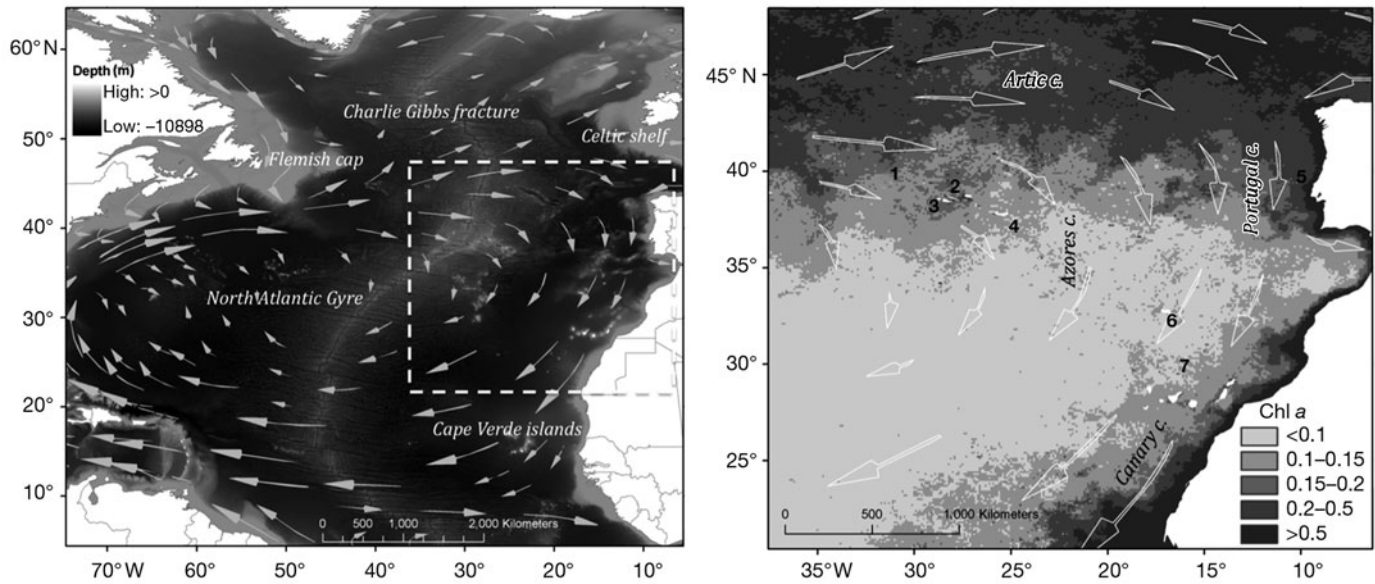


Fig. 1. Broad perspective of the north Atlantic area (left panel) with bathymetric features (labelled; www.ngdc.noaa.gov/mgg/bathymetry/relief.html), the main oceanic gyre influencing the north Atlantic and a detailed view (right panel, corresponding to the area within the dashed line) of the Cory's shearwater breeding colonies where data loggers were deployed. 1, Corvo island; 2, Praia islet (Graciosa island); 3, Faial island; 4, Vila islet (Sta. Maria island); 5, Berlengas island; 6, Deserta Grande island (Madeira archipelago); 7, Selvagem Grande island (Selvagens archipelago). Chl *a* concentration (mg m^{-3}) represents the mean chlorophyll composites for all months and years of study (June to September, 2005 to 2008) and was extracted from <http://ocean-color.gsfc.nasa.gov/>. Arrows: direction of the main oceanic currents influencing the study area (provided by the Portuguese Hydrographic Institute)

Table 1. Environmental characteristics of each study area interpreted from satellite imagery: mean SST and mean chl *a* levels within a radius of 60 km around the colony site from 2005 to 2008. SST, chl *a* and bathymetry data were downloaded from: <http://poet.jpl.nasa.gov/>, <http://oceancolor.gsfc.nasa.gov/>, www.ngdc.noaa.gov/mgg/bathymetry/relief.html. Values in **bold** relate to the sampling periods

Location	SST ($^{\circ}\text{C}$)					Chl <i>a</i> (mg m^{-3})					Distance to nearest seamount feature (km)	Min. distance to canyon or sea channel (km)	Min. distance to isobaths (km) ^a	
	May	Jun	Jul	Aug	Sep	May	Jun	Jul	Aug	Sep				
Berlengas														
Berlenga	15.0	17.6	17.3	16.7	18.2	0.32	0.29	0.32	0.32	0.33	255	54	17, 23, 55	
Azores														
Corvo (occidental group)	16.9	17.7	20.5	22.9	22.8	0.34	0.19	0.16	0.18	0.25	74	74	5, 19, 314	
Faial and Graciosa (central group)	16.6	17.2	20.0	22.4	21.8	0.36	0.21	0.16	0.20	0.16	19	22	6, 44, 494	
Sta. Maria (oriental group)	18.4	18.8	20.9	22.4	22.3	0.13	0.12	0.12	0.11	0.19	50	49	4, 19, 56	
Madeira														
Deserta Grande	18.5	20.2	21.6	22.2	23.2	0.19	0.17	0.17	0.17	0.15	249	198	2, 9, 37	
Selvagens														
Selvagem Grande	19.7	20.8	21.6	22.1	23.2	0.14	0.14	0.15	0.16	0.12	248	301	1, 5, 53	

^aIn the order: continental shelf-break (200 m), continental slope (1000 m), pelagic waters (3000 m) (after Yen et al. 2004)

Table 2. *Calonectris diomedea*. Data logger deployments on Cory's shearwaters and data acquired from 2005 to 2008. Minimum trip duration was 1 d for all study areas. Mean trip duration (\pm SD) includes foraging trips from both compass and pressure loggers (CL, PL)

Year	Month	Place	Breeding phase	Birds	CL	PL	Total no. of CL trips	—Trip duration (d)—	
								Mean \pm SD	Maximum
2005	Sep	Berlenga (Berlengas)	Late chick-rearing	18	16	2	24	1.2 \pm 0.9	3
2006	Jun	Faial (Azores)	Early incubation	12	12		17	8.3 \pm 5.8	11
	Jun	Graciosa (Azores)	Early incubation	4	4		7	6.1 \pm 5.4	12
	Jul	Desertas (Madeira)	Late incubation	9	9		13	9.2 \pm 8.1	19
	Aug	Faial (Azores)	Early chick-rearing	12	12		34	2.3 \pm 5.2	11
	Sep	Berlenga (Berlengas)	Late chick-rearing	20	17	3	19	1.9 \pm 3.2	7
	Sep	Desertas (Madeira)	Late chick-rearing	7	7		9	2.8 \pm 4.5	12
2007	Jun	Berlenga (Berlengas)	Early incubation	8	8		12	4.6 \pm 6.3	13
	Jul	Sta. Maria (Azores)	Late incubation	7	7		9	9.6 \pm 7.1	16
	Jul	Corvo (Azores)	Late incubation	11	11		23	9.2 \pm 6.8	14
	Aug	Corvo (Azores)	Early chick-rearing	23	17	6	45	2.2 \pm 5.9	13
	Sep	Berlenga (Berlengas)	Late chick-rearing	28	19	9	39	1.4 \pm 1.1	3
	Sep	Selvagem (Selvagens)	Late chick-rearing	8	6	2	12	2.1 \pm 3.7	8
2008	Aug	Selvagem (Selvagens)	Early chick-rearing	21	21		39	2.4 \pm 4.3	9
Total				187	165	22	302		

amounting to 339 foraging excursions, of which 98.7% were successfully retrieved, and 96.8% had data of sufficient quality for analysis. We had to discard a residual number of foraging excursions either because of electrical problems with the bearings of one compass or because the temperature sensor was broken. We analysed a total of 302 foraging trips from 165 adult Cory's shearwaters equipped with compass loggers to inspect differences in behaviour and time allocation when feeding at sea. In addition, we tracked 22 Cory's shearwater individuals with pressure loggers during the chick-rearing phase to assess differences in the patterns and characteristics of dives between birds foraging on/near the continental shelf and in the oceanic habitat (Table 2).

