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**THE ROLE OF INDIVIDUAL FORAGING SPECIALIZATION
IN THE TROPHIC RELATIONSHIPS BETWEEN SEABIRDS AND
THE MARINE ENVIRONMENT**

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The role of individual foraging specialization in the trophic relationships between seabirds and the marine environment

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Abstract

Trophic relationships are central in ecology and play a crucial role in species survival, as availability of food resources varies over time and space. The spatio-temporal variation in food sources at sea has many ecological implications on marine top predators such as seabirds. However, most ecological studies of resource use and population dynamics treat conspecific individuals as ecologically equivalent, but intra-specific variation in individual foraging strategies can be large and many apparently generalized populations are in fact composed of specialized individuals that use a small subset of the available resources over time (individual consistency). Studies on the incidence of individual specialization suggest that it may vary among species and among populations, but they are scarce, particularly for seabirds, and the mechanisms that generate inter-individual variation are not well understood. The main goal of this study is to corroborate the existence of individual specialization over time in three different species from four seabirds' populations exploiting different marine environments. Furthermore, it investigates whether individual specialization is associated with the environment and resources exploited and assesses its ecological implications at the population and individual levels.

The hypothesis of this thesis was tested using wandering albatross *Diomedea exulans*, Cory's shearwater *Calonectris diomedea* and yellow-legged gull *Larus michahellis* as model seabird species, and fieldwork was conducted respectively in Bird Island (South Georgia, Antarctica), Corvo Island (Azores archipelago, Portugal) and Berlenga Island (Portugal). Two populations of Cory's shearwater were studied, one from an oceanic environment (Corvo Island) and other from a neritic environment (Berlenga Island). A total of 199 birds were sampled during the breeding season of each species, from 2009 to 2012. Together with conventional dietary methods a combination of intrinsic and extrinsic markers were used, such as stable isotope analyses (from tissues with different turnover rates) and electronic devices (GPS loggers), to corroborate the existence of individual specialization and examine its relative incidence. Using three environmental parameters (bathymetry, sea-surface temperature and chlorophyll a concentration) to characterize marine habitats and recent developments based in a Bayesian framework, namely stable isotope mixing models (Stable Isotope Analysis in R: SIAR) to estimate individual prey consumption, and recent metrics to estimate populations' niche width (Stable Isotope Bayesian Ellipses in R: SIBER), data were analysed to investigate

ecological implications of individual specialization and its relationships with the environment and resources exploited.

Patterns of individual consistency in habitat use and/or prey consumption were found in all studied species. However, these patterns varied spatio-temporally according to the population, evidencing the role of individual specialization in the foraging dynamic of these species. Inter-annual differences in the feeding ecology and foraging behaviour of birds during the breeding season were associated with the availability of food resources around the colonies, which influenced the patterns of individual consistency in Cory's shearwater, but not in yellow-legged gulls. Results also suggest that these differences could have an impact on the reproductive performance of Cory's shearwater and on the body condition of the yellow-legged gulls, but evidences of relationships between these ecological consequences and individual specialization at the individual level were not found.

Overall, this study corroborates the existence of individual specialization over time within studied seabird populations. Therefore, such trait may be potentially widespread across several related seabird species. Such consistency, however, varied among species and populations and results showed that it was more stable in yellow-legged gulls than in Cory's shearwaters. Fluctuations on individual consistency were related to temporal changes in the availability and predictability of resources, which means that the more specialized species may be more sensitive to that. It also corroborates that individual variability within a seabirds' population may be regulated by small differences in breeding location (< 2km), suggesting that studies assuming a colony or sub-colonies as ecologically homogeneous in terms of foraging ecology can be biased. This study supports the hypothesis that individual specialization may have important ecological implications, such as the reduction of intra-specific competition and, consequently, a high impact on ecological processes and foraging dynamics. Further investigation is required to identify the mechanisms that generate individual specialization and its ecological implications at both population and individual level.

Key-words: foraging ecology, individual consistency, intra-specific competition, niche width, predator-prey interactions, stable isotopes, tracking devices.

Resumo

O papel das relações tróficas em ecologia é crucial, e fundamental para a sobrevivência das espécies, uma vez que a disponibilidade de recursos alimentares varia espacial e temporalmente. Esta variação espaço-temporal das fontes de alimento no mar tem numerosas implicações ecológicas nos predadores de topo, tais como as aves marinhas. A maioria dos estudos ecológicos que focam a exploração de recursos e dinâmica populacional assumem que os indivíduos de uma mesma população são ecologicamente semelhantes, no entanto, a variação intra-específica na ecologia alimentar pode ser grande e muitas populações aparentemente generalistas serem de facto compostas por indivíduos especializados que exploram subconjuntos dos recursos disponíveis ao longo do tempo (consistência individual). A ocorrência de especialização individual pode variar entre espécies e entre populações, mas os estudos que a corroboram são atualmente escassos, especialmente para aves marinhas, e os mecanismos que motivam a variação inter-individual não são ainda bem compreendidos. O principal objectivo desta tese foi estudar a existência de especialização individual ao longo do tempo em três espécies de aves marinhas, de quatro populações diferentes, que exploram ambientes marinhos distintos. Especificamente, foram analisadas associações entre a especialização individual com o ambiente marinho e os recursos explorados e avaliadas as suas implicações ecológicas ao nível populacional e individual.

A hipótese desta tese foi testada no albatroz-viageiro *Diomedea exulans*, na cagarra *Calonectris diomedea* e na gaivota-de-patas-amarelas *Larus michahellis*, respectivamente em Bird Island (Geórgia do Sul, Antártida), Ilha do Corvo (Açores, Portugal) e Ilha da Berlenga (Portugal). Entre 2009 e 2012, foi amostrado um total de 199 aves durante o período reprodutor. Para validar a existência de especialização individual e avaliar a sua ocorrência relativa utilizou-se uma combinação de marcadores intrínsecos e extrínsecos, tais como análises de isótopos estáveis (de tecidos com diferentes períodos de síntese) e dispositivos GPS, juntamente com amostragens convencionais de dieta. Adicionalmente, foram usadas três variáveis ambientais (profundidade, temperatura da superfície do mar e concentração de clorofila *a*) para caracterizar os habitats marinhos, assim como modelos recentes suportados por uma inferência bayesiana, nomeadamente modelos mistos de isótopos estáveis (SIAR) para estimar a proporção de presas consumidas por cada indivíduo e métricas recentemente desenvolvidas para estimar o tamanho de nicho das populações (SIBER). Estes dados

foram analisados para investigar as implicações ecológicas da especialização individual e as suas relações com o meio ambiente e os recursos explorados.

Foram encontrados padrões de consistência individual no uso de habitat e/ou no consumo de presas em todas as espécies estudadas. No entanto, a sua ocorrência variou espaço-temporalmente de acordo com a população estudada, evidenciando o papel da especialização individual na dinâmica de ecologia alimentar destas espécies. Diferenças inter-anuais no comportamento e ecologia alimentar das aves durante o período reprodutor estiveram associadas com a disponibilidade de recursos alimentares perto das colônias, que influenciaram os padrões anuais de consistência individual na cagarra, mas não na gaivota-de-patas-amarelas. Os resultados sugerem que tais diferenças na disponibilidade de recursos podem ter um impacto no sucesso reprodutor da cagarra e na condição corporal da gaivota-de-patas-amarelas, mas não foram encontradas evidências ao nível individual de relações entre essas consequências ecológicas e a especialização individual. Este estudo confirma também que a variabilidade intra-populacional na ecologia alimentar de aves marinhas pode ser regulada por pequenas distâncias na localização dos ninhos (< 2km).

No geral, este estudo valida a existência de especialização individual ao longo do tempo nas diferentes populações de aves marinhas estudadas, o que sugere uma potencial generalização em outras espécies de aves marinhas de características análogas. No entanto, os resultados mostram que a consistência variou entre espécies e entre populações, sendo mais estável na gaivota-de-patas-amarelas e mais sujeita a flutuações na cagarra. As flutuações na consistência individual relacionaram-se com variações temporais na disponibilidade dos recursos alimentares, o que sugere que as espécies mais especializadas possam ser mais sensíveis a tais variações. Este estudo suporta a hipótese de que a especialização individual pode ter implicações ecológicas relevantes, tais como a redução da competição intra-específica e, conseqüentemente, um grande impacto na dinâmica da ecologia alimentar das aves marinhas. No entanto, são necessários estudos complementares para identificar os mecanismos que determinam a especialização individual e as suas implicações ecológicas, tanto a nível populacional como a nível individual.

Palavras-chave: aves marinhas, áreas de distribuição, competição intra-específica, ecologia alimentar, especialização individual, isótopos estáveis, relações tróficas.

General Introduction



Wandering Albatross

(Diomedea exulans)

Cory's Shearwater

(Calonectris diomedea)

Yellow-legged Gull

(Larus michahellis)

"The best way to observe a fish is to become a fish."

Jacques Yves Cousteau

Seabirds as marine organisms and modern tools to study trophic ecology

Information on the trophic relationships between key-species and top predators, and their distribution, is required to understand the structure and function of marine ecosystems (Paine 1988). Key-species of primary consumers include zooplankton and several species of epipelagic fish, which are then consumed by secondary predators, including different species of marine birds, in all habitats from coastal to pelagic (Furness & Monaghan 1987). Seabirds are integral components of marine ecosystems as they spend up to 90% of their life-time at sea and have a widespread geographic distribution exploiting marine habitats, from polar to tropical regions and from coastal to pelagic environments. They are the most conspicuous of large marine predators and may be used as sentinel organisms, providing a valuable approach into ecosystem conditions and processes (Furness & Camphuysen 1997; Montevecchi et al. 2006). As marine top predators, seabirds are closely dependent on the food resources they can find at sea, but food sources are patchy and unpredictably distributed (Weimerskirch 2007). To cope with this difficulty, seabirds developed specific morphological characteristics and foraging strategies that enable them to conserve the maximum energy possible while foraging at sea. Thus, most of these species' adaptations are strongly related to their foraging and feeding methods to succeed in their own exploited environments (Fig. 1).

Seabirds are the most threatened group of all birds worldwide and face unprecedented challenges and uncertain futures (Butchart et al. 2004). In particular, the pelagic group of the Procellariiformes (e.g. albatrosses, shearwaters and petrels), are the least known, due to the technical difficulties associated to their study, and the most representative of pelagic ocean ecosystems. They can be highly sensitive to changes in food availability during the breeding season and show important interactions with fisheries. Thus, they can provide early indications of fluctuations in fish stocks and marine environmental health (Parsons et al. 2008). On the other hand, some seabird species, such as many gull species, have become problematic due to its opportunistic behaviour associated with human-altered environments that caused a dramatic increase in their numbers throughout Europe and other regions in recent decades, with several ecological and social impacts (Pedro et al. 2013). Their inter-annual fluctuations, reproductive performance and foraging behaviour are assumed to be a reliable indicator of natural

and local resource availability from both natural and anthropogenic sources (Ramos et al. 2011, Ramírez et al. 2012, Christel et al. 2012).

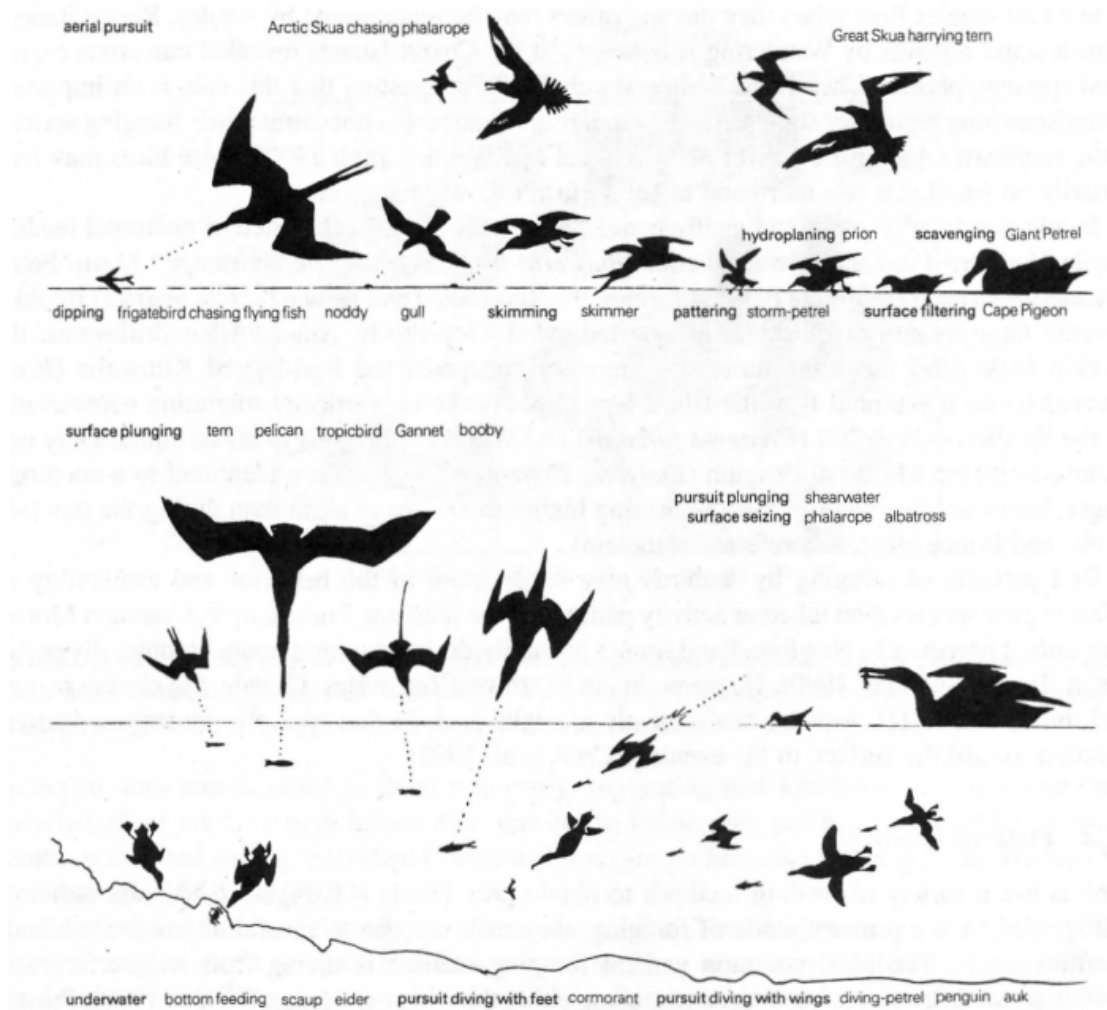


Figure 1. Foraging strategies used by different seabird species (from Nelson 1980).

The fact that seabirds are most often colonial and long-lived species has several benefits as bioindicators of food supplies and pollution across large temporal and spatial scales (Furness & Camphuysen 1997). Nevertheless, to be functional, a bioindicator must act in a sensitive response to alterations in the variable for which it is a proxy measure (Furness & Greenwood 1993). Therefore, we should select as a bioindicator tool such rapid and sensitive responses as state variables of breeding population size, reproductive success, adult condition status, and diet composition or even include further ecological traits such as foraging ecology or trophic niche width to assess challenging and crucial purposes. For instance, given their general wide foraging range, seabirds are ideal

indicator species to define resource hotspots, which could be incorporated into networks of marine protected areas (Louzao et al. 2010).

Many seabird species are good model species to test several ecological theories that still need validation and support but only recently, with the development of new technology, it became possible to investigate accurately their foraging ecology (e.g. Masello et al. 2010; Wanless & Harris 1993). For instance, stable isotope analyses (SIA) of carbon and nitrogen have been used to evaluate seabird trophic relationships (e.g. Cherel 2008; Hobson 2009; Phillips et al. 2011), and tracking devices to study seabird foraging behaviour at sea and spatial distribution (e.g. Christel et al. 2012; Masello et al. 2010; Navarro & González-Solís 2009). These techniques are particularly useful in the study of ecological niche mutually in space, time and trophic dimensions, especially when their use is combined. The development of these new approaches to the study of trophic and ecological interactions provides a complementary approach to investigate the structure of marine trophic relationships in general, and the long-term monitoring of seabird diet and behaviour in particular at both population and individual levels. Understanding these interactions at the individual level becomes a challenge that should highlight some traits that appeared masked when considering the community and population levels.

The foraging niches of seabirds

“Natural systems are dynamic and continually changing, with distance from equilibrium being an important unknown” (Paine 1988). In this context, trophic relationships are central in ecology and play a crucial role in species survival, as the availability of food resources varies over time and space. This balance is mostly driven by two general types of processes that regulate marine ecosystems and ecosystem dynamics: top-down and bottom-up interactions (more rarely by ‘wasp-waist’ interactions, Cury et al. 2000). Top-down effects imply control through predation, including fisheries, while bottom-up effects imply control through food abundance, often assumed to be driven by oceanographic features (e.g. oceanic fronts and upwelling areas) and marine productivity (Frederiksen et al. 2006).

All seabirds are central-place foragers during the breeding season. Therefore, according to the principle of competitive exclusion (Pianka 2011), ecologically-similar species breeding in sympatry are expected to partition their use of available resources, leading

to niche divergence. The ecological niche of a population or species is a fundamental concept in ecology, but there are many niche concepts, each of which emphasizes a different aspect of a species' ecological characteristics (Newsome et al. 2007). In the foraging niche point of view, ecological segregation could arise via differences in space, time and trophic niche (Navarro et al. 2013). Under conditions where competition for resources is likely to be particularly intense, the coexistence of ecologically-similar species should be possible only if there is a degree of ecological segregation presumably to reduce inter-specific competition for food (Phillips et al. 2004, Masello et al. 2010, Navarro et al. 2013). However, when the relative strengths of competition change, niche width should change accordingly and there are evidences that ecological release from inter-specific competition can lead to increases in niche width (Bolnick et al. 2010). Therefore, high overlap in the ecological niche within seabird communities and the non-partitioning of resources among species could be a consequence of a superabundance of food resources and low inter-specific competition (Forero et al. 2004).

The role of individual specialization and temporal consistency

Traditionally, ecologists have long used niche theory to define the ecological niche of a species or population as a whole, assuming that all individuals are similarly affected and ecologically equivalent. However, many apparently generalized species and natural populations are in fact composed of ecologically heterogeneous individuals that use different subsets of the available resources (Bolnick et al. 2002, Svanbäck & Bolnick 2007, Araújo et al. 2007). Such intra-specific variation in individual foraging strategies can be large and vary according to factors such as sex, age, morphology and individual specialization (Bolnick et al. 2003). Individual specialization refers to the use of a relatively limited fraction of the possible range of available resources, resulting in inter-individual niche variation, and temporal consistency conveys the timescale over which the niche variation was observed; therefore, some degree of individual specialization exists if niche variation among individuals within a population is greater than within individuals. For instance, although bull sharks *Carcharhinus leucas* are known as a 'generalist' species showing a broad isotopic niche width at the population level, they differ considerably at the individual level showing a small isotopic niche variance over time, indicating individual consistency in their diets (Matich et al. 2010). Typically, a given population or species could be considered as 'specialist' or 'generalist' according to the feeding habits of its conspecific individuals. A specialist population assumes that

all its individuals are preying on the same food resources and have similar ecological niches resulting in an overall small dietary niche width. On the other hand, generalist populations that show a large dietary niche width might be composed by generalist individuals all taking a wide range of food types (Type A generalization), or individuals each specializing on a different but narrow range of food types (Type B generalization) (Bearhop et al. 2004, Fig. 2).

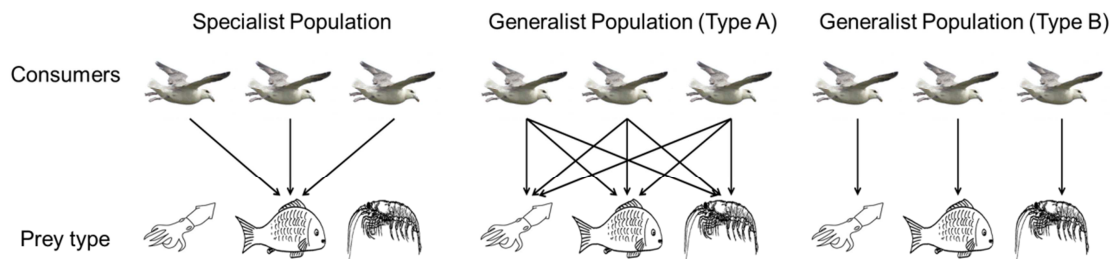


Figure 2. Regimes of predator-prey systems representing extremes of the specialist, Type A generalist and Type B generalist populations. Species pictures are merely representative of consumers and prey type (adapted from Bearhop et al. 2004).

Although individual specialization is known to be widespread across a diverse set of taxa (Bolnick et al. 2003), including several seabird species (e.g. Bearhop et al. 2006; Votier et al. 2010; Woo et al. 2008), the ecological implications of such trait are poorly known. Some studies addressed this issue at the individual level throughout time within the same population (e.g. Matich et al. 2010; Vander Zanden et al. 2010; Woo et al. 2008), and there are evidences that such consistency in foraging niches may reduce intra-specific competition among individuals promoting their ecological segregation (see Bolnick et al. 2003 for a review). However, as seabirds are presumably not territorial at sea it is difficult to take any specific conclusions and hence intra-specific competition for food in pelagic seabirds is difficult to demonstrate (Furness & Birkhead 1984, Lewis et al. 2001). The fact that individuals of the same species or population may use different resources across time is crucial for constructing models of intra-specific competition, predator-prey interactions and food web structure. However, understanding this issue using conventional approaches (e.g. pellets, regurgitates or stomach contents) requires laborious sampling of individuals over extended time periods, which is often difficult to achieve, especially when working with seabirds as they spend most of their time at sea. Here, the use of SIA to infer diet and habitat selection is a powerful approach as stable isotope ratios can integrate dietary information over different temporal scales depending on the tissue analyzed (Inger &

Bearhop 2008). Tracking devices can be used simultaneously to obtain information on successive foraging trips, foraging locations and long-range movements of individual birds in the wild (Weimerskirch et al. 2002). These characteristics of SIA and tracking devices make them appealing to examine isotopic variance and differences in feeding behaviour within and among individuals, and thus can be an effective way to investigate specialization, temporal consistency and the ecological niche (Newsome et al. 2007; but see Matthews & Mazumder 2004). Using these classic and recent tools, this study assesses trophic relationships of different seabird species in relation to their marine environment in general, and evaluates population and individual foraging specialization over time in particular.

Objectives

The main goal of this PhD thesis was to study the influence of environmental variation on the individual specialization of seabirds from different species and populations. Particularly, in the case of providing evidence of individual specialization, this study determines whether intra-specific relationships among seabirds within the same population are associated with the environment and the resources exploited, and investigates the ecological implications of individual foraging specialization in these relationships. Three different seabird species with different characteristics, from four different populations exploiting specific marine environments, were chosen to examine the relative incidence of individual specialization and its ecological implications, focusing particularly in less known aspects such as foraging ecology and behaviour (Table 1). To achieve the proposed goal, the following specific objectives were pursued:

1. Test for short- and long-term consistency in the foraging niche (habitat use and trophic level) of wandering albatrosses, within and among individuals, of a breeding population from Bird Island, South Georgia, Antarctica. Determine the degree of such consistency within the population and investigate whether it is associated with sex, age and body condition of birds.
2. Measure differences in the patterns associated with spatial distribution at sea, habitat use and diet between two sub-colonies of Cory's shearwater, separated by only 2 km, from the same population breeding in Corvo Island. Determine whether small-scale differences in breeding location (and thus at the individual

level) could potentially be related to intra-specific differences in foraging ecology at sea.

3. Use Cory's shearwater as a model species of a wide-ranging top predator breeding in Berlenga Island along three years (2010-2012), during both the pre-laying and chick-rearing periods, to determine whether variations in spatial distribution at sea, trophic niche and short-term consistency in foraging niche are associated.
4. Test for short- and long-term consistency in feeding ecology of yellow-legged gull breeding adults from Berlenga Island in two consecutive years (2011 and 2012), with markedly different baseline diet and oceanographic conditions. Investigate the extent to which the plasticity of this generalist and opportunistic species allow individuals to vary its feeding ecology and foraging behaviour at the population and individual level.

The inter-individual variation in resource use may have a strong impact on ecological processes and population dynamics (Bolnick et al. 2003). To document its incidence and to investigate its implications is crucial to understand trophic relationships between seabirds and the marine environment in order to support theoretical ecological hypotheses and develop conservation strategies.

Table 1. Study species/populations and their general marine environment.

Study Species	Marine Environment
Wandering Albatross (<i>Diomedea exulans</i>)	Oceanic (Polar region)
Cory's Shearwater (<i>Calonectris diomedea</i>)	
Berlenga Island	Neritic (Temperate region)
Corvo Island	Oceanic (Temperate region)
Yellow-legged Gull (<i>Larus michahellis</i>)	Coastal (Temperate region)

Chapter 1

Short- and long-term consistency in the foraging niche of wandering albatrosses

Filipe R. Ceia, Richard A. Phillips, Jaime A. Ramos, Yves Cherel, Rui P. Vieira, Pierre Richard & José C. Xavier



Abstract

The wandering albatross (*Diomedea exulans*) is regarded as a generalist predator, but can it be consistent in its foraging niche at an individual level? This study tested short- and long-term consistency in the foraging niche in terms of habitat use, trophic level and, by inference, prey selection. Fieldwork was carried out at Bird Island, South Georgia, in May-October 2009, during the chick-rearing period. Blood (plasma and cells) and feathers for stable isotope analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were sampled from 35 adults on their return from a foraging trip during which they carried stomach temperature, activity and Global Positioning System loggers. Results suggest short-term consistency in foraging niche in relation to both oceanic water mass and trophic level, and long-term consistency in use of habitat. Consistent differences among individuals partly reflected sex-specific habitat preferences. The proportion of consistent individuals (i.e. with a narrow foraging niche) was estimated at c. 40% for short-term habitat and trophic level (prey) preferences, and 29% for longer-term habitat preference, suggesting this is an important characteristic of this population and potentially of pelagic seabirds in general. Foraging consistency was not related to body condition or level of breeding experience, instead it may reduce intra-specific competition.

Key-words: albatross ecology, foraging strategies, habitat choice, individual specialization, prey selection, stable isotopes

Introduction

According to optimal foraging theory, animals should distribute themselves to maximize their foraging efficiency, which, during breeding is dependent upon the ability to find food within the range of accessible habitat (MacArthur & Pianka 1966; Schoener 1971). Foraging strategies of individual birds can differ substantially (Fritz et al. 2003, Weimerskirch 2007) and vary according to factors such as sex, age, morphology and individual specialization (Bolnick et al. 2003), resulting in the exploitation of different niches by individuals, which could be consistent over time. The degree of variation among individuals in these characteristics has implications for susceptibility to anthropogenic threats, for example from fisheries, and other

environmental changes, and hence for the persistence of populations and species (Phillips, Bearhop, et al. 2009, Dias et al. 2010).

Many populations of generalist predators are now known to include individual specialists, reflecting the often extensive intra-population variation in foraging niche (Bolnick et al. 2003; Woo et al. 2008; Matich et al. 2010). However, few studies have quantified the proportion of specialists in a population and whether this is constant over time. Typically, individual specialization is calculated from a “snapshot” analysis of diet or gut contents, and suffers from stochastic sampling effects. This reflects the logistical and other constraints involved in obtaining repeated diet samples, especially when working with seabirds. However, with the development of new approaches, including the use of data logging devices and stable isotope analysis (SIA), there has been a recent increase in studies of consistency in habitat use and diet (Bearhop et al. 2006, Weimerskirch 2007, Votier et al. 2010). This represents an important development, as an improved understanding of variation in foraging patterns within and among individuals is crucial for determining the major factors contributing to population change (see Bolnick et al. 2003 for a review). Niche variation among individuals, and hence the degree of intra-specific competition, has major ecological and evolutionary implications (Araújo et al. 2007). For example, Weimerskirch et al. (1997) and Jaeger et al. (2009) found differences in habitat use between sexes of wandering albatrosses *Diomedea exulans* (Linnaeus, 1758) during the chick-rearing period and the non-breeding season, respectively. Differences in behaviour between age classes were also found for the wandering albatross (Weimerskirch et al. 2007; Lecomte et al. 2010), suggesting that sex, age and body mass are important factors to take into account when evaluating niche consistency.

During the breeding season, wandering albatrosses are central-place foragers, travelling great distances (up to 15 000 km) in a single foraging trip (Xavier et al. 2004, Weimerskirch et al. 2007). Given their wide foraging range, they are ideal indicator species for defining resource hotspots, which could be incorporated into networks of marine protected areas (Louzao et al. 2010). Wandering albatrosses are top marine predators, feeding mainly on fish and cephalopods and, to a lesser extent, on carrion (Xavier et al. 2004; Weimerskirch et al. 2005). However, nothing is known about short- or long-term consistency in the foraging niche of individuals. Here, we evaluate individual consistency in feeding habitat and diet during the breeding season in a wild

population of wandering albatrosses of known sex and age. Specifically, we used SIA of multiple tissues with different turnover rates, together with the deployment of logger devices and conventional diet samples, to test for short- and long-term consistency in habitat use ($\delta^{13}\text{C}$) and trophic level ($\delta^{15}\text{N}$) within and among individuals. Using this combination of methods, we addressed the following questions; (i) Are individuals consistent in trophic level and foraging habitat over short- and long-term periods? (ii) What is the degree of individual foraging consistency within the population? (iii) Can foraging consistency be related to age or body mass index? (iv) Is there sexual variation in the consistency of the foraging niche?

Materials and methods

Fieldwork was carried out on wandering albatrosses rearing chicks at Bird Island, South Georgia (54°S 38°W) in May-October 2009, during the austral winter. A total of 35 breeding adults (18 males and 17 females) were sampled in May (six), June (six), July (six), August (eight), September (six) and October (three). The age was known for 28 individuals ringed as chicks, and birds were sexed from plumage and morphology (Tickell 1968). Three types of device - GPS and activity recorders and, when possible, a stomach temperature probe - were deployed on birds attending chicks, and removed at the end of the subsequent foraging trip (details of the devices below). Blood samples (1 ml blood from the tarsal vein) and 6-8 randomly selected breast feathers were collected from each bird on recapture, for later SIA. Stomach contents were also sampled by water-offloading, following Xavier et al. (2004). Bill length and width were measured, and birds weighed before the foraging trip. The procedure of capture, deployment or retrieval of devices, collection of samples and release took 10-15 min. No birds were sampled more than once, nor a sample taken from the partner of a previously sampled bird. The blood samples were separated into plasma and red blood cells (RBC) using a centrifuge (15 min at 3000 rpm), stored frozen, and later freeze-dried and homogenized prior to SIA.

Diet sampling and analysis

Food samples collected from each individual reflected recent prey ingestions. Following Xavier et al. (2004), regurgitates were separated into oil and solid mass. Each component (cephalopod, fish, crustacean and carrion) was weighed separately, and individual prey items identified to species where possible. The identification of

cephalopod beaks followed Xavier and Cherel (2009) and of fish otoliths followed Hecht (1987), Williams and McEldowney (1990), and Smale et al. (1995). Fresh squid and fish (with beaks and otoliths attached, respectively) were stored frozen for SIA.

Stable isotope analysis (SIA)

Stable isotopes analyses of carbon and nitrogen can provide useful insights into seabird diet and they are a natural and crucial tool in contemporary studies of the ecological niche (Newsome et al. 2007). Carbon stable isotope value ($\delta^{13}\text{C}$) mainly reflects the consumers' foraging habitat while nitrogen stable isotope value ($\delta^{15}\text{N}$) is mainly used to define consumers' trophic position. Moreover, different tissues have different turnover rates, and therefore can reflect temporal changes in trophic position and foraging habitat (i.e. a change in isotopic niche) (reviewed in Rubenstein and Hobson 2004; Bond and Jones 2009). We analysed $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) in plasma, RBC and breast feathers from each adult, and in prey items obtained from stomach contents. Plasma and RBC retain information on diet (carbon source and trophic level) from a few days prior to sample collection, to the previous 3-4 weeks, respectively (Hobson and Clark 1993; Votier et al. 2010). Hence, the isotopic signature of plasma is representative of the food and feeding ecology of the birds during their single tracking trip (Jaeger et al. 2010b). Breast feathers represent diet during the moult, since feather keratin is metabolically inert after synthesis, which in wandering albatrosses occurs during the non-breeding period (Jaeger et al. 2009). Therefore, based on SIA of different tissues from the same bird we are able to test for short- and long-term consistency in individual foraging niche.

Lipids are depleted in ^{13}C relative to whole tissues and were removed from plasma using successive rinses in a 2:1 chloroform-methanol solution (Cherel et al. 2005b). The low lipid content of whole blood (or RBC) does not typically require lipid extraction (Cherel et al. 2005a). Prior to SIA, feathers were cleaned of surface contaminants using successive rinses in a 2:1 chloroform-ether solution, air-dried and then ground to a fine powder in a freezer mill operating at liquid nitrogen temperature. Flesh samples from regurgitates were stored frozen, and then freeze-dried and ground to a fine powder before SIA. Lipids were extracted from flesh using a 2:1 chloroform-methanol solution.

Nitrogen and carbon isotope ratios were determined by a continuous-flow isotope ratio mass spectrometer (Delta V Advantage, Thermo Scientific) coupled to an elemental

analyser (Flash EA1112, Thermo Scientific). Approximately 0.3 mg of each sample was combusted in a tin cup for the simultaneous determination of nitrogen and carbon isotope ratios. Results are presented in the usual δ notation based on the PeeDee Belemnite (PDB) for carbon and atmospheric N₂ (AIR) for nitrogen. Replicate measurements of internal laboratory standards (acetanilide) indicate measurement errors <0.1‰ both for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

Tracking data collection and analysis

In total, 35 breeding adults of both sexes were fitted concurrently with a GPS (19.5 g, 46.5 x 32 x 18.5 mm, Earth & Ocean, Kiel, Germany) and activity recorder (MK 7, 3.6 g, 18x18x6.5 mm, British Antarctic Survey, Cambridge) before they departed for a single foraging trip at sea. The GPS loggers have an accuracy of 10 m; they were attached to feathers in the mantle region with Tesa tape and recorded the position of the albatross every 20 min. GPS data were obtained from 30 of the 35 loggers deployed, and were used to determine latitude and longitude at the point of inflection, which was the location furthest from the colony and assumed to represent the point at which the bird began its return, maximum distance from colony (km), and trip duration (days). The activity recorders check for saltwater immersion every 3 s, record every change of state from ‘wet’ (indicating sitting on the sea surface) to ‘dry’ (indicating flying or on land) that lasts ≥ 6 s, and were used to determine the percentage of time spent flying in each trip, and by daylight and darkness (civil twilight). Additionally, 26 of these birds were also equipped with a stomach temperature logger (51.5 g in total including the spring, Earth & Ocean, Kiel, Germany), of which 22 were retrieved and downloaded successfully. These incorporated a temperature sensor with a relative resolution of 0.1°C, inside a cylindrical titanium housing of 150 mm x 19 mm in diameter. The anchoring spring hinders the regurgitation of the probe while the bird is at sea. Loggers record temperature changes in the proventriculus, with sudden drops in temperature indicating ingestion of cold prey (Wilson et al. 1992). Housings were specifically designed to be large enough to sample temperature for most of the stomach volume and not become covered by food after ingestion of only a few prey items (Wilson et al. 1995). Temperature was logged every 20 s and was used to estimate the number of prey ingestions. Changes in temperature were bimodal; those of the first peak (< 4°C) usually reflect ingestion of water or very small prey (Weimerskirch et al. 2007) and were

excluded from the analyses. The total mass of the three devices was below 3% of adult mass (0.6-1.0%), as recommended by Phillips et al. (2003) (but see Passos et al. 2010).