Technical details of the data loggers used: We equipped Cory's shearwaters with compass-temperature loggers (Compass-Tlog, hereafter named compass loggers). These direction recorders for birds are a type of dead-reckoning data logger (Wilson et al. 2007) and have an outer diameter of 16 mm, a total length of 65 mm and a mass of ~14.5 g, representing 1.3 to 2.1% of the bird's body mass. Intervals for bearing (precision of 1 binary value) and temperature (to the nearest 0.001°C) measurements were set to between 1 and 4 s for the chick-rearing period (memory lasts for 4 to 12 d), and 5 and 6 s for the incubation period (memory lasts for 20 to 24 d; earth & OCEAN Technologies, Kiel, Germany). Shorter intervals between bearing and temperature measurements allow better discrimination of behaviours and track reconstruction, but because of the memory limit, intervals need to be set according to the expected duration of the foraging excursion at sea. The precision temperature-depth recorders (PTD loggers, hereafter

named pressure loggers) have an outer diameter of 19 mm, a total length of 80 mm and a mass of ~23 g, which represents 2.0 to 2.7% of the bird's body mass. Intervals for temperature (to the nearest 0.001°C) and pressure (to the nearest 0.01 bar) measurements were set at 1 s (memory lasts for 6 d; earth & OCEAN Technologies, Kiel, Germany). The data collected from these devices allowed analysis of more than 500 dives in terms of their patterns, rate of occurrence and duration.

Logger deployment: A metal identification ring was placed on the bird's tarsus and biometric measurements were collected from all birds used for logger deployments. Biometric measurements included body mass, wing length, tarsus length, head and bill, culmen, bill height at the gonys (the keel or more salient lower outline of the bill) and height at the base of the bill (at the upper posterior border of nares). These measurements were used in a discriminant function described by Granadeiro (1993) to determine sex. Both types of devices were attached with Tesa® tape (Wilson et al. 1997) to the 4 central tail feathers. Biometric measurements and attachment of tags took 10 to 15 min and birds were returned immediately to their nest. After retrieval of the devices, birds were always weighed, as they should have gained weight either to replace their mate on the nest (incubation period) or to feed their chick (chick-rearing period). All but 3 individuals, in which a maximum decrease of 7% (63 ± 7 g) was recorded, maintained or increased their weight during a foraging trip with loggers, considering both incubation and chick-rearing periods. During the incubation period, all tracked birds from the different study sites ($N = 51$) were again weighed on the day after their logger removal to obtain a better measure of mass

assimilated; 93 % of the birds increased their weight (mean = 18.1 g, range 9 to 53 g). Moreover, the change in the individual bird mass was similar between tracked (mean change = 6.2 ± 2.1 %) and non-tracked (mean change = 6.7 ± 1.9 %) individuals (arcsine transformed data: $t_{98} = 0.12$, $p = 0.9$). On Berlengas, during the chick-rearing period of 2007, birds carrying devices ($N = 28$) had a similar weight increment (measured after removal of devices) to that of birds without devices ($N = 20$; birds with loggers = 91.2 ± 25.6 g vs. birds without loggers = 86.1 ± 33.4 g; $t_{46} = 0.82$, $p = 0.5$). Weight of equipped (894.5 ± 65.4 g) and non-equipped (855.2 ± 54.2 g) adults (with empty stomach) was similar (arcsine transformed data: $t_{46} = 0.82$, $p = 0.5$) ensuring an unbiased comparison. Moreover, fledging success of Berlengas birds with and without loggers was similar (83.3 %, $N = 28$ vs. 84.1 %, $N = 20$; $\chi^2_1 = 0.98$, $p = 0.32$). Both types of loggers always represented less than 3 % of the bird's body weight, which has been reported to have no deleterious effects on seabird species (Phillips et al. 2003), including Cory's shearwaters (Igal et al. 2005), during short-term deployments.

Environmental data: Monthly composites of remote sensing data were used to characterise the marine environment surrounding Cory's shearwater breeding colonies (Table 1) and assess the reasons influencing foraging choices. A radius of 60 km was selected as representing 'colony surroundings' based on the median of the maximum distances travelled by adults during feeding events (median = 57 ± 28 km) during their short foraging excursions. Diverse environmental data were extracted for a grid between 43 and 5° W, and 15 and 57° N. Namely, night-time values of sea surface temperature (SST, $^\circ\text{C}$), chlorophyll *a* (chl *a*) concentration (mg m^{-3}) and bathymetry (m) were obtained from the following websites: <http://poet.jpl.nasa.gov/>, <http://oceancolor.gsfc.nasa.gov/> and www.ngdc.noaa.gov/mgg/bathymetry/relief.html. SST data was downloaded with a spatial resolution of 0.04° (approx. 4 km), chl *a* with a spatial resolution of 0.1° (approx. 9 km) and bathymetry data with a spatial resolution of 0.01° (approx. 1 km). Data was downloaded as ASCII files and grid cells with erroneous data (e.g. cloud cover) were removed both for SST (values < 255) and chl *a* (values $\neq -999$). Files were then converted to raster data by interpolation (Inverse Distance Weighted method) using the Spatial Analyst toolbox of ArcView GIS.

Data analysis and statistics: The MT-Comp v6 software (Jensen Software System, Kiel, Germany) was used for track reconstruction and interpretation of behavioural data. This software reconstructs flight, swimming or other movements using a dead-reckoning technique (Dall'Antonia et al. 1995, Thaxter et al. 2009). The routes taken by Cory's shearwaters were reconstructed using the archived directional informa-

tion together with their speed (general cruising speed for Cory's shearwater = 10 m s^{-1} ; Rosén & Hedenström 2001, Paiva et al. 2010), and the directional information was converted into a vector. Vectors were calculated for each subsequent data point and combined to reconstruct the full foraging track. As wind drift could influence the foraging routes of birds at sea, especially on trips lasting several days, we tried to minimise drift error by including information on wind speed and direction. This information was obtained for daily composites from: http://cersat.ifremer.fr/data/discovery/by_parameter/ocean_wind/mwf_quikscat on a 0.5° grid, and after processing, added and interpolated to raster data on a GIS system. The input of wind characteristics into the MT-Comp software was made in 3 main steps: (1) The track was reconstructed without any wind characteristics (because we had no pre-assumption as to where the birds were going). (2) After checking the approximate position and timing of the bird track each day on a GIS system, we added the wind characteristics information to each location using the Zonal Statistics tool from the Spatial Analyst toolbox (ArcView GIS). When grid squares had no data for an intended day (i.e. due to cloud cover or technical problems), the closest day with data for that square was used. (3) We again reconstructed the track and applied a start-endpoint correction (i.e. the bird's nest site) (earth & OCEAN Technologies, Kiel, Germany). When the compass logger is used, an external temperature sensor further indicates phases when seabirds sit on the sea surface, enabling flight and non-flight phases to be identified. Diving locations of birds at sea were examined under ArcView GIS using fixed kernel density (FKD) estimates with least-squares cross-validation (Worton 1989, Beisiegel & Mantovani 2006). We considered the 75 % FKD estimates to represent the core area of diving activity.

Diving behaviour was analysed using MultiTrace-Dive v2.3.3.2006 (Jensen Software Systems, Kiel, Germany). Vertical immersions were considered dives when they were deeper than 0.2 m; with shallower measurements attributed to bathing and preening of the bird. This allowed us to interpret dive patterns and time allocation of birds while feeding.

Normality (Shapiro-Wilk's test) and homoscedasticity (Bartlett's test) of the data were verified before each statistical test.

Our measurements of foraging distribution and effort comprised (1) diving rate (no. dives h^{-1}), as a measure of the bird's effort to obtain its food along the whole foraging trip. Cory's shearwaters are surface-feeders and locate prey visually from the air, so the number of dives should be a good proxy for prey-encounter rate; (2) SST around midnight (minimum, maximum and mean midnight SST), as a mean value of

SST (°C) taken from the temperature sensor probe data when Cory's shearwaters were swimming. We used these 3 different measurements of SST because they were not always cross-correlated and should provide a more complete perspective of the habitats exploited by the birds. Night-time was selected for measurement of water temperature because the temperature amplitude should be lower than in the daytime. When a bird spent several days at sea, a mean midnight SST value was obtained from all measurements taken close to midnight. This should give an indirect indication of the productivity in the areas visited by the bird, because low SST values are normally associated with high productivity patterns (e.g. Bez et al. 1995); (3) percentage of time spent travelling (= % travel), which is another measure of prey availability based on the searching effort of the individual. Time at the nest was excluded and only time at sea was considered; (4) trip duration (d) was used as an indirect measure of the distance from the colony to the foraging areas. For comparisons among birds of the same colony (between sexes or year of study), we also used mean values of (5) latitude and (6) longitude as dependent variables, to assess differences in the spatial distribution of the birds; (7) dive depth and (8) dive duration (both with mean and maximum values) were used to assess differences in diving strategy among areas; (9) number of U-shaped dives per trip and (10) number of V-shaped dives per trip were used as a proxy for type of diet, as birds will perform a higher percentage of U-shaped dives if their main prey items are mesopelagic (Rodary et al. 2000). Dive shape was determined by inspecting the evolution of depth through time on the MultiTrace-Dive software. Typically, V-shaped dives are relatively short and shallow, and U-shaped dives are relatively long and deep (Garthe et al. 2000). The U-shaped category was assigned if the birds stayed at a relatively constant depth for at least six 1 s depth measurements (R. P. Wilson pers. comm.).

All foraging and diving variables were compared among study sites and reproductive phase using generalised linear mixed models (GLMM, Faraway 2006), fitted by the Laplace approximation. Bird identity was included as a random factor to control for pseudoreplication, because more than one foraging trip per individual was recorded. The GLMM used a quasi-Poisson error distribution with a logarithm link function for the count data (Schall 1991). GLMM analysis was selected when, after running a model check script (mcheck) as suggested by Crawley (2007), our residuals were not normally distributed. The association between chl *a* values and the percentage of short trips birds performed was assessed using a Spearman's rank correlation test. For the chick-rearing period, the effects of breeding site and trip type (fixed factors) on the forag-

ing parameters were tested with a multivariate analysis of variance (MANOVA) randomly choosing 1 trip per bird. All multiple comparisons were made using post-hoc *t*-test with Bonferroni correction. In order to avoid Type I errors (the rejection of a null hypothesis purely by chance), *p*-values from the other statistical tests were also Bonferroni corrected. A principal component analysis (PCA), using variables 1 to 4 derived from compass loggers, was performed to describe patterns in the behavioural parameters of Cory's shearwaters from the different breeding sites. In total, 6 variables were loaded into the PCA analysis, namely (1) diving rate, (2) mean midnight SST, (3) minimum midnight SST, (4) maximum midnight SST, (5) percentage of time spent travelling, and (6) trip duration. Only the first trip per bird was used in the PCA to avoid pseudoreplication. All analyses were performed with STATISTICA v.8 and R v.2.7.2 (R Development Core Team 2008) with a significance level of $p < 0.05$. Results given are mean \pm SD.

RESULTS

Behavioural parameters for the same study area and breeding period (mid-chick-rearing for Berlengas 2005 to 2007 and Selvagens 2007 and 2008) showed no significant differences among years for diving rate, midnight SST, % travel (i.e. time spent flying, in contrast to time in the water) and trip duration (GLMM: all $p > 0.09$), suggesting that comparisons between study years may be possible if made within the same phase of the reproductive period.

Dual foraging strategy

The frequencies of trip duration for the whole data showed a natural cut-off point between short and long foraging trips at 4 d (Fig. 2), which was maintained when each of the 4 archipelagos were analysed (Fig. A1). Therefore, after the visual exploration of the histograms, trips were considered short (≤ 4 d) or long (≥ 5 d). The patterns of foraging trip duration were very similar for Berlengas and Corvo during both incubation and chick-rearing periods, with a prevalence of short trips over long trips. On the contrary, birds from Faial and Desertas made a higher number of long trips than those from Berlengas and Corvo, especially during incubation, with 1 individual from Desertas staying 19 d at sea (Fig. A1). As loggers were deployed on the birds for several days, it was possible to verify the dual foraging strategy when the same individual performed alternating short and long foraging excursions. During incubation, the most repeated pattern was 1 short trip

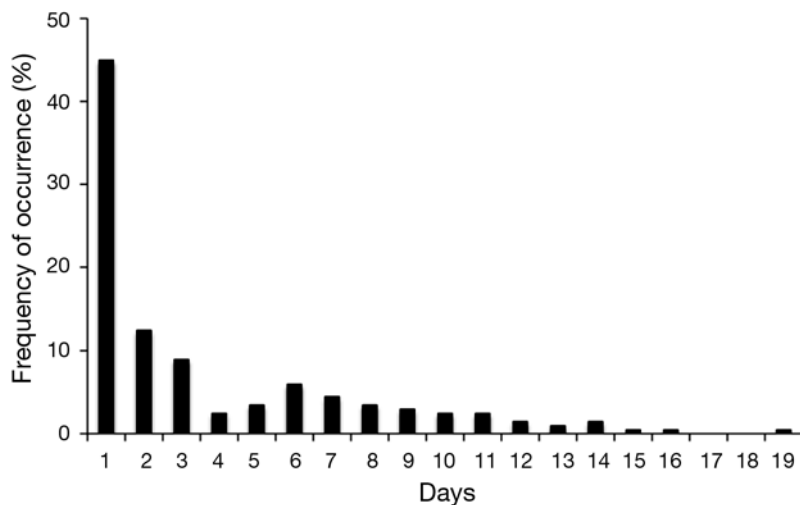


Fig. 2. *Calonectris diomedea*. All foraging trips recorded from 2005 to 2008 during incubation and chick-rearing periods. The bimodal frequency distribution was attributed to short (≤ 4 d) and long (≥ 5 d) foraging trips

(mean for all 7 study sites = 1 d) and 1 long trip for several days (mean for all study sites = 7 d). During chick-rearing, each individual usually alternated 4 short trips (mean for all study sites = 1 d) with 1 long one (mean for all study sites = 5 d).