Data analysis

We regressed stable isotope ratios in plasma on those in RBC to obtain an index of consistency in carbon source (water mass) and trophic level. Since $\delta^{13}\text{C}$ has a trophic component, we used the residuals of the relationship with $\delta^{15}\text{N}$ in the same tissue (Plasma: $F_{1,33} = 15.2$, $P < 0.001$, $r = 0.562$; RBC: $F_{1,33} = 14.8$, $P < 0.001$, $r = 0.556$) to determine the degree of short-term repeatability in $\delta^{13}\text{C}$ (between RBC and plasma), independently of trophic effects (Bearhop et al. 2006, Votier et al. 2010). Each tissue has a different turnover rate and therefore represents different timescales. However, integration of prey isotopes into body tissues is a continuous, dynamic process, and the analyses of short-term consistency were performed using the same blood sample, separated into plasma and RBC, which could lead to a temporal overlap in the synthesis of these tissues. Longer-term foraging consistency was estimated by regressing stable isotope values in RBC with those in feathers. We used again the residuals to correct the trophic component associated with $\delta^{13}\text{C}$ by regressing these values upon $\delta^{15}\text{N}$ signatures in feathers ($F_{1,33} = 27.2$, $P < 0.001$, $r = 0.672$). Overlap between samples in this comparison will be negligible as wandering albatrosses do not replace breast feathers during breeding. Residuals from the significant relationships were used as a measure of consistency of each individual. We used the absolute value of the residuals for statistical analyses and assumed that values greater or less than the median represented, respectively, more or less consistent individuals. However, to establish the degree of foraging consistency within the population, we cautiously assumed residual values below 0.2 as consistent individuals. This is a conservative estimation, as 0.2 was always lower than the median of the residuals for all individuals. One outlier which had a significant influence on the results for $\delta^{13}\text{C}$ (1.0 in Fig. 4b) even after data transformation was excluded from further analyses. Although birds were sampled from May to October, month had no influence in the stable isotope and consistency values. This was expected because this study was carried out only during the chick-rearing period. Therefore, data for the six months period was pooled to analyse foraging consistency patterns.

Mixing models can be used to estimate the relative proportion of different dietary sources. We adopted a Bayesian multi-source stable isotope mixing model (SIAR: Stable Isotope Analyses in R; Parnell et al. 2010) to estimate ranges of probable contributions of each prey to the diet of each individual, and hence its specialization on particular prey items. All possible combinations of each source contribution were examined using the isotope values from plasma and RBC for each bird, and the mean and standard deviation of each of the four main prey sources. There are no diet-blood fractionation factors available for wandering albatrosses; hence, we used the average values generally accepted for birds: 1‰ and 3‰ enrichment for carbon and nitrogen, respectively (Kelly 2000; Caut et al. 2009), as adopted in studies of other seabirds (Hobson and Clark 1992; Bearhop et al. 2002; Cherel et al. 2005a). A standard deviation of $\pm 0.5\%$ was taken into account, considering potential differences in fractionation factors among species.

We used the standard residuals of the relationship between body mass (at initial capture) and bill length ($F_{1,33} = 42.3$, $P < 0.001$, $r = 0.749$) to estimate the body mass index (BMI) of all sampled birds, an index primarily reflecting body lipid reserves (Zwarts et al. 1996).

All data were tested for departures from a normal distribution; trip duration was \log_{10} transformed, maximum distance to colony and number of prey ingestions overall were square root transformed and all proportions were arcsine transformed. If no transformation normalised the data, non-parametric tests were used. The proportion of consumed prey types was compared between males and females, and between the more and the less consistent individuals, using ANOVA (for data obtained with the SIAR mixing model) and Mann-Whitney U Test (for data from the stomach contents). All statistical tests were performed with Statistica 7.0.

Results

General diet and stable isotope analysis

The diet of the 35 wandering albatrosses sampled was composed mainly of fish (59.4% by mass) and cephalopods (38.4%), a small amount of carrion (2.2%) and trace crustaceans (0.02%). No significant differences were found between sexes in the proportion of each of these components. Similarly, mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of plasma,

which provides an indication of recent meals, did not differ significantly between sexes (Table 2). However, there were significant differences between sexes in $\delta^{13}\text{C}$, but not $\delta^{15}\text{N}$, in RBC and feathers; females showed enrichment in ^{13}C , suggesting some sexual segregation of foraging habitat.

Table 2. Comparison in stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in plasma, red blood cells (RBC) and feathers of male and female wandering albatrosses. Values are mean \pm SD. Significant results in bold.

Tissue type	All birds (n=35)	Males (n=18)	Females (n=17)	T-value	P
$\delta^{13}\text{C}$ (‰)					
Plasma	-20.0 \pm 0.6	-20.2 \pm 0.5	-19.9 \pm 0.5	1.9	0.070
RBC	-20.1 \pm 0.5	-20.3 \pm 0.3	-19.9 \pm 0.6	2.1	0.042
Feathers	-17.5 \pm 0.8	-17.8 \pm 0.8	-17.1 \pm 0.6	3.3	0.002
$\delta^{15}\text{N}$ (‰)					
Plasma	14.3 \pm 0.4	14.3 \pm 0.5	14.4 \pm 0.4	0.4	0.673
RBC	14.1 \pm 0.3	14.1 \pm 0.2	14.2 \pm 0.4	0.9	0.385
Feathers	16.0 \pm 0.3	16.0 \pm 0.7	16.0 \pm 0.6	0.3	0.774

The most frequent fresh prey found in stomach samples from wandering albatrosses were Patagonian toothfish *Dissostichus eleginoides* (Smitt, 1898), blue antimora *Antimora rostrata* (Günther, 1878), giant warty squid *Kondakovia longimana* (Filippova, 1972) and glass squid *Taonius* sp. B (Voss) (Steenstrup, 1861). Mean $\delta^{15}\text{N}$ was much higher in the two fish species, *D. eleginoides* and *A. rostrata* than in the squid, reflecting their higher trophic position (Table 3). As expected, $\delta^{15}\text{N}$ in the blood of wandering albatrosses was higher than in their prey.

Table 3. Stable isotopic signature of carbon and nitrogen and C/N mass ratio (means \pm SD) of the four main prey species recorded in regurgitates collected from wandering albatrosses breeding in Bird Island.

Prey species	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C/N
<i>Dissostichus eleginoides</i>	5	-19.9 ± 0.4	13.8 ± 0.9	3.17 ± 0.06
<i>Antimora rostrata</i>	4	-20.7 ± 0.3	12.2 ± 0.8	3.13 ± 0.02
<i>Taonius</i> sp. B (Voss)	2	-21.4 ± 0.3	11.3 ± 0.8	3.14 ± 0.02
<i>Kondakovia longimana</i>	4	-22.5 ± 0.8	8.7 ± 1.2	3.12 ± 0.07

SIAR mixing model indicated that based on blood and prey isotope values, fish was the largest component (56.4%) in the diet of the sampled birds, followed by cephalopods (43.6%); proportions which were similar to those from analysis of regurgitates. According to the model, some individuals obtained a much greater proportion of their diet from cephalopods than others (Fig. 3). Although the credibility intervals overlapped, the model revealed a high degree of heterogeneity in the proportion of the four main prey types in the diet of different individuals, with the exception of *A. rostrata* that was relatively constant for all individuals. Several individuals (e.g. 2, 12, 28, 31 and 34 in Fig. 3) appeared to have specialized on particular types of prey. This was unrelated to sex, as there were no significant differences in the proportions of the four prey items in the diet estimated by the model between males and females.

Short- and long-term consistency in foraging niche

Strong significant positive relationships were found in residual $\delta^{13}\text{C}$ (hereafter $\delta^{13}\text{C}$), and in $\delta^{15}\text{N}$ between RBC and plasma of individual adults ($F_{1,33} = 35.0$, $P < 0.001$, $r = 0.718$, and $F_{1,33} = 18.7$, $P < 0.001$, $r = 0.601$, respectively; Fig. 4). These results suggest short-term foraging consistency within individuals in relation to both the use of particular water masses and trophic level (\approx relative proportion of fish and squid). Males and females showed similarly significant correlations between RBC and plasma in $\delta^{13}\text{C}$ (Males: $n = 18$, $P = 0.001$, $r = 0.710$; Females: $n = 17$, $P = 0.003$, $r = 0.674$), and in $\delta^{15}\text{N}$ (Males: $n = 18$, $P = 0.007$, $r = 0.614$; Females: $n = 17$, $P = 0.006$, $r = 0.641$).

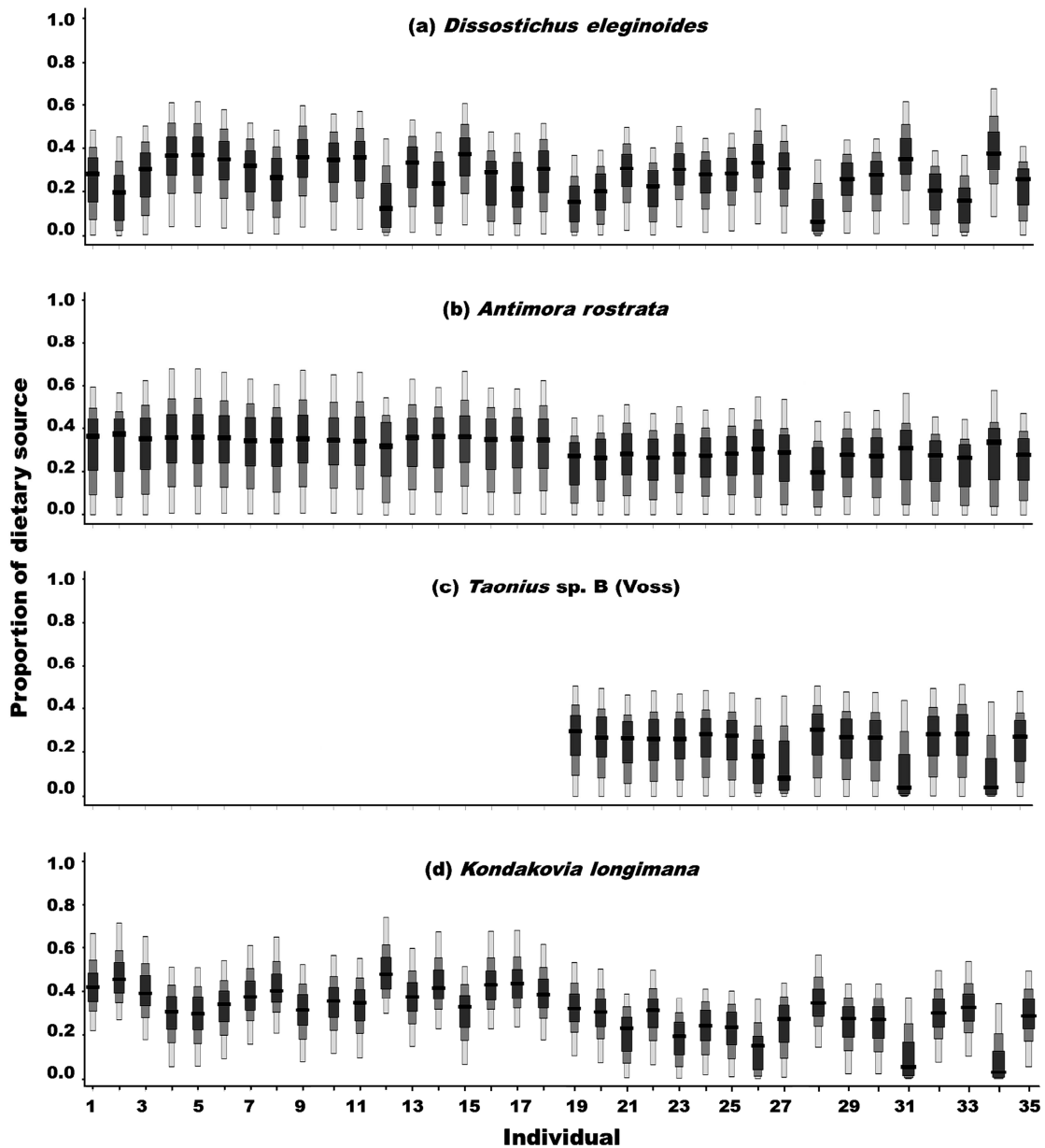


Figure 3. Range of possible proportions of (a) *Dissostichus eleginoides*, (b) *Antimora rostrata*, (c) *Taonius* sp. B (Voss) and (d) *Kondakovia longimana* in the diet of individual wandering albatrosses during chick-rearing. Decreasing bar widths represent 5, 50, 75 and 95% Bayesian credibility intervals computed by Stable Isotope Analysis in R (SIAR; Parnell et al. 2010).

A significant positive relationship was found between feathers and RBC in $\delta^{13}\text{C}$ ($F_{1,33} = 8.6$, $P = 0.006$, $r = 0.454$), which suggest consistent longer-term use of specific water masses (Fig. 4e). However, when split by sex, this relationship was not significant, although stronger in males (Males: $n = 18$, $P = 0.089$, $r = 0.413$; Females: $n = 17$, $P = 0.223$, $r = 0.312$). No relationship was found between $\delta^{15}\text{N}$ in feathers and RBC in the pooled sample ($F_{1,33} = 0.7$, $P = 0.405$, $r = 0.145$), or in separate analyses for each sex

(Males: $n = 18$, $P = 0.940$, $r = 0.019$; Females: $n = 17$, $P = 0.274$, $r = 0.281$). Hence birds apparently did not show long-term consistency in trophic level.

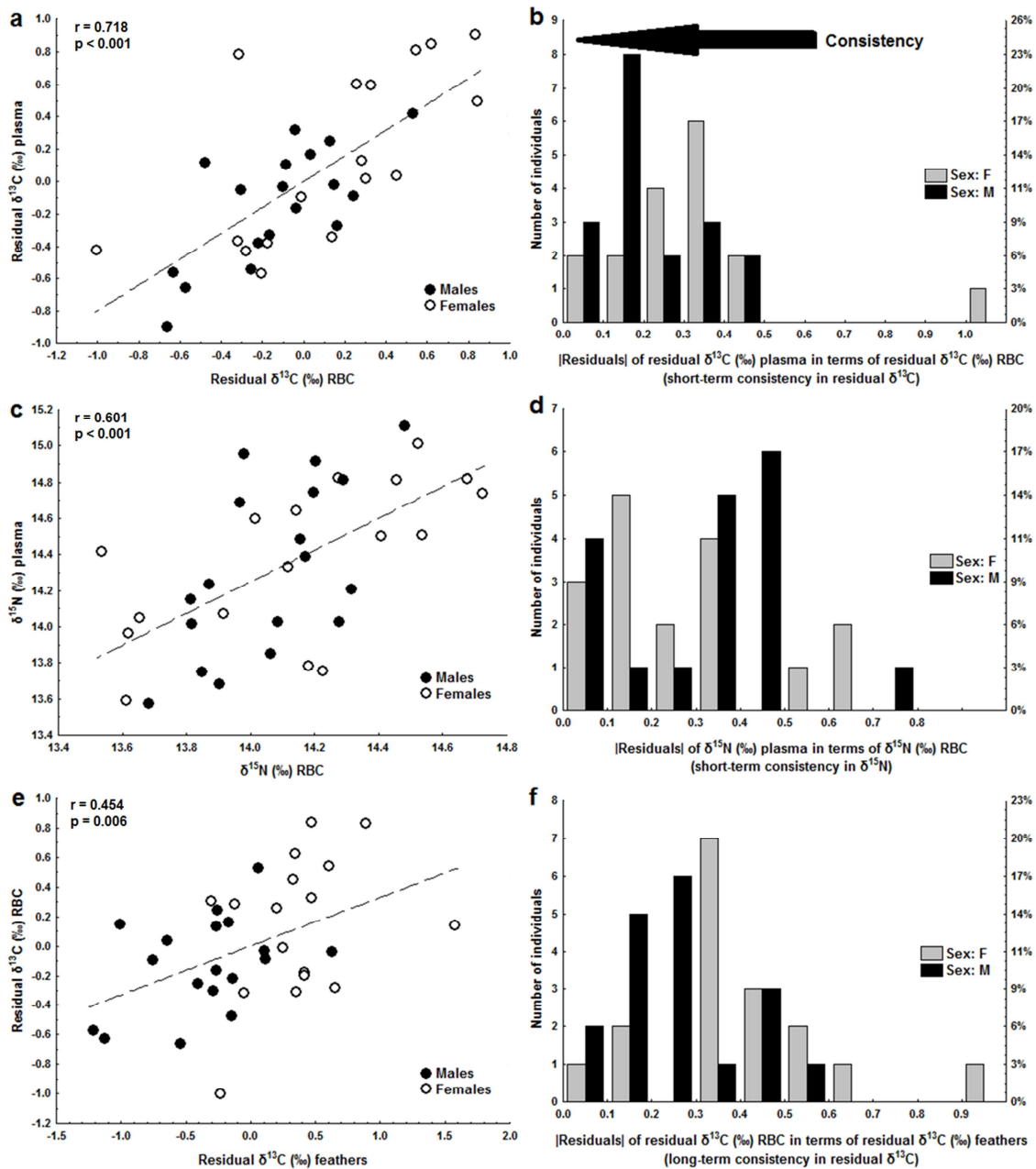


Figure 4. Relationships between (a) residual $\delta^{13}\text{C}$ values in red blood cells (RBC) and plasma, (c) $\delta^{15}\text{N}$ values in RBC and plasma and (e) residual $\delta^{13}\text{C}$ values in feathers and RBC of wandering albatrosses. Histograms indicate the number of males and females showing varying degrees of consistency in residual $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ values (b) short-term consistency in residual $\delta^{13}\text{C}$, (d) short-term consistency in $\delta^{15}\text{N}$ and (f) long-term consistency in residual $\delta^{13}\text{C}$. ($n = 35$). Individual wandering albatrosses with consistency values below 0.2 were considered as consistent.