After controlling for the breeding phase, the GLMM explained 39% of the initial deviance of trip duration among breeding sites during chick-rearing ($F_{4,64} = 8.23$, $p < 0.001$) and 28% of the deviance during incubation ($F_{4,162} = 5.68$, $p < 0.001$). Considering only the areas where birds were sampled both during incubation and chick-rearing ($N = 4$ sites, Fig. 2), the GLMM explained 52% of the original deviance on trip duration and showed that its variability was explained both by breeding site ($F_{3,183} = 9.45$, $p < 0.001$) and breeding phase ($F_{3,183} = 7.32$, $p < 0.001$). The proportion of long trips varied significantly between incubation and chick-rearing for all sites, except for Desertas (61.5% and 45.0% for incubation and chick-rearing, respectively; Fig. 3). Moreover, a significant correlation was found between the percentage of short foraging trips that birds performed during chick-rearing in the different study areas and the concentration of chl *a* in the waters around the breeding colonies ($r_s = 0.55$, $p = 0.05$, $N = 7$; Fig. 4). Data from the incubation period were used for the correlation in the case of Graciosa and Sta. Maria, as

those sites were not sampled during chick-rearing.

Differences in the spatial distribution patterns of individuals from all study sites between short and long foraging excursions were very evident. During short trips, birds foraged very close to their breeding colonies, both during incubation and chick-rearing periods. During long trips, they visited areas further away from the colonies (Fig. 5): (1) all individuals from the Azores, as well as birds from Berlengas, headed north; (2) birds from Desertas also headed north and reached similar latitudes to birds from the Azores and Berlengas, but extensively used an area with several high banks and seamounts between Madeira and the Portuguese mainland; and (3) adults from Selvagens foraged exclusively in areas near to or above the continental

shelf of the African coast (Fig. 5).

Overall, during the chick-rearing period, the foraging parameters varied significantly between short and long trips (MANOVA, Wilks' lambda, $F_{5,73} = 17.45$, $p < 0.001$), among different populations (MANOVA, Wilks' lambda, $F_{5,73} = 6.16$, $p < 0.001$) and in the interaction between trip type and breeding site (MANOVA, Wilks' lambda, $F_{5,73} = 4.03$, $p = 0.003$) (Table 3). Specifically, changes in each foraging parameter revealed that (1) adults from Berlengas made fewer dives (1.4 ± 0.9

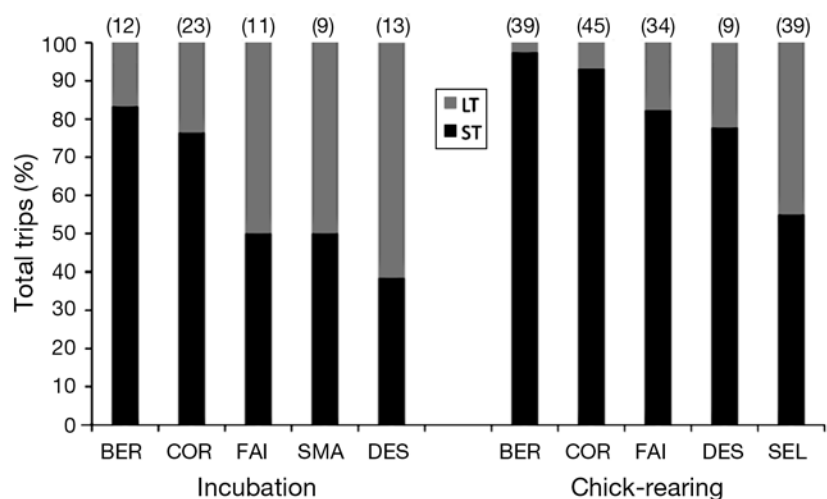


Fig. 3. *Calonectris diomedea*. Differences in the frequency distribution between long (LT: ≥ 5 d) and short (ST: ≤ 4 d) trips in relation to sampling sites and reproductive phase. BER: Berlengas; COR: Corvo; FAI: Faial; SMA: Sta. Maria (Vila islet); DES: Desertas; SEL: Selvagens. Number of foraging trips in parentheses

dives h^{-1}), exploited colder waters ($16.7 \pm 2.8^\circ C$) and travelled less ($29.2 \pm 12.3\%$) within each foraging trip than birds from Faial, Desertas, Corvo or Selvagens, and (2) birds from all breeding sites performed fewer dives (2.4 ± 1.0 dives h^{-1}) and travelled less per forag-

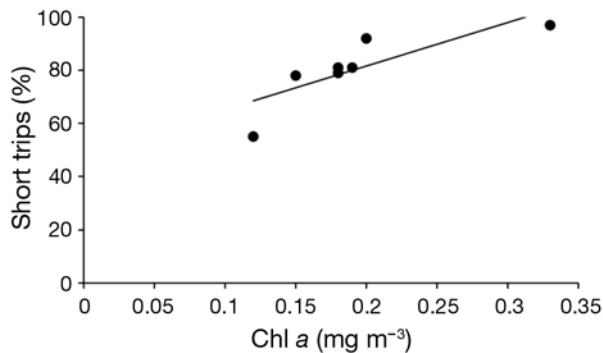


Fig 4. *Calonectris diomedea*. Relationship between the number of short trips and the concentration of chl *a* in the waters around the breeding colonies during chick-rearing. Data from the incubation period were used for Graciosa and Sta. Maria

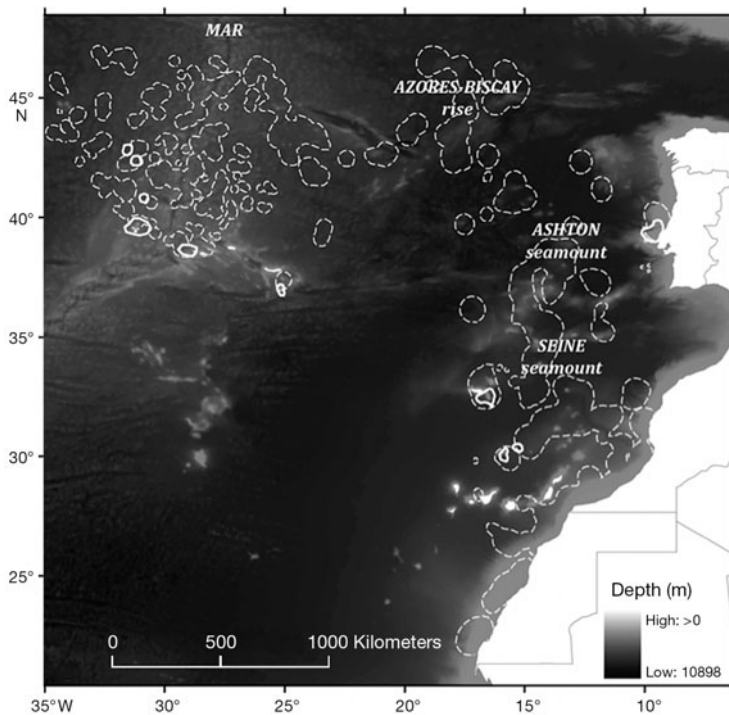


Fig. 5. *Calonectris diomedea*. The 75% Fixed Kernel Density estimates for diving locations of short (continuous lines) and long (dashed lines) foraging excursions. Bathymetry (www.ngdc.noaa.gov/mgg/bathymetry/relief.html) of the north Atlantic is represented in the background. MAR: Mid-Atlantic Ridge. Ashton and Seine seamounts represent the extreme features of an area with several high banks and seamounts