Individual foraging consistency

Absolute value of residuals for the level of consistency in tissue isotope values within individuals ranged from 0 to 1 for short- and long-term (Fig. 4bdf). The median values were 0.22 for short-term (plasma vs. RBC) in $\delta^{13}\text{C}$, 0.31 for short-term (plasma vs. RBC) in $\delta^{15}\text{N}$, and 0.31 for long-term (RBC vs. feathers) in $\delta^{13}\text{C}$, and the percentage of individuals that were consistent (based on the absolute value of residual of < 0.2 ; see methods) was 42.9, 37.1 and 28.6%, respectively. These results suggest that around 40% of the individuals in this population show short-term consistency in both prey carbon source (foraging habitat) and trophic level, and 29% of individuals showed long-term consistency in foraging habitat. Despite a slight tendency for greater short-term consistency in foraging habitat use of males ($\delta^{13}\text{C}$), and in trophic level of females ($\delta^{15}\text{N}$), no differences were found between sexes for the absolute values of residuals for short-term (plasma vs. RBC; Fig. 4bd). However, significant differences were found between sexes for the absolute values of residuals for long-term in $\delta^{13}\text{C}$ (RBC vs. feathers; t-test: $df = 33$, $T\text{-value} = 2.6$, $P = 0.014$), with males showing higher consistency in the longer-term than females (Fig. 4f).

Linking foraging niche consistency with diet, foraging behaviour, age and body mass index

The proportion of fish and cephalopods found in the diet of wandering albatrosses collected using conventional sampling, and the proportion of the four main prey items estimated by the SIAR mixing model applied to prey and blood values, did not differ significantly between the more and the less consistent individuals in $\delta^{15}\text{N}$ (Table 4). From the 35 individuals, 14 consumed more than 80% fish (“fish specialists”), 13 consumed more than 80% cephalopods (“squid specialists”), and eight combined the consumption of both these prey groups (generalists) during their last trip, which suggests that individuals specialized in specific prey items during trips. However, results from SIA of plasma and RBC suggest that the less consistent individuals changed the proportion of prey items consumed during preceding weeks.

Table 4. Proportion of fish and cephalopods (based on the stomach contents), and the four main prey species (based on the SIAR mixing model) recorded in regurgitates collected from wandering albatrosses showing high or low levels of consistency in $\delta^{15}\text{N}$ (diet and distribution), and for all birds. Values are mean \pm SD (minimum – maximum).

	All birds (n=35)	More consistent (short-term in $\delta^{15}\text{N}$; n=17)	Less consistent (short-term in $\delta^{15}\text{N}$; n=18)
Fish (%)	50.9 \pm 43.2 (0 – 100)	55.5 \pm 40.2 (0 – 100)	46.6 \pm 46.6 (0 – 100)
Cephalopods (%)	44.9 \pm 43.2 (0 – 100)	43.2 \pm 41.3 (0 – 100)	46.5 \pm 46.1 (0 – 100)
<i>Dissostichus eleginoides</i> (%)	26.8 \pm 5.8 (16 – 39)	27.7 \pm 6.4 (18 – 39)	26.0 \pm 5.2 (16 – 35)
<i>Antimora rostrata</i> (%)	29.5 \pm 4.3 (22 – 36)	29.6 \pm 4.3 (23 – 36)	29.5 \pm 4.5 (22 – 36)
<i>Taonius</i> sp. B (Voss) (%)	11.9 \pm 12.5 (0 – 27)	12.6 \pm 12.4 (0 – 27)	11.2 \pm 13.0 (0 – 27)
<i>Kondakovia longimana</i> (%)	31.7 \pm 9.3 (14 – 50)	30.1 \pm 9.6 (14 – 48)	33.3 \pm 9.0 (19 – 50)

Trip duration in the last foraging trip was significantly greater in individuals that showed greater consistency in $\delta^{13}\text{C}$ in RBC and plasma (Table 5). No differences in trip characteristics were found between sexes. Absolute value of residuals for short-term in $\delta^{13}\text{C}$ was negatively correlated with trip duration ($F_{1,32} = 5.0$, $P = 0.032$, $r = -0.368$; Fig. 5). However, when split by sex, this relationship was significant only in males (Males: $n = 18$, $P < 0.001$, $r = -0.592$; Females: $n = 16$, $P = 0.525$, $r = -0.172$). No relationships were found between foraging consistency in trophic level and any foraging behaviour parameters recorded during the previous trip.

Table 5. Comparison of foraging parameters of wandering albatrosses showing high or low levels of short-term consistency in residual $\delta^{13}\text{C}$ (foraging habitat), and for all birds. Some data transformed before analysis. Civil twilight (cut-off between daylight and darkness). Values are mean \pm SD (sample size). Significant results in bold.

	All birds	More consistent (short-term in residual $\delta^{13}\text{C}$)	Less consistent (short-term in residual $\delta^{13}\text{C}$)	<i>T</i> -value	<i>P</i>
Trip duration (days)	6.4 \pm 5.0 (35)	7.6 \pm 4.4 (17)	5.1 \pm 5.3 (18)	-2.4	0.020
Latitude (point of inflection)	-47.3 \pm 7.2 (30)	-46.2 \pm 7.2 (13)	-48.1 \pm 7.3 (17)		
Longitude (point of inflection)	-44.0 \pm 8.1 (30)	-48.1 \pm 9.6 (13)	-42.6 \pm 6.1 (17)		
Maximum distance from colony (km)	1071 \pm 793 (30)	1338 \pm 738 (13)	867 \pm 794 (17)	-1.8	0.087
Percentage of time spent flying overall	62.4 \pm 14.1 (35)	58.3 \pm 12.1 (17)	66.3 \pm 15.2 (18)	1.8	0.080
Percentage of time spent flying during daylight	69.3 \pm 14.6 (35)	64.6 \pm 15.3 (17)	73.7 \pm 12.9 (18)	2.0	0.059
Percentage of time spent flying during darkness	57.6 \pm 17.4 (35)	53.5 \pm 14.2 (17)	61.4 \pm 19.7 (18)	1.5	0.142
Number of prey ingestions overall	16.3 \pm 14.1 (22)	25.9 \pm 14.6 (10)	8.3 \pm 7.0 (12)	-3.5	0.003
Number of prey ingestions per day	3.3 \pm 1.6 (22)	3.2 \pm 1.4 (10)	3.3 \pm 1.8 (12)	0.2	0.856

No relationships were found between the age or body mass index (BMI) and their level of short- and long-term consistency in $\delta^{13}\text{C}$ (age: $F_{1,25} = 0.0$, $P = 0.835$, $r = 0.042$ and $F_{1,26} = 2.7$, $P = 0.115$, $r = 0.305$, respectively; BMI: $F_{1,32} = 0.8$, $P = 0.382$, $r = 0.158$ and $F_{1,33} = 0.0$, $P = 0.946$, $r = 0.012$, respectively) or short-term consistency in $\delta^{15}\text{N}$ (age: $F_{1,26} = 0.6$, $P = 0.436$, $r = 0.153$; BMI: $F_{1,33} = 0.1$, $P = 0.817$, $r = 0.041$).

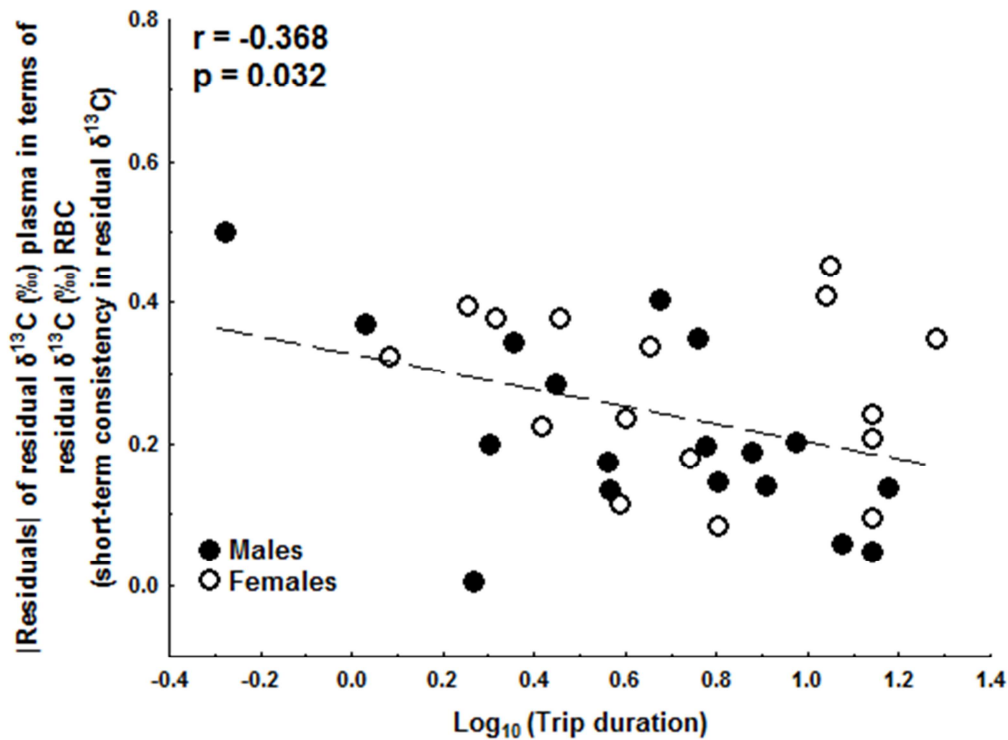


Figure 5. Relationship between Log_{10} (trip duration) and short-term consistency in residual $\delta^{13}\text{C}$ of wandering albatrosses (estimated from the absolute value of the residuals between red blood cells (RBC) and plasma in residual $\delta^{13}\text{C}$ values; $n = 34$).

Discussion

Our results suggest that there is a high level of short-term consistency within individuals in the use of particular water masses and in trophic level (proportion of fish *vs* cephalopods) in wandering albatrosses during chick-rearing at South Georgia. The correlations in stable isotope ratios between different tissues (RBC and plasma for short-term, and feathers and RBC for long-term) can highlight particular details of seabird ecology, such as the degree of foraging specialization. Previous work has shown foraging specialization in a large range of species, mainly reflecting high site fidelity or a consistent pattern in foraging behaviour (data loggers: Weimerskirch et al. 2005; Cook et al. 2006; Elliott et al. 2009; stable isotopes: Cherel et al. 2007; Anderson et al. 2009; Jaeger et al. 2010a; or in combination: Phillips et al. 2009; Weimerskirch et al. 2009; Votier et al. 2010). However, as far as we are aware, ours is the first study to estimate the proportion of consistent individuals within a population.

Wandering albatrosses are top predator species consuming varying proportions of prey according to local or regional resource availability (Review in Cherel and Klages 1998; Xavier et al. 2004; Weimerskirch et al. 2005). However, focusing at an individual level, perceptible preferences in diet were found within the study population at South Georgia. Analyses of regurgitates showed that several birds fed mainly (> 80% of prey items by mass) on fish or on cephalopods in their last trip (42.9 and 34.3%, respectively), whereas others (22.8%) consumed both prey in different proportions. SIAR mixing model estimated that fish were the most consumed resource in the short-term based on analysis of stable isotope ratios in blood (Fig. 3). However, the relative contribution to the diet from different prey species varied considerably among individuals. For some individuals the proportion of cephalopods was higher. According to Bolnick et al. (2007) the use of a narrow range of resources by each individual (specialization) might minimize intra-specific competition. Specialization in particular prey items does not seem to be related to sex in wandering albatrosses from South Georgia, because no differences were found between males and females in ratio of the components found in regurgitates or in the diet predicted by the SIAR mixing model, although Weimerskirch et al. (1997) showed that males deliver fish more often than females at Crozet Islands.

A high, positive correlation in $\delta^{13}\text{C}$ (corrected for trophic fractionation) between RBC and plasma (Fig. 4a) indicates that individual wandering albatrosses foraged in isotopically similar areas in the short-term. However, it does not mean necessarily that individuals show fine-scale site fidelity, but that they consistently use the same water mass. $\delta^{15}\text{N}$ values were also strongly correlated in RBC and plasma (Fig. 4c), suggesting short-term consistency in trophic level. Such relationships, however, are partly attributable to temporal overlap in the synthesis of plasma and RBC (Votier et al. 2010). Nevertheless, the correlation in $\delta^{13}\text{C}$ between feathers and RBC indicates that individuals exhibit longer-term consistency in habitat use that persists over many months, since $\delta^{13}\text{C}$ in RBC represents the breeding period (at least a few weeks before sampling), and in body feathers represents the previous non-breeding season. This relationship was stronger in males than females (corroborated by the relative proportion of consistent individuals; Fig. 4f). These results are in accordance with differences in $\delta^{13}\text{C}$ values in feathers, which suggest sexual segregation in habitat during the non-breeding season (Weimerskirch and Wilson 2000; Jaeger et al. 2009; Phillips et al. 2009). Presumably males are more likely to forage consistently in isotopically similar

water masses throughout the year, whereas females may shift their distribution further to the north, to exploit warmer waters during the nonbreeding season, which may reduce competition for resources (Weimerskirch and Wilson 2000; Phillips et al. 2011).

A significant degree of foraging consistency within a population does not necessarily mean that all individuals are consistent. Our estimation of the proportion of individuals that were consistent was conservative, by selecting only those with very small residuals (absolute value < 0.2) from the fitted regression line. Still, there were high proportions of individuals that showed short-term consistency in habitat use (43%) and trophic level (37%), and longer-term consistency in habitat use (29%). Therefore, this characteristic may be widespread in this population and related species. In this context, we explored relationships between short-term foraging consistency and several other characteristics, including diet and foraging behaviour recorded using data loggers in order to clarify this phenomenon. In terms of diet, our results shows that of the more consistent individuals, around 42% were specialists on fish, 29% on cephalopods, and 29% were generalists. Consistent generalists must consume similar proportions of all prey items over time in order to show similar isotope values. On the other hand, the great majority (78%) of individuals classified as generalists nevertheless seemed to have specialised on a particular prey category during the last trip, based on the single conventional diet sample collected on their return. However, these individuals must, in fact, be generalists that fed on different prey during previous weeks. This underlines the problem in determining the ratio of specialists to generalists from a “snapshot” diet analysis, particularly as a generalist predator might have ingested one prey species immediately prior to capture and collection of stomach contents (Warburton et al. 1998). In contrast, stable isotopes are much more suitable for analysing temporal diet consistency from days to weeks or months, depending on the tissue sampled (Araújo et al. 2007).

Similar to other studies of marine predators, we found differences in foraging behaviour at an individual level (see Weimerskirch 2007 for review), in this case, linked to foraging consistency. Presumably the significant correlation of trip duration with short-term consistency in $\delta^{13}\text{C}$ (plasma vs. RBC; Fig. 5) simply reflects a greater proportion of RBC that was synthesized during the trip in birds that have been at sea (feeding on the same carbon source/in the same water mass) for longer. On the other hand, birds that made short trips would have produced more of their RBC during previous trips where they could have been feeding somewhere different. Nevertheless, it is equally possible

that differences in trip duration could indicate foraging behaviour segregation between the more and the less consistent individuals in foraging habitat (mainly males), corroborated by the significant correlation of trip duration with short-term consistency in $\delta^{13}\text{C}$, as a result of more targeted specialization. At least around 43% of birds were consistent and selective in foraging habitat during longer trips. Performing shorter trips at smaller spatial scales, the immediate prey encounter rate is expected to play a major role and prey predictability is assumed to be smaller in contrast with longer trips (Weimerskirch 2007), as birds travelling longer distances to find food may consistently seek specific water masses, in order to refill their condition and compensate for travelling longer distances. Consistency in foraging behaviour during the chick-rearing period has rarely been investigated in the past, but previously reported for other species (Quillfeldt et al. 2008; Woo et al. 2008; Jaeger et al. 2010a). Thus, short-term consistency in foraging habitat of wandering albatrosses, particularly males, during the chick-rearing period could be related to the regularity that many birds perform longer trips to specific water masses. This suggestion is in accordance with the fact that many seabird species concentrate their efforts on persistent and predictable food sources (Weimerskirch et al. 2005; Woo et al. 2008; Votier et al. 2010).