ing trip ($39.4 \pm 13.2\%$) during short trips than during long excursions (5.9 ± 2.1 dives h^{-1} and $59.3 \pm 22.1\%$, respectively). During long trips (1) birds from Berlengas decreased the diving rate (1.23 ± 0.9 vs. 2.9 ± 1.1 dives h^{-1}); (2) Corvo and Selvagem birds exploited colder habitats (19.2 ± 0.7 vs. $22.8 \pm 0.9^\circ C$ and 19.6 ± 1.2 vs. $23.7 \pm 0.1^\circ C$); (3) Faial and Corvo birds travelled longer (48.9 ± 23.8 vs. $28.4 \pm 20.6\%$); (4) Faial, Berlengas and Corvo birds exploited higher latitudes (41.9 ± 2.2 vs. 38.7 ± 0.26 , 39.5 ± 0.4 vs. 37.8 ± 0.8 and 43.0 ± 0.3 vs. $39.6 \pm 0.3^\circ N$, respectively); and (5) Corvo birds foraged further west (31.1 ± 0.1 vs. $28.7 \pm 0.4^\circ W$) while Selvagens birds exploited more easterly areas (13.2 ± 2.3 vs. $15.7 \pm 0.2^\circ W$; Table 3).

Foraging behaviour and time allocation

The PCA analysis with 6 variables derived from compass loggers, namely, diving rate, mean, minimum and maximum midnight SST, percentage of time spent travelling and trip duration, reduced the original variables to 2 principal components (PC1 and PC2) that accounted for 67% of the total variance in the data

Table 3. *Calonectris diomedea*. Effect of breeding site (FAI, Faial; DES, Desertas; BER, Berlengas; COR, Corvo; SEL, Selvagem), trip type (ST, short trip: ≤ 5 d; LT, long trip: ≥ 5 d) and first order interaction terms on the different foraging parameters during the chick-rearing period. Univariate result of the 5 response variables from a MANOVA, followed by post-hoc *t*-tests using Bonferroni correction. Berlengas data from 2005 and 2006 excluded as no long trips were detected. Sample sizes as the number of birds tracked with compass loggers are given in Table 2. SST was measured with the temperature sensor of compass loggers

	<i>F</i>	<i>df</i>	<i>p</i>	Effect
Breeding site				
Dive rate (dives h^{-1})	5.89	4, 75	<0.001	BER < other sites
Midnight SST ($^\circ C$)	7.44	4, 75	0.04	BER < other sites
Time travelling (%)	4.66	4, 75	<0.001	BER < other sites
Mean latitude	-	-	-	-
Mean longitude	-	-	-	-
Trip type				
Dive rate (dives h^{-1})	9.53	1, 75	0.02	ST < LT
Midnight SST ($^\circ C$)	0.98	1, 75	0.48	
Time travelling (%)	7.05	1, 75	0.02	ST < LT
Mean latitude	-	-	-	-
Mean longitude	-	-	-	-
Breeding site \times Trip type				
Dive rate (dives h^{-1})	3.92	4, 75	0.02	BER: ST > LT
Midnight SST ($^\circ C$)	3.78	4, 75	0.02	COR, SEL: ST > LT
Time travelling (%)	6.23	4, 75	<0.001	FAI: ST < LT
Mean latitude	2.33	4, 75	0.05	FAI, BER, COR: ST < LT
Mean longitude	2.95	4, 75	0.03	COR: ST < LT SEL: ST > LT

(Table 4). The next principal components (PC3 and PC4) explained a minor portion of the overall variance (7 and 5% of the variance, respectively) and were not considered in the interpretation of loadings. PC1 was primarily associated with 4 variables, including mean, minimum and maximum midnight SST and diving effort. Foraging trips with higher scores in PC1 were made by birds exploiting warmer sea areas and showing higher diving effort. PC2 was negatively linked with trip duration and percentage of time spent travelling. Therefore, these 2 principal components were largely associated with environmental characteristics (PC1) and with the dual foraging strategy and percentage of time spent travelling (PC2; Fig. 6). The variables from PC1 allowed us to separate the foraging behaviour of populations exploiting a near continental shelf environment (= neritic areas, Berlengas) from that of those foraging in oceanic areas (populations from Azores, Madeira and Selvagens). To a certain extent, differences registered on both axes were also related to the differential effort (i.e. percentage of time spent travelling and diving rate) that parents made to provide for their chick. Although the highest values for PC1 (foraging effort) were obtained from a mixture of oceanic populations, birds from Faial and Corvo represented the extreme situations (Fig. 6). In fact, the percentage of time spent travelling of birds from Corvo ($50.5 \pm 21.1\%$, $N = 44$) was significantly higher than that of birds from Faial ($40.3 \pm 21.2\%$, $N = 34$; GLMM: $\chi^2_1 = 6.32$, $p = 0.01$) but Corvo birds made significantly shorter trips (1.6 ± 1.6 d, $N = 45$) than Faial birds (2.3 ± 2.7 d, $N = 34$; GLMM: $\chi^2_1 = 8.63$, $p < 0.01$).

When comparing foraging behaviour of birds from the same archipelago or from close islands, significant

differences were registered: (1) during the incubation period, areas exploited by birds from Corvo were significantly warmer ($20.9 \pm 1.4^\circ\text{C}$) than those exploited by birds from Faial ($17.1 \pm 0.6^\circ\text{C}$) and Sta. Maria ($18.9 \pm 1.9^\circ\text{C}$); and (2) while chick-rearing, birds from Selvagens foraged in habitats with significantly lower SST ($18.1 \pm 0.6^\circ\text{C}$) than birds from Desertas ($20.4 \pm 1.6^\circ\text{C}$, Table 5).