The adaptive significance of the foraging specialisations observed in wandering albatrosses remains unclear. Some studies clearly demonstrate that intra-population variation is due to age or sex, while others attribute it to individual preference (Bolnick et al. 2003). Despite no significant differences in absolute value of residuals in the short-term between sexes, the slight tendency of higher short-term consistency in habitat use by males, as well as significant differences in $\delta^{13}\text{C}$ values in RBC could reflect sexual segregation in habitat use during chick-rearing (Weimerskirch et al. 1997; this study). This has also been inferred for the non-breeding season from differences in stable isotope ratios in feathers (Jaeger et al. 2009; this study), and considered to reflect habitat specialisation, possibly driven by competitive exclusion of females by males (Phillips et al. 2011). However, the variation in short-term consistency in the foraging niche was unrelated to sex, indicating that other factors were responsible. We found no evidence that foraging niche consistency was related with age and hence probably not with experience. However, we only sampled breeding adults (11-33 years), and not immature birds. Weimerskirch et al. (2005, 2007) and Lecomte et al. (2010) found differences in behaviour between age classes, and suggested that younger birds may

have different foraging strategies, perhaps resulting from a poorer knowledge of the foraging habitat. However, there was apparently no difference in foraging success of young compared with older birds. Moreover, in the present work, there was no relationship between foraging consistency and body mass index, suggesting that the specialists and generalist have similar levels of body condition.

Foraging consistency in wandering albatrosses is not a consequence of experience in adult breeders and does not appear to confer an advantage in terms of body condition, so it remains unclear why there are such a high number of consistent individuals within the population. The advantages may relate to improvements in several traits such as reproductive success, chick food delivery rates or chick condition which requires further investigation. It may also contribute to reduce intra-specific competition among individuals.

In summary, we observed that: (i) wandering albatrosses from South Georgia showed high short-term consistency at both habitat use and trophic level, and long-term consistency in habitat use; (ii) the degree of individual consistency in both habitat use and trophic level within the population was around 40% in the short-term, and 29% in the long-term habitat use; (iii) foraging consistency was not related to age or body mass index and so is not a consequence of experience nor does it affect body condition; and (iv) consistency in habitat use tended to be greater over long time periods in males than females. As well as documenting the existence of individual specialization, further studies should explore the relative incidence in different populations, species and communities, and the implications for fecundity and survival.

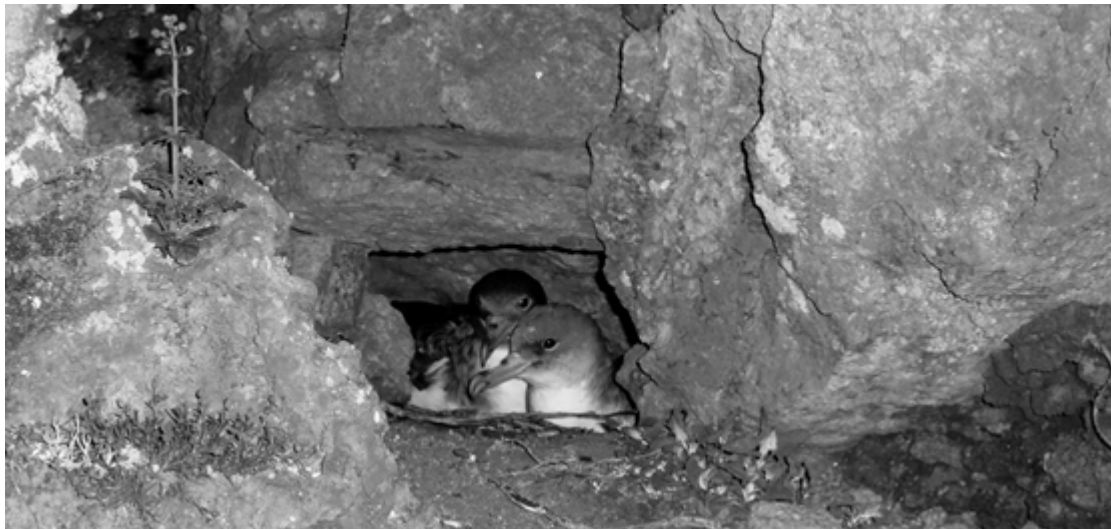
Acknowledgements

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Chapter 2

Spatial foraging segregation by close neighbours in a wide-ranging seabird

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Abstract

Breeding seabirds are central-place foragers and therefore exploit food resources most intensively around their colonies. When nesting aggregations are close to one another density-dependent competition is likely to be high, potentially promoting foraging segregation. However, little is known about dietary and spatial foraging difference between closely adjacent colonies, particularly for wide-ranging foraging species. The extent of foraging segregation between two sub-colonies in a wide-ranging seabird, the Cory's shearwaters (*Calonectris diomedea*), separated by only 2 km, was assessed on a small Island in the North Atlantic in order to evaluate the effects of at-sea intra-specific competition for food resources. During the 2010 chick-rearing period a total of 43 breeding adults of both sexes were sampled at both sub-colonies. A GPS logger was deployed on each individual and removed after several foraging trips at sea. Blood samples (plasma and red blood cells) were collected from each tracked individual for stable isotope analysis (SIA) and breeding parameters were monitored during the whole season (from May to October). Results suggested that spatial segregation was apparent in short (= 1 day) but not in long (≥ 2 days) foraging trips. Birds from different sub-colonies did not only forage at different locations, exploring areas with different oceanographic conditions in the short trips during the chick-rearing period, but also showed significant differences in $\delta^{13}\text{C}$ of red blood cells, suggesting foraging segregation in habitat use during the incubation period. Interestingly, no differences were found in the exploited habitat between birds from both sub-colonies during the chick-rearing period, suggesting that birds concentrated their feeding activity in small concentrated patches of similar habitat. We provide evidence that widely-ranging seabirds from two sub-colonies exhibited colony-specific foraging areas during short trips, most likely to reduce intra-specific competition.

Key-words: feeding ecology, GPS tracking, individual specialization, intra-specific competition, stable isotopes

Introduction

Competition between conspecifics, which is frequently density-dependent, may result in the partitioning of resources between individuals or groups (Wakefield et al. 2009). As

seabirds are presumably not territorial at sea, intra-specific competition for food in pelagic seabirds is difficult to demonstrate (Furness & Birkhead 1984, Lewis et al. 2001), but there is evidence that it may drive foraging segregation among neighbouring colonies in several seabird species (e.g. Masello et al. 2010; Wiley et al. 2012). High intra-specific competition is mainly attributed to large colonies during the breeding season, which could result in prey depletion in their vicinity and longer foraging ranges to obtain food (Furness & Birkhead 1984, Lewis et al. 2001, Garthe et al. 2011). Breeding seabirds are central-place foragers, leading populations to exploit resources around their colonies under the influence of distribution of prey (Phillips et al. 2009), for which may be drivers or proxies local oceanographic conditions (e.g. bathymetry, sea-surface temperature, chlorophyll *a* concentration; Masello et al. 2010). Therefore, we can expect segregation both in foraging areas and prey between geographically distant breeding populations, which may lead to diversification of foraging tactics among populations. To minimize intra-specific competition, Cairns (1989) predicted that seabird colonies should be spaced so that their closer foraging areas do not overlap. In this study we tested the hypothesis that due to density-dependent competition for food, foraging segregation occurs between geographically proximate seabird sub-colonies. In accordance to Cairns (1989) prediction, several studies (e.g. Grémillet et al. 2004; Yamamoto et al. 2011; Wiley et al. 2012) demonstrated foraging segregation between colonies in pelagic seabirds, but these were separated by tens or hundreds of kilometres. Studies demonstrating spatial foraging segregation among seabirds of the same species, breeding in colonies as close as 2 – 2.5 km from each other, are very scarce (Wanless and Harris 1993; Masello et al. 2010). Those authors studied Blue-eyed Shags *Phalacrocorax atriceps* and three different penguin species which generally have smaller foraging ranges at sea. To our knowledge no studies have examined segregation between closely spaced colonies of more wide-ranging species.

Large populations of Cory's shearwaters *Calonectris diomedea borealis* breed in the Azores, a chain of nine islands aggregated in three groups (western, central and eastern) straddling the mid-Atlantic ridge over a distance of about 600 km. Corvo Island is the smallest (ca. 17 km², Fig. 6) and it holds greater densities of Cory's shearwater than any other in the archipelago (mean = 2732 birds km⁻¹, Furness et al. 2000). Given the high density of birds nesting on Corvo, it is an appropriate site to test for between-sub-colony foraging segregation. The most appropriate period to address this issue is during the

early chick-rearing period, when birds' foraging effort is highest and most intensively concentrated in the vicinity of the colony (Granadeiro et al. 2000, Paiva, Geraldes, Ramírez, Meirinho, et al. 2010a). We expected that density-dependent competition is likely to be more intense close to Corvo, therefore segregation is more likely to occur during short than during long foraging trips.

Specifically, we hypothesized that: (1) central-place foragers reduce competition by partitioning available space (i.e. geographical location) and habitats (i.e. a set of environmental conditions) during the early chick-rearing period; and (2) individuals (according to sub-colony and sex) display dietary segregation throughout the breeding period (incubation and chick-rearing). Our goal is to measure differences and patterns associated with spatial distribution at sea, habitat use and diet to determine whether small-scale differences in breeding location could potentially be related to intra-specific differences in foraging ecology at sea. In order to test our hypotheses we tested for foraging segregation using conventional dietary sampling, stable isotope analysis (SIA) and individual movement data. We used these techniques to evaluate the effects of at-sea intra-specific competition for food resources between two sub-colonies of Cory's shearwater from the same population separated by only 2 km. Cory's shearwater is dimorphic in size and bill dimensions (Granadeiro 1993, Ramos, Granadeiro, et al. 2009) suggesting possible at-sea foraging differences between sexes that could confound the sub-colony differences. We therefore controlled for potential differences between males and females. We used a combination of GPS loggers, SIA of multiple tissues with different turnover rates, conventional diet samples, environmental covariates and breeding success, to address spatial, habitat and dietary segregation between sub-colonies.

Materials and methods

Fieldwork was conducted in Corvo Island (39°40'N, 31°06'W; Fig. 6) in the Azores archipelago, Portugal, during the 2010 chick-rearing period. The islands of the Azores have relatively narrow peri-insular shelves and are surrounded by deep, oceanic waters.

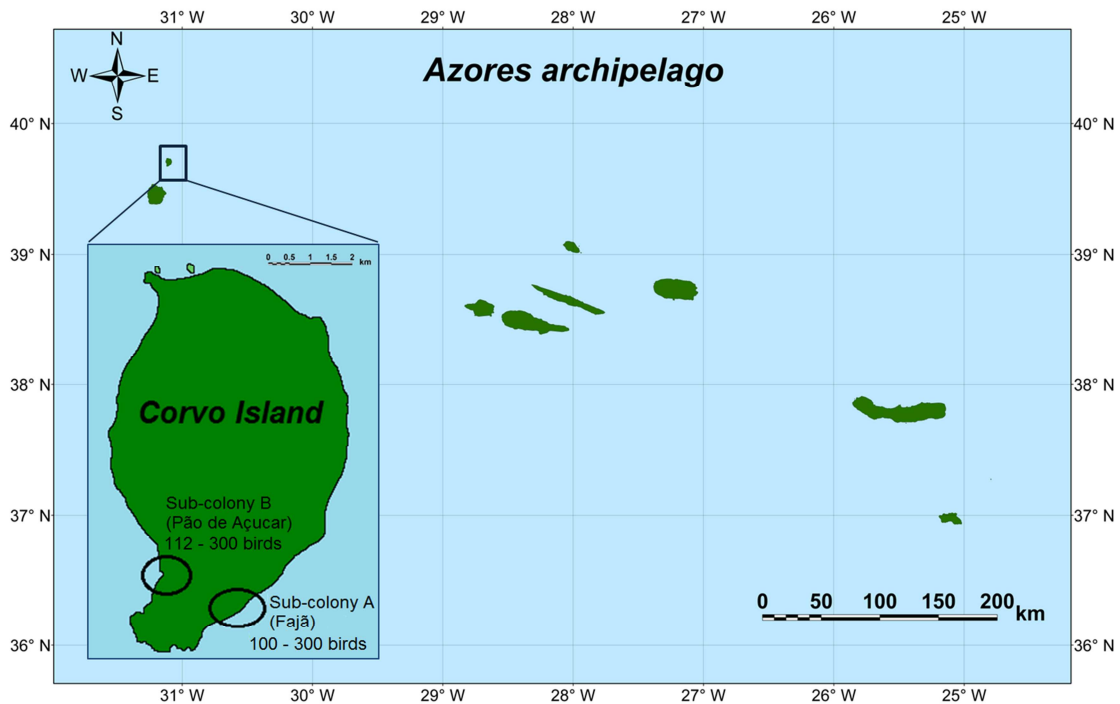


Figure 6. Location of the Cory's shearwater *Calonectris diomedea* sub-colonies (A and B) studied at Corvo Island, Azores, Portugal (39°40'N, 31°06'W).

A total of 43 breeding adults of two sub-colonies of Cory's shearwaters separated by 2 km on Corvo Island (sub-colony A (Fajã): 14 males and 9 females, sub-colony B (Pão de Açúcar): 10 males and 10 females; Fig. 6) were sampled during a period of 35 days, from 30 July to 2 September. The time between capture and recapture ranged from 2 to 30 days (14.9 ± 5.5 days). Captured birds were ringed, weighed both on capture and recapture, and wing and tarsus length were measured. Sex was already known for the majority of birds; however, the bill was also measured (culmen, bill height at the gonys and at the base) to determine the sex of remaining birds (using a discriminant function established by Granadeiro 1993). A GPS logger was deployed on birds attending chicks, and removed after several foraging trips (details of the devices below). Birds from the two sub-colonies were tracked simultaneously (Fig. 7). Blood samples (0.5-1 ml from the tarsal vein) were collected from each bird on capture and recapture using 25 gauge needles and, within 2-3 h, separated into plasma and red blood cells (RBC) using a centrifuge (15 min at 3000 rpm). Hematocrit was recorded and samples were then stored frozen until preparation for SIA. Stomach contents were sampled from 20 tracked individuals of both sub-colonies by water-offloading, following Wilson (1984). We weighed chicks (age between 6-40 days) reared by tracked adults every two days to estimate linear chick growth. In addition, all sampled birds were monitored every day

from May 26 until hatching to determine laying and hatching date using a burrow-scope (elongated remote camera). Afterwards, the presence of adult and/or chick was monitored every week until October 21 to determine fledging success. Deployment or retrieval of devices, collection of samples and release took 10-15 min and birds were returned immediately to their nests.

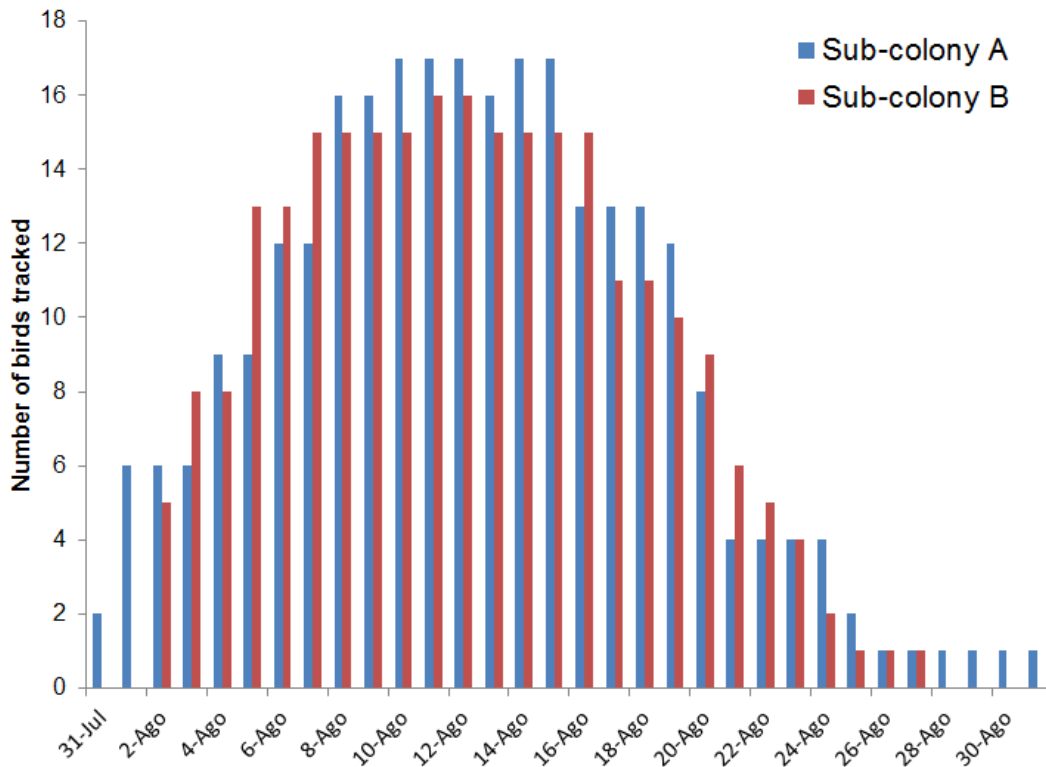


Figure 7. Number of Cory’s shearwaters *Calonectris diomedea* tracked per day from each sub-colony during the early chick-rearing period of 2010 in Corvo Island.

Tracking data collection

Each bird was fitted with a GPS logger (CatTraq GT-120, Perthold Engineering LLC). The plastic case was removed and replaced by a 7 cm long thermo-retractile rubber sleeve reducing the total weight to 17 g. This corresponded to 1.6-2.6% of studied individuals’ mass, which is below the 3% of adult mass reported to have no deleterious effects on seabird species during short-term deployments (Phillips et al. 2003; but see Vandenabeele et al. 2012), including Cory’s shearwaters (Iguar et al. 2005). The GPS loggers were attached to feathers in the mantle region with Tesa® tape and set to record the birds’ position (median error of < 10m) every 5 min. We tracked birds continuously from 2 to 17 days (12.7 ± 3.7 days)

Environmental data

We characterized Cory's shearwater habitat use using three environmental indices: bathymetry (m), August 2010 mean chlorophyll-a concentration (Chl *a*, mg m⁻³) and sea surface temperature (SST, °C) (Paiva et al. 2010b). Bathymetry data were extracted from a grid of 0.01° (approx. 1 km) from <http://www.ngdc.noaa.gov/mgg/global/global.html> (we selected the ETOPO1 blended product). Chl *a* and SST data were downloaded for a spatial resolution of 0.04° (approx. 4 km) of Aqua-MODIS mapped products from <http://oceancolor.gsfc.nasa.gov/cgi/13>.

Diet sampling and identification

All regurgitates came from breeding individuals; birds with empty stomachs were not considered in the analysis. Following Xavier et al. (2004), regurgitates were separated into oil and solid fractions. Each solid component (fish and cephalopod) was sorted, counted and weighed separately, and individual prey items identified to species-level whenever possible. Fresh squid and fish (with beaks and otoliths attached, respectively) were stored frozen for SIA.

Stable isotope analyses

Stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of plasma and RBC retain information on diet (carbon source and trophic level) from a few days prior to sample collection, up to the previous 3-4 weeks, respectively (Hobson and Clark 1993, Votier et al. 2010). In each individual, we analysed $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) in RBC from initial capture and plasma from recapture (between 2 and 30 days difference) in order to minimize overlap between the samples (Votier et al. 2010). $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) of fresh prey items obtained from stomach contents were also analysed to create a basis for the interpretation of the tissues' isotopic signatures and construction of mixing models (see data analysis below).

Samples were freeze-dried and homogenized prior to SIA. Because high lipid concentrations in plasma and in flesh from prey items can lead to depleted $\delta^{13}\text{C}$ values, lipids were removed using successive rinses in a 2:1 chloroform-methanol solution (Cherel et al. 2005). Nitrogen and carbon isotope ratios were determined via Finningan conflo II interface to a Thermo Delta V S mass spectrometer coupled to a Flash EA1112 Series elemental analyser. Approximately 0.3 mg of each sample was combusted in a tin

cup for the simultaneous determination of nitrogen and carbon isotope ratios. Isotope ratios are presented in the usual δ notation based on the PeeDee Belemnite (PDB) for carbon and atmospheric N₂ (AIR) for nitrogen, and expressed as ‰. $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = [(R_{\text{sample}}/ R_{\text{standard}}) - 1] \times 1000$, where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicate precision $< 0.2\text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

Data analysis

As Cory's shearwaters typically use a dual foraging strategy to exploit the environment (Magalhães et al. 2008; Paiva et al. 2010b; but see Phillips et al. 2009), we expected differences in the habitats explored by individuals between short and long foraging trips. Although birds did not exhibit bimodality in this study either in trip duration or maximum distance from colony (see Fig. 8), all analysis were performed separately for long (≥ 2 days) and short (= 1 day) foraging trips, since density-dependent competition is likely to be more intense during shorter trips than longer trips.

The nonparametric fixed kernel density (FKD) estimator was used to calculate the 25, 50 and 75% density contour areas, and respective areas (km²), of each trip using functions (“*kernelUD*”, “*getvolumeUD*”, “*getverticeshr*” and “*kernel.area*”) of the *adehabitat* package ($h = 0.03$ for short trips, $h = 0.13$ for long trips, *grid* = 500; Calenge 2006) under R 2.14.0 (R Development Core Team 2011). GPS locations at the colony were excluded from analyses and we only used foraging-point kernels, which exclusively represented the areas where birds were presumed to be foraging (determined by trip sinuosity index ≥ 3 ; adapted from Grémillet et al. 2004). The intra-specific overlap in the estimated foraging range among individuals within each sub-colony and among individuals between sub-colonies was assessed following Fieberg and Kochanny (2005). The 25, 50 and 75% FKD overlap were calculated for each bird (within and between sub-colonies) using the function “*kerneloverlap*” of the *adehabitat* package (*meth* = “VI”; Calenge 2006) under R 2.14.0. Spatial segregation was assessed by determining that FKD (25, 50 and 75%) overlap among individuals between sub-colony A and B was smaller than the FKD (25, 50 and 75%) overlap among individuals within each sub-colony.

Zones of area-restricted search (ARS) were estimated for each trip applying first-passage time (FPT) analysis (see Fauchald and Tveraa 2003 for more details) and using

functions (“*as.ltraj*”, “*fpt*”, “*varlogfpt*” and “*meanfpt*”) of the *adehabitat* package (Calenge 2006) under R 2.14.0 and some custom-built functions. Usually, positions which corresponded to when the bird was sitting on the water result in very small-scale ARS zones (< 100 m diameter), increasing the variance in FPT and reducing the ability to detect larger-scale ARS zones (Weimerskirch et al. 2007). To address this problem, we removed bouts on the water (speed < 9 km h⁻¹) and interpolated locations to obtain a distance interval of 1 km for FPT analysis (Pinaud 2008). Following the recommendations of Pinaud (2008), FPT analysis was performed in two steps: (1) to detect large-scale ARS we run the analysis on the whole path, estimating the FPT every 25 km for a radius *r* from 1 to 300 km; (2) to detect small spatial scale events we run again FPT analysis every 1 km for an *r* varying between 1 and 50 km. The plot representing variance in log (FPT) as a function of *r* allowed us to identify the ARS scales by peaks in the variance. In this calculation, FPT was log transformed to make the variance independent of the magnitude of the mean FPT (Fauchald & Tveraa 2003). The mean scale at which variance in FPT peaked at the individual level was 3.2 ± 2.6 km during short trips and 17.5 ± 11.3 km during long trips; there was no significant differences between the two sub-colonies (short trips: sub-colony A = 3.2 ± 2.9, sub-colony B = 3.1 ± 1.7, ANOVA: $F_{1,40} = 0.0$, $P = 0.86$; long trips: sub-colony A = 16.1 ± 11.9, sub-colony B = 19.5 ± 10.5 ANOVA: $F_{1,30} = 0.7$, $P = 0.41$). The centroid of geographic position at each ARS zone (latitude and longitude) was calculated for each trip and used to assess differences between sub-colonies in the exploited zones.

Given the geometry of the two colonies within Corvo Island (sub-colony A, east side; sub-colony B, west side), we tested whether the breeding site had an effect on direction adopted by birds for each foraging trip. Following Robson et al. (2004), the bearing (degrees) of the most distant location recorded during each trip from each sub-colony was calculated to evaluate the probability that the observed distribution of trip directions would occur under the null hypothesis of no difference in the direction of foraging trips between sub-colonies. Foraging trip direction was compared between sub-colonies with a Watson-Williams test for circular data using functions (“*graus.rad*”, “*graus.circ*”, “*plot.circular*” and “*watson.williams.test*”) of the *circular* package (Agostinelli and Lund 2011) under R 2.14.0. To avoid pseudoreplication, one trip was randomly selected from each bird.

Mean values of environmental variables inside the kernel contours and ARS zones of each trip were extracted using ArcGIS 9.2. With the exception of circular variables, behavioural indices were modelled using mixed-effects ANOVA, with sex, colony and environmental variables treated as fixed effects and individual as a random effect.

Mixing models were used to estimate the relative proportion of different dietary sources. We adopted a Bayesian multi-source stable isotope mixing model (stable isotope analyses in R: SIAR, function “*siarsolomcmc4*”; Parnell et al. 2010) to estimate contributions for each prey to the diet of each individual. All possible combinations of each source contribution were examined using both isotope values from RBC on capture and plasma from recapture (corresponded to incubation and chick-rearing periods, respectively) for each bird, and the mean and standard deviation of each of the three prey sources. There are no diet-blood fractionation factors available for Cory’s shearwaters; hence, we used the average values of four seabird species available in literature: 0.30 and 2.85‰ enrichment for carbon and nitrogen, respectively (Hobson & Clark 1992, Bearhop et al. 2002, Cherel, Hobson, & Hassani 2005). Due to potential differences in fractionation factors among species, a standard deviation of $\pm 1.0\text{‰}$ was assumed.

We used the standard residuals of the relationship between body mass (mean between capture and recapture) and wing length ($F_{1,39} = 11.5$, $P = 0.002$, $r = 0.478$) to estimate the body mass index (BMI) of 41 sampled birds, which we assume primarily reflects body lipid reserves (Sánchez-Guzmán et al. 2004), to assess whether adults from the two colonies were in a similar health state. In addition, the variation in the hematocrit between the blood sampling on initial capture and recapture was calculated as a proxy of the individuals’ current health condition status (see Fair et al. 2007 for a review). The linear growth rate for each chick was represented as the coefficient of the regression line between chick body mass and age (i.e. the daily increase in body mass), expressed in g day^{-1} (Ramos et al. 2003).

All data were tested for normality and homoscedasticity; foraging area (25, 50 and 75% FKD) and Chl *a* were \log_{10} transformed, bearing (degrees) was transformed into radians, linear chick growth was square root transformed and proportions were arcsine transformed, with exception of those obtained from SIAR mixing model. If no transformation normalized data, non-parametric tests were used. Values are means \pm SD

unless otherwise stated. Circular data analyses were performed under R 2.14.0. All other statistical tests were performed with Statistica 7.0 (StatSoft. Inc. 2004).

Results

We obtained a total of 368 foraging trips from 43 individuals. The frequencies of trip duration for the entire data set showed a clear unimodal distribution during the study period, during which 310 (84.2%) were one day trips made by 42 individuals and 58 (15.8%) were ≥ 2 day trips made by 32 individuals (Fig. 8).

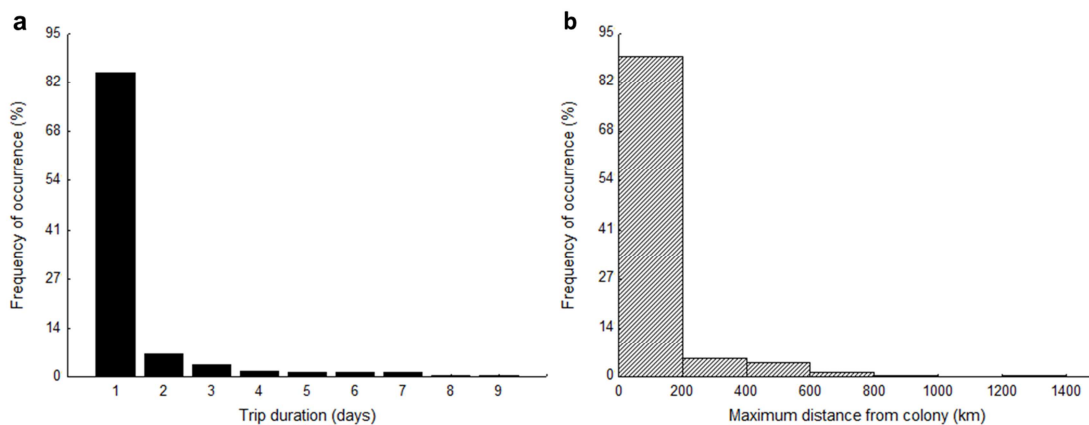


Figure 8. (a) Frequency distribution of trip duration (days) and (b) maximum distance from colony (km) for all 368 Cory's shearwaters *Calonectris diomedea* foraging trips recorded in August 2010 during the chick-rearing period in Corvo Island.

Spatial segregation

During long trips, birds from Corvo headed exclusively north to forage in areas such as the mid-Atlantic ridge and surrounding seamounts (e.g. Altair and Chaucer), with a maximum distance of 1265 km (347 ± 244 km) and a maximum trip duration of 9 days. Short trips were mostly confined to the colony surroundings, within a maximum distance of 216 km (62 ± 39 km).

Birds from the two sub-colonies demonstrated intra-specific spatial segregation at sea during short trips; a significant greater overlap was detected among individuals within each sub-colony (75, 50 and 75% FKD: $19.5 \pm 4.0\%$, $13.2 \pm 3.1\%$ and $8.2 \pm 2.2\%$, respectively) than among individuals between the two sub-colonies (75, 50 and 75% FKD: $16.2 \pm 4.2\%$, $10.5 \pm 3.0\%$ and $6.0 \pm 2.1\%$, respectively) at 75, 50 and 25% FKD (ANOVA: all $P < 0.001$). In addition, FPT analyses indicated that the individuals from the two sub-colonies foraged at significantly different longitudes (hence distinct ARS

zones) during short trips (sub-colony A: $-30.8 \pm 0.4^\circ\text{W}$, $n = 143$; sub-colony B: $-31.0 \pm 0.4^\circ\text{W}$, $n = 142$; $F_{1,40} = 6.5$, $P = 0.015$), while no differences were found in latitude (sub-colony A: $39.8 \pm 0.4^\circ\text{N}$, $n = 143$; sub-colony B: $39.8 \pm 0.4^\circ\text{N}$, $n = 142$; $F_{1,40} = 0.0$, $P = 0.91$). On the other hand, neither spatial nor foraging segregation were detected during long trips; the overlap among individuals within each sub-colony (75, 50 and 25% FKD: $10.6 \pm 4.3\%$, $4.3 \pm 2.3\%$ and $0.7 \pm 0.6\%$, respectively) did not differ significantly with the overlap among individuals between the two sub-colonies (75, 50 and 25% FKD: $11.2 \pm 5.0\%$, $4.6 \pm 2.5\%$ and $0.7 \pm 0.6\%$) at 75, 50 and 25% FKD (ANOVA: all $P > 0.05$); moreover, no significant differences were found in the ARS zones (latitude and longitude) determined by FPT analyses during long trips (ANOVA: all $P > 0.05$). No spatial segregation was detected between males and females within each sub-colony during either short or long trips (ANOVA: all $P > 0.05$). Overall, the spatial segregation was high in short trips, where birds largely foraged on their respective sides of Corvo (sub-colony A, east side; sub-colony B, west side), in contrast to long trips where spatial segregation was not detected (Fig. 9). Furthermore, we found that birds from the two sub-colonies travelled in different directions to forage during short trips (Fig. 10); the bearing from the colony to the most distant location recorded differed significantly between both sub-colonies (sub-colony A: mean 84.4° (circular variance = 38.0°); sub-colony B: mean 251.2° (circular variance = 52.5°); Watson-William test: $F_{1,40} = 8.5$, $P = 0.006$), suggesting a difference in colony-specific foraging areas between breeding sites during short trips. Conversely, no significant differences were found in the direction of long trips (sub-colony A: mean 16.1° (circular variance = 16.7°); sub-colony B: mean 4.2° (circular variance = 16.5°); Watson-William test: $F_{1,30} = 0.5$, $P = 0.50$; Fig. 10).

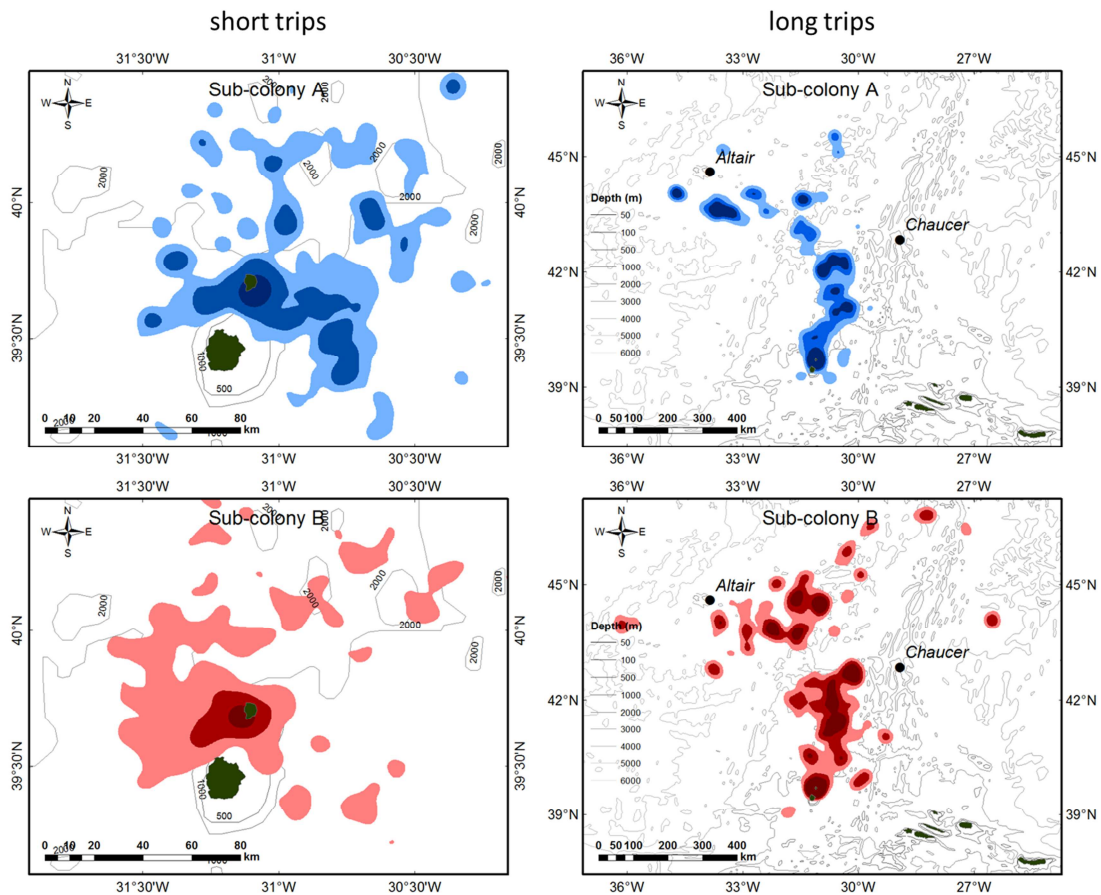


Figure 9. Spatial distribution of Cory's shearwaters *Calonectris diomedea* breeding in two sub-colonies of Corvo Island during the chick-rearing period (sub-colony A: upper panel; sub-colony B: lower panel) in long (≥ 2 days) and short ($= 1$ day) foraging trips. Dark, medium and light shades represent 25, 50 and 75% kernel utilization, respectively, i.e., the areas where the birds spent most of their foraging time.