Dive pattern and diel rhythms in relation to the surrounding environment

There were 2 main dive patterns for Cory's shearwater, the V-shaped dives, representing 52% of the total dives identified, and the U-shaped dives, comprising 42%. A very small number of dives (3%) was also assigned to a third category of W-shaped dives (Fig. A2). This remaining 3% of dives were not considered in the analysis, because they could not be included in the previous categories and, most importantly, they could represent errors of the pressure sensor. Using the data from the pressure loggers, we found a significant difference in dive frequency and pattern between birds feeding in neritic areas and those feeding in oceanic areas (Table 6). Cory's shearwaters exploiting neritic areas performed shallower and shorter dives than those feeding in oceanic waters. Moreover, the dominance of V-shaped dives in the neritic environment contrasted with the dominance of U-shaped dives in oceanic regions. In addition, there was an obvious difference in the depths of U- and V-shaped dives, with V-shaped dives being shallower than U-shaped dives for both neritic and oceanic habitats (mean depth = 1.74 ± 0.45 m vs. 4.3 ± 3.2 m; GLMM: $\chi^2_1 = 10.2$, $p = 0.01$, $N = 22$). The same pattern was obtained for dive duration, with shorter dives (for both V- and U-shaped) over the continental platform and longer diving periods in oceanic areas. Not surprisingly, U-shaped dives lasted longer than V-shaped dives for birds feeding in both environments (7.8 ± 3.2 vs. 2.3 ± 0.5 s, GLMM: $\chi^2_1 = 15.4$, $p < 0.001$, $N = 22$) (Fig. 7).

Table 4. *Calonectris diomedea*. Component loadings of 6 explanatory variables from daily foraging trips on the first 2 principal components, which collectively explained 67.2% of the total variance in the data. PC3 and PC4 both explained less than 12% of the overall variance. Time travelling was the period of time the bird spent flying in contrast to time in the water and excluding time in the colony. Parameters accounting for most of the variation in each principal component are shown in **bold**. *Significant correlations, $p \leq 0.05$

Descriptives	PC1	PC2
Eigenvalues	3.23	1.99
Variance explained (%)	46.2	25.0
Cumulative variance (%)	46.2	67.2
Variables		
Trip duration	-0.09	-0.41
Mean midnight temp	0.99 *	0.04
Min. midnight temp	0.94 *	0.14
Max. midnight temp	0.92 *	-0.10
Dive rate (h^{-1})	0.59	-0.19
% travel	0.15	-0.96 *

DISCUSSION

Foraging plasticity to cope with habitat heterogeneity

Our results show that Cory's shearwater exhibits great behavioural plasticity when exploiting heterogeneous marine environments, as different populations differed in several parameters of at-sea activity, suggesting the existence of diverse habits adapted to dif-

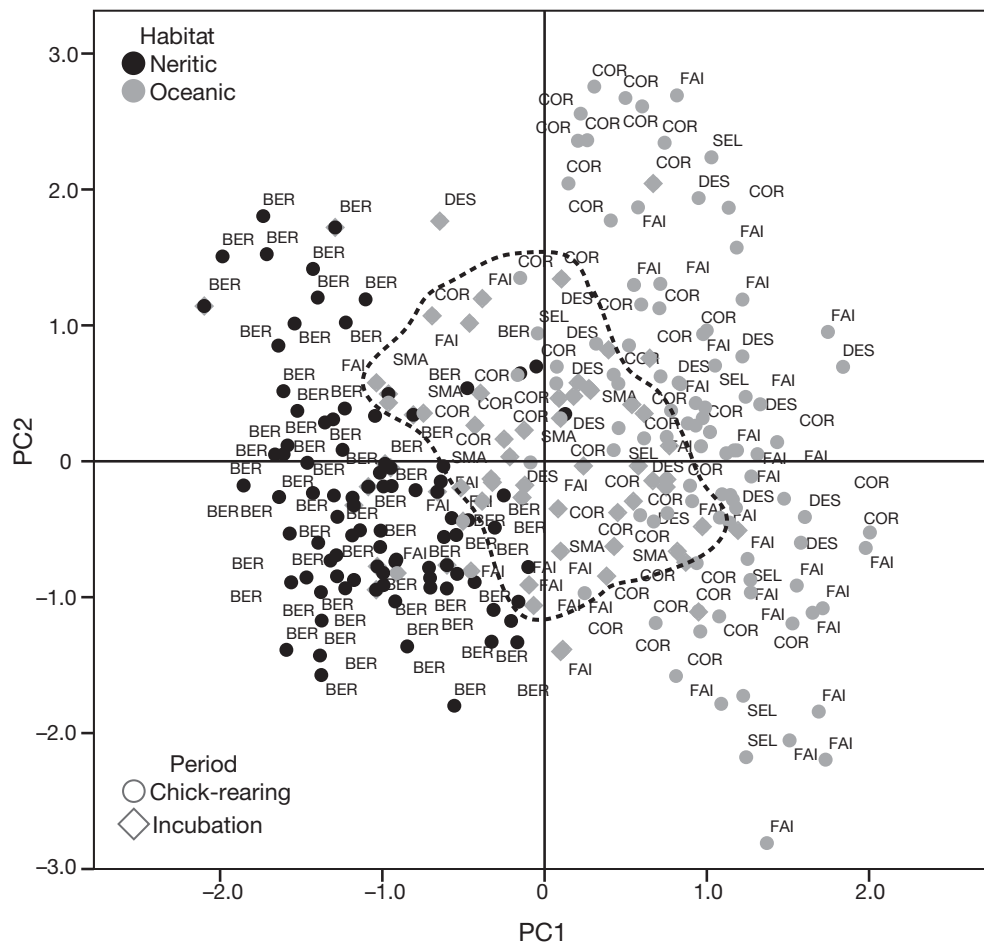


Fig. 6. *Calonectris diomedea*. Component loadings of 6 variables from daily foraging trips into the first 2 principal components (PC1, PC2). PC1 is mainly related to a productivity gradient (mostly on a longitudinal scale) and PC2 to the investment in a dual foraging strategy. Neritic habitat: an island within a long continental shelf (≤ 200 m depth); Oceanic habitat: islands with a short continental shelf and mainly surrounded by an oceanic platform (> 200 m depth). Dotted line represents the separation between incubation data (inside the circle) and chick-rearing data (outside the circle). BER: Berlengas (N = 94 foraging trips); FAI: Faial and Graciosa (N = 58); COR: Corvo (N = 68); DES: Desertas (N = 22); SEL: Selvagens (N = 51); SMA: Sta. Maria (N = 9)

Table 5. *Calonectris diomedea*. Comparison of the foraging parameters of different populations breeding on diverse islands within the Azores archipelago (Corvo, Faial and Sta. Maria) and on Madeira and the Selvagens archipelago. Time travelling was the period of time the birds spent flying in contrast to time in the water, and excluding time in the colony. Data was analysed only for the chick-rearing period. Values are mean \pm SD, number of foraging trips is given in parentheses. All tests were performed by GLMM fitted by the Laplace approximation. SST was measured with the temperature sensor of compass loggers

Parameters	Azores			Madeira Desertas 2006	Selvagens Selvagem 2007	$F_{2,47}$	p	Madeira vs. Selvagem	
	Corvo 2007	Faial 2006	Sta. Maria 2007					χ^2_1	p
Dive rate (h^{-1})	4.6 \pm 2.4 (23)	5.8 \pm 2.3 (17)	4.4 \pm 2.7 (9)	4.6 \pm 2.4 (9)	5.3 \pm 2.9 (12)	0.10	0.98	2.98	0.10
Midnight SST ($^{\circ}C$)	20.0 \pm 1.4 (23)	17.9 \pm 0.5 (17)	18.7 \pm 0.9 (9)	20.4 \pm 1.6 (9)	18.1 \pm 0.6 (12)	4.05	0.04	4.06	0.05
Time travelling (%)	40.0 \pm 17.6 (23)	35.7 \pm 13.5 (17)	35.8 \pm 10.2 (9)	42.0 \pm 16.7 (9)	37.5 \pm 11.5 (12)	1.27	0.30	1.74	0.24
Trip duration (d)	9.2 \pm 6.8 (23)	8.3 \pm 5.8 (17)	9.6 \pm 7.1 (9)	2.8 \pm 4.5 (9)	2.1 \pm 3.7 (12)	0.92	0.59	0.91	0.48

ferent ecological niches. These adaptations applied to lower dive rates, lower percentages of time spent travelling per trip and shorter foraging trip durations for birds exploiting neritic areas if compared with those exploiting oceanic areas. These differences are attributed to the different levels of marine productivity around the breeding areas. In fact, the lower diving rate of birds from Berlengas is in accordance with the cold and rich upwelling waters in that area (Mann &