Differences were also found in the foraging areas during short trips, where birds from sub-colony A apparently foraged over larger areas than those from sub-colony B at 50% FKD (sub-colony A: $61 \pm 32 \text{ km}^2$, $n = 156$; sub-colony B: $53 \pm 25 \text{ km}^2$, $n = 149$; $F_{1,40} = 5.1$, $P = 0.031$) and 25% FKD (sub-colony A: $23 \pm 14 \text{ km}^2$, $n = 156$; sub-colony B: $19 \pm 8 \text{ km}^2$, $n = 149$; $F_{1,40} = 7.8$, $P = 0.009$), but not at 75% FKD (sub-colony A: $158 \pm 63 \text{ km}^2$, $n = 156$; sub-colony B: $153 \pm 204 \text{ km}^2$, $n = 149$; $F_{1,40} = 0.1$, $P = 0.72$). On the other hand, no differences were detected at 75, 50 and 25% FKD between sub-colonies in the foraging areas during long trips (ANOVA: all $P > 0.05$), and between males and females during both short and long foraging trips (ANOVA: all $P > 0.05$).

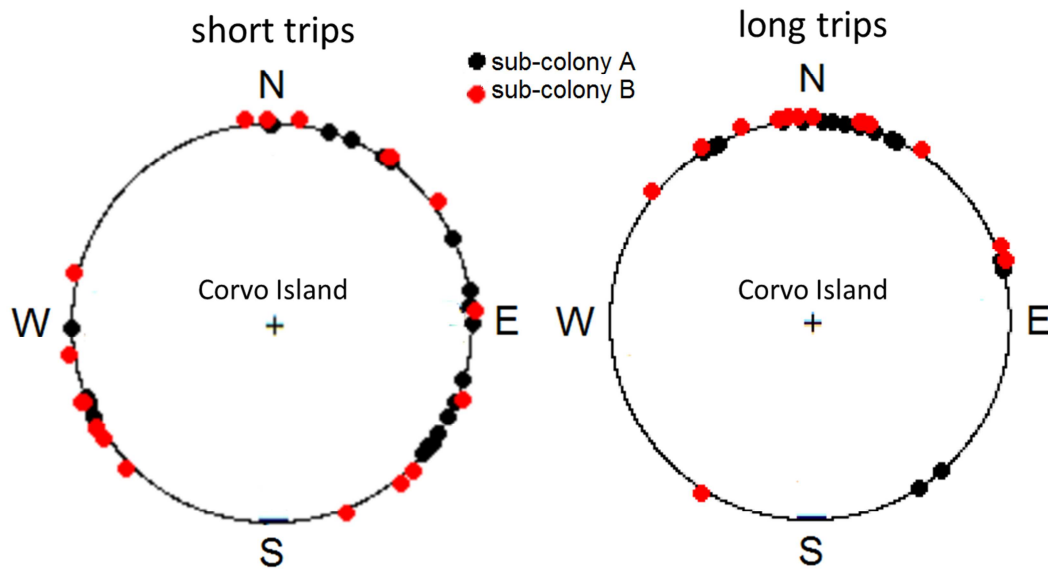


Figure 10. Bearing showing the direction from the breeding site to the most distant location recorded of Cory's shearwaters *Calonectris diomedea* breeding in two sub-colonies of Corvo Island and tracked during the chick-rearing period for long and short foraging trips.

Oceanographic habitat

FKD (75, 50 and 25%) showed that oceanographic parameters (SST, Chl *a* and bathymetry) diverged significantly between the areas visited by the individuals of the two sub-colonies during short trips (ANOVA: all $P < 0.05$; Fig. 11). Overall, birds from sub-colony B utilised shallower and warmer areas with greater Chl *a* during short trips. Interestingly, there were no significant differences in the oceanographic parameters at ARS zones estimated by FPT analyses (ANOVA: all $P > 0.05$) during short trips, suggesting that although individuals from the two sub-colonies passed through areas with different oceanographic conditions they foraged in patches of similar habitat. No differences were found in oceanographic parameters estimated by FKD (75, 50 and 25%) between sub-colonies during long trips (ANOVA: all $P > 0.05$). However, FPT analyses indicated that birds from sub-colony B foraged in areas with greater Chl *a* than those from sub-colony A (sub-colony A: $0.129 \pm 0.054 \text{ mg/m}^3$, $n = 34$; sub-colony B: $0.167 \pm 0.064 \text{ mg/m}^3$, $n = 24$; $F_{1,30} = 5.6$; $P = 0.031$, Fig. 11) during long trips. There were no significant between-sex differences in the oceanographic conditions experienced during either short or long trips, estimated by FKD (75, 50 and 25%) and FPT analyses (ANOVA: all $P > 0.05$).

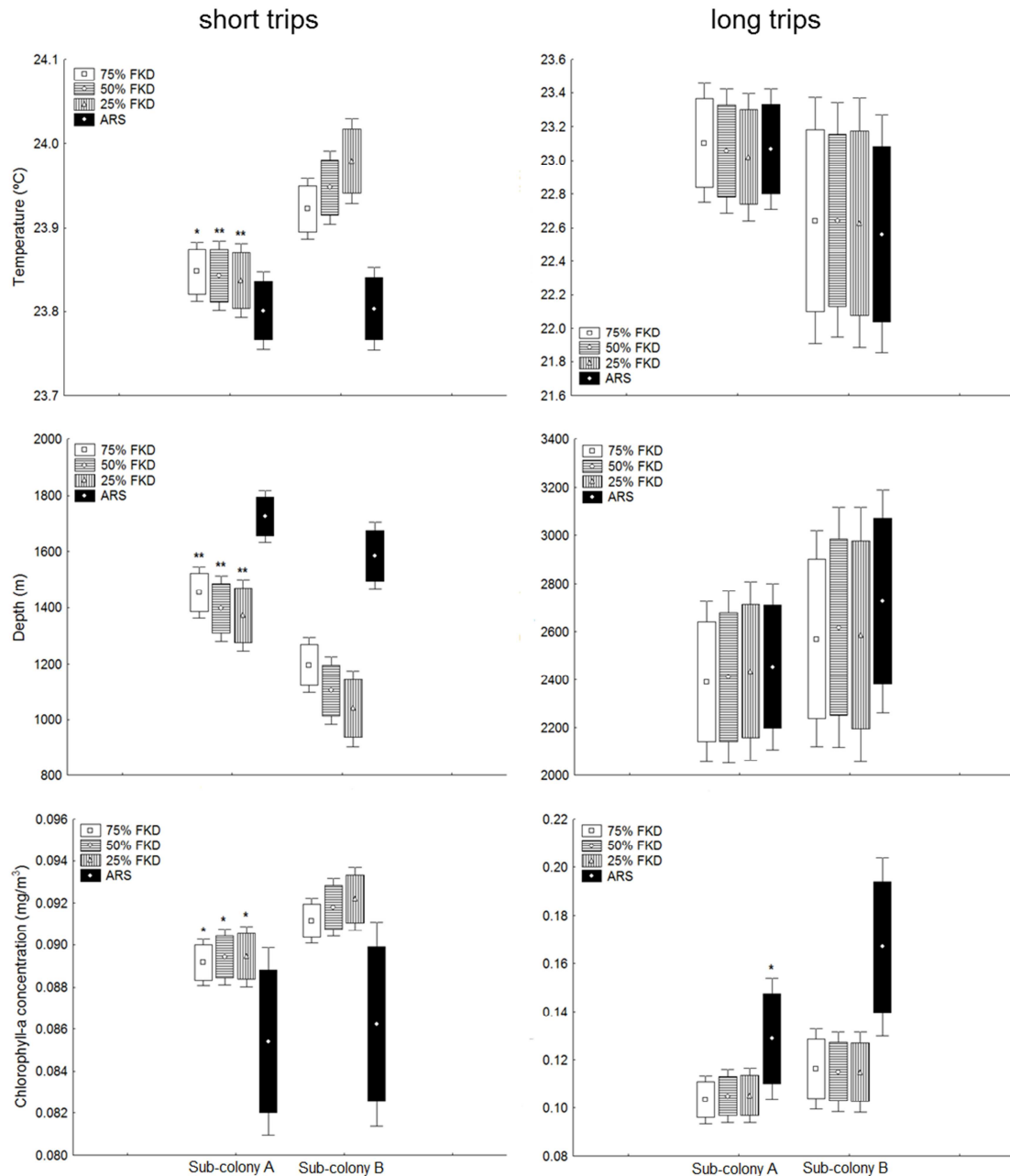


Figure 11. Differences between sub-colonies (A and B) of Cory's shearwaters *Calonectris diomedea* breeding in Corvo Island for the oceanographic conditions (SST, Chl *a* concentration and bathymetry) of foraging areas during the chick-rearing period in short and long foraging trips, calculated using 25, 50 and 75% fixed kernel density (FKD) and zones of area-restricted search (ARS). Points represent means, bars and lines represent ± 0.95 and ± 0.99 confidence intervals, respectively. Significant differences between the sub-colonies are presented with * ($P < 0.05$) and ** ($P < 0.01$).

Diet and stable isotope analysis

Complete or partial diet samples were obtained by stomach irrigation from 18 birds. These mainly comprised fish (98.5% by mass and 90.7% by numerical frequency) and a small amount of cephalopods (1.5% by mass and 9.3% by numerical frequency). No

significant differences were found between sub-colonies or sexes in the mass proportion or numerical frequency of each of these components (Mann-Whitney U Test: all $P > 0.05$). The three prey species identified in regurgitates collected from Cory's shearwaters were boarfish *Capros aper*, blue jack mackerel *Trachurus picturatus* and cock-eyed squid *Histioteuthis* sp..

Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were greater in the cephalopod species *Histioteuthis* sp. followed by the two fish species, *T. picturatus* and *C. aper*, respectively. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in the plasma and RBC from 43 individual Cory's shearwaters were greater than in their prey (Fig. 12). The mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of Cory's shearwaters plasma did not differ significantly between sub-colonies, sex and sub-colony*sex (factorial ANOVA: all $P > 0.05$). However, there were significant differences between sub-colonies in $\delta^{13}\text{C}$, but not in $\delta^{15}\text{N}$ for RBC ($\delta^{13}\text{C}$: $F_{1,39} = 5.0$, $P = 0.032$; $\delta^{15}\text{N}$: $F_{1,39} = 1.9$, $P = 0.174$); birds from sub-colony B showed enrichment in $\delta^{13}\text{C}$, suggesting some segregation of foraging habitat during the incubation period. There were also significant differences between males and females in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for RBC ($\delta^{13}\text{C}$: $F_{1,39} = 4.2$, $P = 0.042$; $\delta^{15}\text{N}$: $F_{1,39} = 7.1$, $P = 0.011$); females showed enrichment in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ which suggests some sexual segregation in isotopic niche. No sub-colony*sex interaction was found in either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ for RBC.

The SIAR mixing model based on plasma, RBC and prey isotope values indicated that *C. aper* was the largest component in the diet of Cory's shearwaters during the chick-rearing and the incubation periods (40.3 and 41.9%, respectively) followed by *T. picturatus* (31.7 and 31.1%, respectively) and *Histioteuthis* sp. (28.0 and 27.0%, respectively). No significant differences were found in the proportions of the three prey items in the diet of Cory's shearwaters estimated by the model based in plasma isotope values (hence representing the chick-rearing period) between sub-colonies, sexes and sub-colony*sex (factorial ANOVA: all $P > 0.05$). Moreover, there were no significant differences in the proportions of the three prey items in the diet estimated by the model based in RBC isotope values (which reflect the incubation period) between sub-colonies ($F_{2,38} = 1.9$, $P = 0.166$), and sub-colony*sex ($F_{2,38} = 2.1$, $P = 0.140$). However, significant differences were found in the proportions based in RBC isotope values between males and females for all prey items combined ($F_{2,38} = 4.3$, $P = 0.020$) or

independently (factorial ANOVA: all $P < 0.01$); females ingested more *T. picturatus* and *Histioteuthis* sp., and less *C. aper* than males.

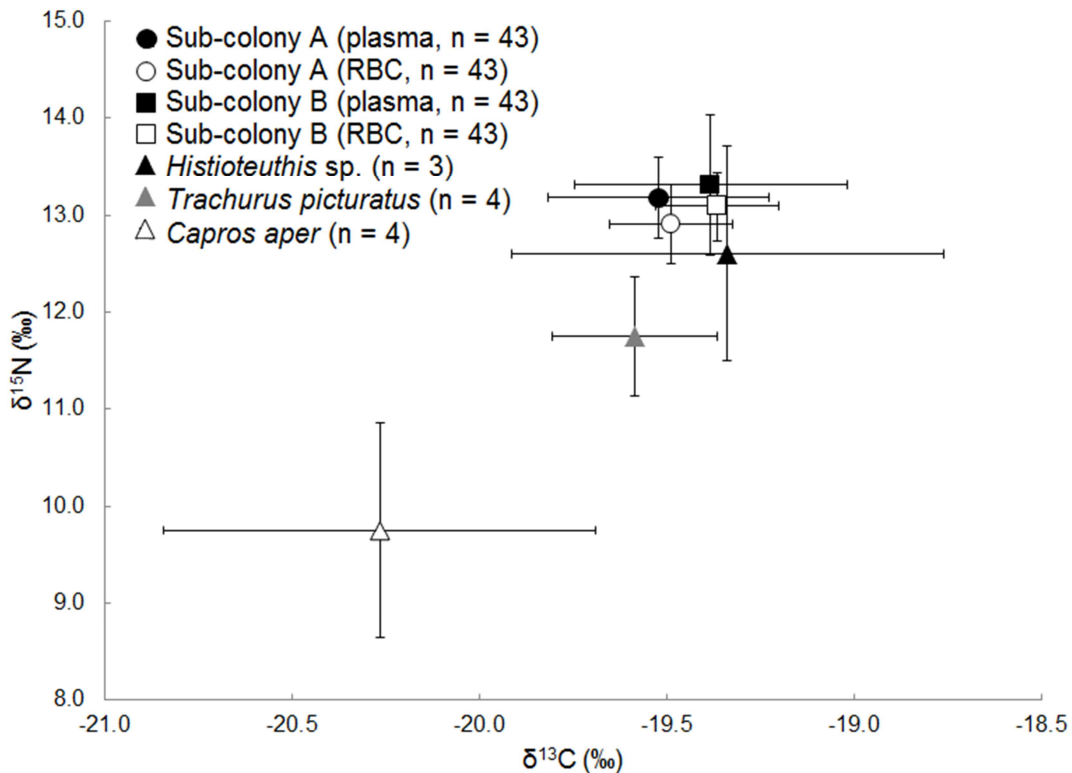


Figure 12. Stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) (means \pm SD) in plasma and red blood cells (RBC) of Cory's shearwaters *Calonectris diomedea* breeding in Corvo Island during the chick-rearing period, and prey species recorded in regurgitates.

Body mass index, condition status and breeding success

No significant differences were found in BMI between the individuals from the two sub-colonies ($F_{1,37} = 3.5$, $P = 0.068$) and there was no interaction of sub-colony*sex ($F_{1,37} = 1.5$, $P = 0.222$). However, males showed significantly greater BMI than females ($F_{1,37} = 8.4$, $P = 0.006$). There was no effect of sub-colony ($F_{1,39} = 1.5$, $P = 0.221$), sex ($F_{1,39} = 3.2$, $P = 0.080$) and no interaction of sub-colony*sex ($F_{1,39} = 0.4$, $P = 0.543$) on the haematocrit variation.

Breeding parameters of tracked birds did not differ significantly between the two sub-colonies at Corvo Island (Table 6). No significant differences were found in laying and hatching dates ($Z = 0.5$, $P = 0.60$; $Z = -1.3$, $P = 0.19$, respectively), although chicks from sub-colony A hatched on average two days before those from sub-colony B. The

linear chick growth rate did not differ between the two sub-colonies ($T = -0.5$, $P = 0.60$; Table 6).