Lazier 2005, Sousa et al. 2008). Birds exploiting oceanic environments exhibited higher diving effort, which agrees with the higher SSTs (either satellite and temperature sensor data) that are known to be related to less productive and profitable waters (e.g. Bez et al. 1995). In both cases (continental shelf areas or open ocean habitats), the activity of Cory's shearwaters can be linked to prey patch availability, and dive rate should therefore be considered as a measure of the

birds' effort to obtain food. This variety in productivity that influences the behaviour of birds at sea has recently been reported to also influence life strategies of Cory's Shearwaters, namely timing of moulting (Alonso et al. 2009) and brood-guarding behaviour (Cтры et al. 2009). Nevertheless, because Cory's shearwaters feed on mobile fish and not on more static primary producers, care should be taken when concluding that high levels of chl *a* and low values of SST are the reasons for the presence of foraging individuals (e.g. Grémillet et al. 2008).

Table 6. *Calonectris diomedea*. Diving characteristics (from pressure loggers) during short (≤ 4 d) foraging excursions in neritic (birds breeding on Berlengas) and oceanic (birds breeding on Corvo and Selvagens) environments. Values are mean \pm SD (number of foraging trips). All tests were performed by GLMM fitted by the Laplace approximation

	Neritic (n = 14)	Oceanic (n = 8)	χ^2_1	P
Dive depth (m)	1.3 \pm 0.59	2.6 \pm 0.53	2.97	0.10
Maximum dive depth (m)	4.9 \pm 2.3	9.8 \pm 2.4	6.98	0.02
Dive duration (s)	3.0 \pm 1.7	4.9 \pm 3.8	0.97	0.38
Maximum dive duration (s)	17.0 \pm 2.2	32.0 \pm 5.8	4.78	0.04
Percentage of U-dives per trip	38 \pm 4 %	80 \pm 5 %	7.56	0.02
Percentage of V-dives per trip	62 \pm 8 %	20 \pm 4 %	6.89	0.02

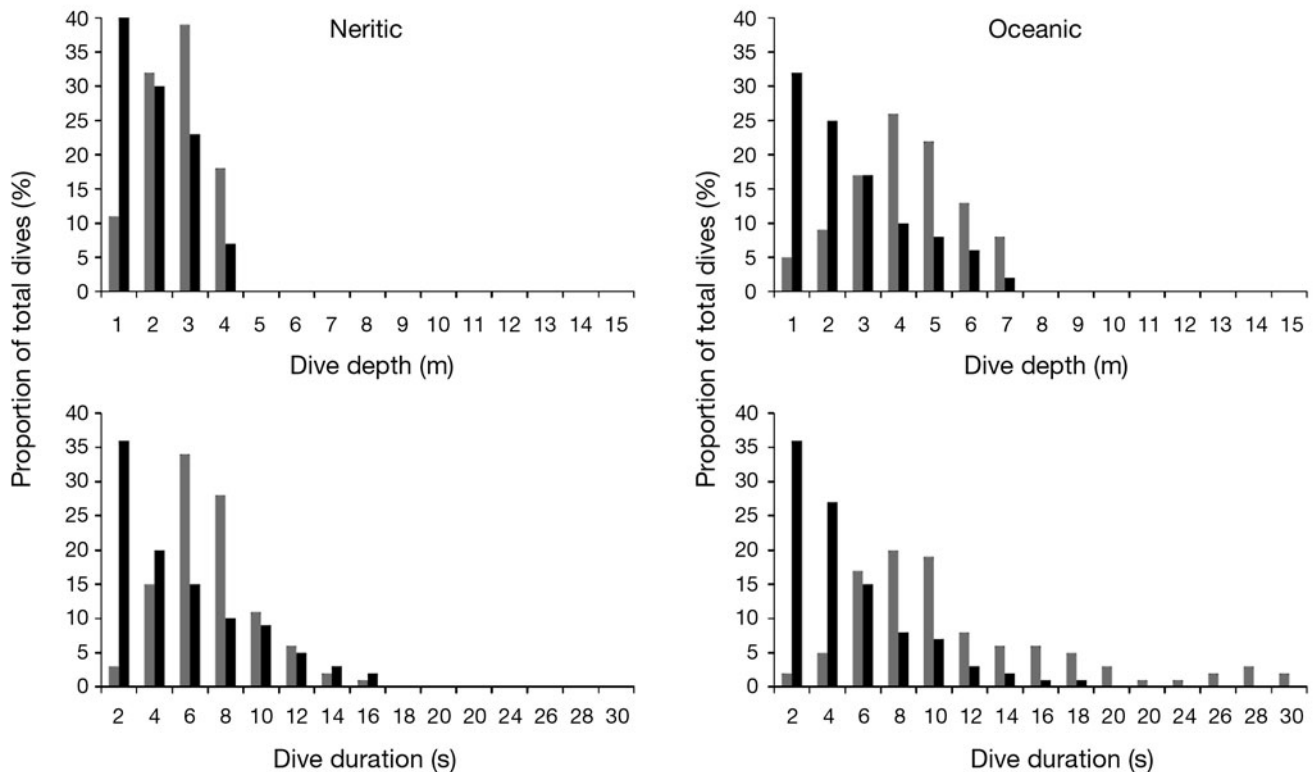


Fig. 7. *Calonectris diomedea*. Comparison of the frequency distribution of dive depth and duration during short foraging excursions (≤ 4 d), between a neritic (left, Berlengas) and an oceanic environment (right, Corvo and Selvagens). V-shaped dives in black and U-shaped dives in grey

As the PCA emphasised, the foraging effort of birds (mainly revealed by changes in dive rate and trip duration) was greater during the chick-rearing period, because birds had to face the additional challenge of feeding their chick at a frequency high enough to avoid chick starvation (Granadeiro et al. 2000, Navarro et al. 2007). Birds from Corvo and Faial apparently faced more difficulties in obtaining food for their chicks because, in each foraging trip, Corvo birds were obliged to travel for a longer proportion of time (% travel), and Faial birds had to travel for more days (trip duration) to reach productive areas. Once again, birds from Berlengas presented a lower foraging effort, suggesting a high productivity profile of the neritic waters around Berlengas. Similarly, Grémillet et al. (2008) reported that Cape gannets *Morus capensis* nesting close to a strong upwelling region showed a lower foraging effort than those breeding close to a weak upwelling region. However, the authors also point out that this is an indirect interpretation, as Cape gannets do not feed on primary production. Nonetheless, these results show the high importance of oceanic phenomena (in this case upwelling regions) for the optimisation of foraging efforts of sea animals. The boundary and extension of the upwelling along the Portuguese coast are well characterised (Sousa et al. 2008) and may have been important in the at-sea behaviour adopted by Berlengas birds. In this study, Cory's shearwaters spent almost 40% of their time flying, and the rest of the time sitting on the water or diving. This value is in accordance with those measured for seabirds from temperate or polar waters, such as gannets (Garthe et al. 2003), alcids (Kato et al. 2003) or albatrosses (Weimerskirch & Guionnet 2002), and is smaller than those measured for seabirds from tropical areas, like tropical boobies (Weimerskirch et al. 2005), where food resources are scarcer.

A dual foraging strategy as a reflection of ocean productivity

The bimodal foraging strategy was first reported for the blue petrel *Halobaena caerulea* (Chaurand & Weimerskirch 1994). It is known to be an important strategy employed by procellariiform species to solve the problem of distant and unpredictable food resources (Warham 1990). Magalhães et al. (2008) reported that Cory's shearwaters from the Azores typically invest in a dual foraging strategy during the chick-rearing period. Our study shows that this behaviour can actually be extended to other breeding areas of the North Atlantic, indicating that this may be a relevant strategy to maximise energy conservation and breeding success. This strategy was also used by birds during the incubation period, suggesting that the degree of investment into

long trips may be a reflection of the marine productivity around the breeding colonies (Granadeiro et al. 1998a), and not only a way for birds to re-establish their body condition while feeding their chicks.

Strong differences in behavioural parameters of short and long trips were detected among populations from the different geographical areas of the North Atlantic. While feeding their chicks, birds from Selvagens travelled longer distances to reach colder waters. This is likely to be a consequence of the low productivity (i.e. low prey availability) of waters surrounding the Selvagens archipelago (as suggested by the higher SST of that area). This foraging pattern was also described in earlier studies of Cory's shearwaters on Selvagens (Mougin & Jouanin 1997, Granadeiro et al. 1998a), where adult birds performed a greater number of long trips than those from Azores and Berlengas during the chick-rearing period, suggesting that birds from Selvagens exploit more productive upwelling areas along the African coast, (Davenport et al. 2002). The same pattern was exhibited by Cory's shearwaters breeding on Faial, Corvo and Sta. Maria (Azores) and Desertas (Madeira), where the birds need to forage for a longer time and thus travel to more distant areas to use colder and supposedly more productive waters. This result was also reported by Magalhães et al. (2008) for Cory's shearwaters breeding on the different islands of Azores. There, birds exploited regions at higher latitudes during almost all the long foraging excursions. Moreover, birds from Berlengas had no need to search for distant productive waters (during chick-rearing, long trips comprised only 2.5% of all trips for the 3 study years), because there were cold, and presumably profitable, waters in the surroundings of the colony. This would confirm that the proximity to highly productive environments strongly influences the foraging strategy of animals (Navarro & González-Solís 2009). On the other hand, birds from Selvagens had to perform a larger number of long trips to restore their depleted body condition and, presumably, to increase the meal size delivered to their chicks (Granadeiro et al. 1998a) by exploiting south-western areas with colder waters (V. H. Paiva unpubl. data). Thus, Selvagens seems to be the colony with lowest food resources around the breeding area (lowest chl *a* and highest SST of the 7 study sites), which was previously suggested by chick-provisioning rates of Selvagens, Azores and Berlenga birds (Ramos et al. 2003). Additionally, for all study areas, we found that the higher the concentration of chl *a* around the breeding colony, the lower the percentage of long trips performed by birds. This suggests that local productivity (i.e. 60 km around the colony) is a main factor influencing the investment of birds into an optimised dual foraging strategy.

Dive pattern and diel rhythms in relation to the surrounding environment

This is the first time that pressure-temperature devices have been used on Cory's shearwaters. Mean and maximum dive depths (2.6 and 9.8 m in oceanic areas) were greater than those previously reported for Cory's shearwater, which has been described as unable to capture prey deeper than 2 m (Monteiro et al. 1996), and to make deeper dives only sporadically (Martin 1986). Our study shows that the diving behaviour of Cory's shearwaters is quite variable and flexible among heterogeneous environments. Usually, birds inhabiting a more coastal colony perform a larger number of V-shaped dives (Garthe et al. 2000, 2007), with shorter dive duration and less depth, and birds living in oceanic environments perform a larger number of U-shaped dives, also greater in duration and depth (Garthe et al. 2007). This was the pattern that we observed when comparing Cory's shearwater populations visiting neritic versus oceanic environments. Moreover, as deep dives can only be made by underwater propulsion using feet and wings (Garthe et al. 2000), it seems that Cory's shearwaters exploiting oceanic areas use this behaviour to pursue their prey. Birds exploiting a neritic habitat exhibited larger numbers of V-shaped than U-shaped dives, which is likely to be related to the vertical distribution of their main prey along the Portuguese coast. In fact, their main prey in the Portuguese continental shelf area are epipelagic species, such as *Sardina pilchardus* and *Belone belone* (Granadeiro et al. 1998b, V. H. Paiva unpubl. data), which should both occur between 10 and 100 m (Froese & Pauly 2009). On the other hand, birds from Corvo and Selvagens, while exploiting a typical oceanic environment, performed a larger number of U-shaped than V-shaped dives, suggesting that they had to pursue their main prey deeper in these areas. In fact, the main prey for the Azores, *Trachurus picturatus* (Magalhães 2007, V. H. Paiva unpubl. data), usually inhabits shallow neritic areas of island shelves and seamounts (Smith-Vaniz 1986) but may also reach a depth of 370 m (Froese & Pauly 2009). In summary, our study indicates that diverse populations of Cory's shearwater (exploiting heterogeneous environments) display different modes of diving, which are connected to different oceanographic characteristics and may ultimately be related to the particular behaviour of prey available in those areas. In addition, Cory's shearwater is well adapted to the diel migration of some of their prey, especially squid, and also feeds at night (Granadeiro et al. 1998b).

CONCLUSIONS

This study shows the complexity of the foraging behaviour of a seabird species exploiting diverse for-

aging niches in highly variable environments. It illustrates the importance of behavioural plasticity in different populations of the same species and suggests that this is a fundamental trait in the life history of seabirds living in highly variable environments. By means of adapting their at-sea behaviour while searching over vast oceanic areas for scattered prey patches, Cory's shearwaters locate prey associated with different oceanographic features. These features, mainly seamounts and coastal environments, are areas of enhanced productivity through the well-known upwelling phenomenon, and birds adapt their modes of predation to cope with them. The behavioural response of birds is mainly dictated by the heterogeneity of their habitat, that is driven over time by 2 productivity gradients present in the north Atlantic. (1) Productivity is expected to increase from the subtropical warmer waters of Selvagens to the northern colder waters of the Azores archipelago. (2) Oceanic environments are expected to be less profitable than neritic environments (upwelling areas), such as the Portuguese and African coastal environments. (3) Assuming that seabirds adapt their behaviour to cope with environmental heterogeneity, changes in their foraging parameters may be used as bioindicators of ecological changes in the feeding grounds they exploit (Parsons et al. 2008).

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Appendix 1. Variations in trip duration and dive profiles