Table 6. Breeding parameters of Cory’s shearwaters *Calonectris diomedea* in the two studied sub-colonies from Corvo Island during the breeding period of 2010. Sample size, corresponding to the nests of GPS logged individuals, is shown in parenthesis.

	Sub-colony A	Sub-colony B
Laying date	1 Jun \pm 4.6 d (12)	1 Jun \pm 6.8 d (10)
Hatching date	22 Jul \pm 3.7 d (13)	24 Jul \pm 4.4 d (10)
Fledging success (%)	71.4 (14)	80.0 (10)
Chick growth (g day ⁻¹)	20.4 \pm 3.4 (14)	21.3 \pm 5.2 (10)

Discussion

We used Cory’s shearwater as a model wide-ranging higher predator to compare foraging distribution and trophic ecology between two sub-colonies during the breeding season on a North Atlantic island. The studied sub-colonies are much closer to each other (2 km) than the mean foraging range of the species (in this study 62 and 347 km for short and long foraging trips, respectively). We therefore expected a large overlap in foraging areas and in feeding ecology. Although no differences were found during long trips, our results show a marked spatial foraging segregation among birds from the two sub-colonies for short trips during the chick-rearing period. We found that geographic breeding location influenced the travelling direction of birds during short foraging trips resulting in colony-specific foraging areas, probably in an attempt to reduce intra-specific competition as predicted by Cairns (1989). Although differences were found in the habitat visited by birds from both sub-colonies during short trips, no differences were found in the habitat exploited, suggesting that birds were feeding in patches of similar habitat. Consequently, no apparent differences were detected in the feeding ecology of birds during the chick-rearing period, but we observed differences in $\delta^{13}\text{C}$ of RBC indicating a potential dietary segregation during the incubation period. However, these differences apparently had no effect on the breeding success and on the health condition status of birds from both sub-colonies. Some sex-related differences were also found, mainly in regards to the feeding ecology.

Although birds from Corvo typically use a dual foraging strategy, the prevalent unimodal foraging strategy during the present study contrasted with the bimodal strategy observed for this population during the chick-rearing period in 2004 and 2007 (Magalhães et al. 2008, Paiva, Geraldés, Ramírez, Meirinho, et al. 2010a). As many other seabird species, Cory's shearwaters use a dual foraging strategy when local resources are poor such as oceanic environments (but see Phillips et al. 2009), although they increase the number of short trips during the early chick-rearing period. Unimodal or bimodal distributions in the length and duration of the foraging trips may be determined by distance from the breeding colony to productive areas (Granadeiro et al. 1998, Navarro & González-Solís 2009, Paiva, Geraldés, Ramírez, Garthe, et al. 2010), but an unimodal strategy may also reflect a higher diversity of foraging areas available in waters surrounding the colony simply because of prey patchiness (Phillips, Wakefield, et al. 2009). Thus, the unimodal strategy observed suggests that the 2010 chick-rearing period was a profitable year to rely on local food resources at Corvo. Moreover, growth rates of chicks during this study (mean 20.8 g day⁻¹) were greater than those previously recorded in Corvo during the early chick-rearing period (14.2 g day⁻¹; Magalhães et al. 2008).

Kernel and FPT analyses showed that birds from both sub-colonies clearly selected distinct areas to forage during short trips, but not during long trips. This was somehow expected because if segregation arises due to density-dependent competition as predicted by Cairns (1989), spatial segregation would be more likely close to the colonies (i.e. at a smaller scale) than further afield (i.e. at a larger scale). Recently, some studies demonstrated partial or complete segregation in foraging ecology for seabird apex predator species, such as black-browed albatrosses *Thalassarche melanophris* (Huin 2002, Granadeiro et al. 2011), cape gannets *Morus capensis* (Grémillet et al. 2004), hawaiian petrels *Pterodroma sandwichensis* (Wiley et al. 2012) and streaked shearwaters *Calonectris leucomelas* (Yamamoto et al. 2011). However, the potential overlap in foraging areas of such studies is small, particularly during short trips, because the colonies are separated by tens or hundreds of kilometres. Consequently, there would be little gain for birds to travel further and forage in areas already occupied by a more efficient group of conspecifics from closer colonies (Huin 2002). Navarro et al. (2009) detected partial foraging segregation between the two subspecies of Cory's shearwater, *C. d. diomedea* and *C. d. borealis* sympatrically breeding in a Mediterranean colony

(however see Gómez-Díaz et al. 2009). To our knowledge, only Wanless and Harris (1993) and Masello et al. (2010) addressed our main question and, in accordance to Cairns (1989) prediction, found partial and/or complete spatial segregation in birds from very close colonies (only 2 – 2.5 km apart). However, these authors studied Blue-eyed Shags (Wanless & Harris 1993) and three different penguin species (Masello et al. 2010), which are species potentially more limited in foraging range than Cory's shearwaters. Wanless and Harris (1993) attributed inter-colony differences in foraging and diet during the breeding season to highly localized differences in feeding conditions, given the extremely limited foraging range of most individuals (ca. 1 km from the colony). On the other hand, Masello et al. (2010) attributed foraging segregation to intra-specific competition, but also to an effort to reduce predation risk by fur seals *Arctocephalus australis* that were present in the island. Our observations that birds from the two colonies travelled in different directions to forage during short trips suggest colony-specific foraging areas determined by breeding locations. However, this was not verified during longer trips, as no significant differences were found in the direction of foraging trips adopted by birds from both sub-colonies. According to Robson et al. (2004), a simple explanation for the directional persistence within breeding sites might be that individuals constantly initiate a foraging trip on a bearing consistent with the general orientation of the site. Although Robson et al. (2004) studied fur seals *Callorhinus ursinus*, our results corroborated this hypothesis in a wide-ranging seabird species during short foraging trips, despite the small area of Corvo Island and the low altitude of the two studied breeding sites. However, there are scattered birds breeding along the cliffs of Corvo Island, increasing density-dependent competition for food around the colony, which could increase spatial segregation during short foraging trips among individuals according to their geographic breeding location. Although the potential foraging areas fully overlapped, our results demonstrated that birds preferred adjacent areas to their own sub-colony rather than the neighbouring sub-colony during short trips resulting in colony-specific foraging areas, possibly in an attempt to reduce intra-specific competition as predicted by Cairns (1989).

The oceanographic habitat used by study birds was significantly different between birds from the two sub-colonies during short trips. Surprisingly, however, differences detected by kernel analysis (explored areas) were not detected by FPT analysis (ARS zones), which corresponds to an environment where the probability of prey capture

should be higher. Therefore, these results suggest that birds from both sub-colonies explored various wide areas for food but concentrated their feeding activity in small concentrated patches with similar oceanographic characteristics. Top predators appear to forage at locations that usually congregate potential prey due to specific physical processes, such as oceanographic fronts, currents, eddies, seamounts or upwelling zones (Bost et al. 2009), which ultimately could have similar characteristics, especially at a smaller scale where short trips occur (Wakefield et al. 2009). During long trips no differences were found either in the habitat of visited areas or ARS zones (although differences were found in Chl *a* at ARS zones). Cory's shearwaters exploited vast offshore environments, apparently within frontal and seamount areas (Paiva, Geraldes, Ramírez, Meirinho, et al. 2010a), but constantly headed north on their long foraging trips. This pattern seems to show little inter-annual variation, as it was also reported by other studies in 2004 and 2007 for the same island (Magalhães et al. 2008, Paiva, Geraldes, Ramírez, Meirinho, et al. 2010b).

No differences were detected in the diet and stable isotopes ratios of plasma between the two sub-colonies. These results therefore corroborated the lack of differences in the exploited habitat type at ARS zones during both short and long foraging trips. On the other hand, differences in $\delta^{13}\text{C}$ between sub-colonies were found in RBC, suggesting a potential segregation of foraging habitats during the incubation period. Interestingly, the apparent lower energy requirement during the incubation period suggests that this should be the period with a minimal potential for interference competition, in opposition to the early chick-rearing period. Differences were also detected in feeding ecology between males and females during the incubation period. Females showed enrichment in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and ingested significantly more *T. picturatus* and *Histioteuthis* sp. and less *C. aper* (estimated by SIAR) than males. Preference by prey from a higher trophic level during incubation may be related with specific nutrient requirements to compensate egg-laying that could potentially create temporary sex differences in feeding ecology (Lewis et al. 2002, Phillips et al. 2004) and might not be driven by intra-specific competition.

We found no evidence that foraging segregation between birds from both sub-colonies affected BMI, health condition status of individual birds, breeding success and chick growth. Shearwaters present a fixed investment, and adults may increase foraging effort and/or reduce parental investment at the expense of chick condition to maintain their body condition (Navarro & González-Solís 2007). In a food shortage scenario,

differences in foraging segregation and higher intra-specific competition for food could potentially lead to differences in the breeding success between birds from the two sub-colonies.

In summary, we observed that Cory's shearwaters breeding in very close sub-colonies in Corvo showed a high spatial foraging segregation during the chick-rearing period for short trips, but not for long excursions; and no differences were found between males and females. Interestingly, our results suggest that birds from both sub-colonies visited areas with different oceanographic conditions during short trips, but concentrated their feeding activity in patches of similar habitat. Consequently, individuals from both sub-colonies did not display dietary segregation during the early chick-rearing period. However, our results suggest a potential segregation of foraging habitats between sub-colonies during the incubation period, but further studies should be conducted to validate this hypothesis.

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Chapter 3

Relationships among spatial distribution at sea, trophic niche width and consistency in the foraging niche of a pelagic seabird species

Filipe R. Ceia, Vitor H. Paiva, Stefan Garthe, João C. Marques & Jaime A. Ramos



Abstract

The Van Valen (1965) ‘niche variation hypothesis’ postulates that populations with wider niches are more variable than populations with narrower niches. We determine whether variations in foraging spatial distribution at sea, trophic niche and consistency in foraging niche of a pelagic seabird species are associated in order to test this hypothesis and identify patterns of consistency in the foraging niche. The extent of such relationships was assessed using a wide-ranging apex predator, the Cory’s shearwaters *Calonectris diomedea*, as a model marine species, along a three year study (2010-2012), during both the pre-laying and chick-rearing periods. We used individual movement data and stable isotope data, analysed using recent metrics based in a Bayesian framework, of 69 adults breeding on a small neritic island in the North Atlantic. Results confirm that trophic niche expansion arise via increased variation in spatial distribution at sea among individuals, providing support for ‘niche variation hypothesis’ in the context of foraging ecology. Moreover, we found that short-term consistency in the foraging niche was higher and persistent during periods when the population showed an intermediate trophic niche width, and absent when trophic niche was both extremely small and extremely large. These results suggest that foraging consistency is an important characteristic of this population and potentially of pelagic seabirds in general, and should be important to understand the dynamics of foraging ecology and may reduce intra-specific competition during periods with typical average availability in food resources.

Key-words: foraging ecology, GPS tracking, individual specialization, niche variation, stable isotopes

Introduction

The ecological niche of a population is a fundamental concept in ecology, but there are many niche concepts, each of which emphasizes a different aspect of a species’ ecological characteristics (see Newsome et al. 2007 for a review). Concurrently, foraging niche of a population is still poorly understudied, particularly concerning pelagic seabirds. Classical tools (e.g. conventional dietary analyses and census at sea) have been widely used to describe the ecological niche of pelagic seabirds but an

accurate assessment of spatial distribution at sea and foraging ecology of seabirds only recently was possible through the use of recent technology such as tracking devices and stable isotope analyses (SIA). According to the ‘niche variation hypothesis’ (Van Valen 1965) populations with wider niches are more variable than populations with narrower niches. Some studies focusing on morphology or size have failed to support the above theory because they did not find any positive correlation between intra-specific trait variation and population niche width (e.g. Soulé and Stewart 1970; Meiri et al. 2005). However, focusing on foraging ecology, there is a repeated tendency for more generalist populations to exhibit higher niche variation than more specialized populations due to a higher degree of diet variation (Bolnick et al. 2007). Moreover, diet variation within a single population can arise via foraging plasticity among its individuals, resulting in resource use diversity (Svanbäck & Bolnick 2007). Therefore, in accordance with the classic ‘niche variation hypothesis’ we should expect that a higher variation in the foraging spatial distribution among individuals from the same population would lead to a wider trophic niche of such population. This assumption must be validated and to our knowledge no studies have shown relationships between the areas explored by seabird populations and trophic niche width in the marine environment. Recent studies demonstrated relationships between geographic locations and stable isotope signatures for marine predators (e.g. Cherel and Hobson 2007, Phillips et al. 2009, Jaeger et al. 2010), thus we expect to evaluate whether this assumption is true. Moreover, foraging strategies of individual birds can differ substantially and individuals of the same species may use different resources, resulting in the exploitation of different niches, which could be consistent over time (see Bolnick et al. 2003 for a review). Accordingly, there has been a recent increase in studies of individual consistency in the foraging niche within populations (e.g. Bearhop et al. 2006; Votier et al. 2010), suggesting that some individuals have a narrow foraging niche, helping to reduce intra-specific competition (Svanbäck & Bolnick 2007, Matich et al. 2010, Ceia et al. 2012). However, to our knowledge inter-annual and seasonal variation in the consistency of foraging niche was not previously evaluated, and mechanisms that could drive such trait are not well understood.

During the breeding season, Cory’s shearwaters *Calonectris diomedea borealis* are central-place foragers capable of traveling distances up to 5500 km (Magalhães et al. 2008) in a single foraging trip. Such long trips, however, are more expected in oceanic

(i.e. lower productive regions) than in neritic (i.e. higher productive regions) areas, because of prey patchiness and prey distribution along the neritic-oceanic marine productivity gradient (Paiva, Geraldes, Ramírez, Meirinho, et al. 2010a). Similarly, longer trips are relatively more frequent during the early stages of the breeding season, pre-laying and incubation periods, than during later stages, the chick-rearing period, when birds must forage within a shorter range in order to provide food for their chicks (Paiva, Geraldes, Ramírez, Meirinho, et al. 2010a). Given their wide range in foraging patterns according to the breeding stage, prey abundances and oceanographic conditions (Paiva et al. 2013), Cory's shearwaters are a good model species to study spatial variations at sea and their relationships with trophic niche width. Moreover, Cory's shearwaters are pelagic species feeding mainly on fish and cephalopods (Xavier et al. 2011, Neves et al. 2012), which enable to evaluate variation in feeding ecology of individual birds according to spatial or temporal changes in the abundance of these main food sources (Rutz & Bijlsma 2006, Neves et al. 2012), and, consequently, investigate variation on consistency in the foraging niche within and among individuals.

In this study, we used individual movement data (GPS tracking) and isotopic signature ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) from blood of Cory's shearwaters, separated in plasma and cells, to detect spatio-temporal variations in the foraging niche of individuals among years and between periods with markedly different foraging patterns. We test for relationships among spatial distribution at sea, trophic niche width and short-term consistency in the foraging niche along three years (2010-2012), during both the pre-laying and chick-rearing periods, thus totalizing six sampling periods. Specifically, we hypothesized that variability in the foraging ecology within a population of a pelagic marine species drive (1) spatial distribution at sea, (2) trophic niche width, and (3) short-term consistency in the foraging niche of individuals. Our goal was to measure differences and patterns associated with foraging ecology and population dynamics to determine whether variations in spatial distribution at sea, trophic niche and short-term consistency in foraging niche are associated.

Materials and methods

Fieldwork was conducted in Berlenga Island, Portugal (39°24'N, 009°30'W), during the pre-laying (April-May) and chick-rearing (August-September) periods of Cory's shearwaters along 2010, 2011 and 2012. A population of about 800 breeding pairs of

Cory's shearwaters is estimated to breed in Berlenga Island (Lecoq et al. 2011), a small neritic island with ca. 78.8 ha and 11 km in the western coast of Portugal. This island is situated within a large continental shelf characterized by shallow waters and high marine productivity due to the coastal upwelling that lasts from April to September (Sousa et al. 2008).

Sample collection

A total of 69 breeding adults were sampled along 2010, 2011 and 2012 (pre-laying period: 10, 8 and 12, respectively; chick-rearing period: 19, 11 and 9, respectively). A GPS logger was deployed on each bird and removed after 1 to 18 foraging trips at sea (details of the devices below). In order to examine the relationship between foraging trips and trophic ecology, blood samples (~0.5-1 ml from the tarsal vein) were collected from each bird on recapture (and on capture and recapture during the 2010 chick-rearing period) and, within 2-3 h, separated into plasma and red blood cells (RBC) using a centrifuge (15 min at 3000 rpm). Hematocrit was recorded as the proportion of RBC in total blood volume and samples were then stored frozen until preparation for SIA. Captured birds were ringed, wing and tarsus length were measured, and weighed both on capture and recapture. In addition, a total of 65 nests including the nests of all sampled birds were monitored twice, in May and late September, to determine laying and fledging success, respectively. Deployment or retrieval of devices and collection of samples took 10-15 min and birds were returned immediately to their nest.

Tracking data collection

Each individual bird was fitted with a GPS logger (CatTraq GT-120, Perthold Engineering LLC). The plastic case was removed and replaced by a 7 cm long thermo-retractile rubber sleeve reducing the total weight to 17 g. This corresponded to 1.7-2.6% of studied individuals' mass, which is below the recommended 3% threshold reported to have no deleterious effects on seabird species during short-term (Phillips et al. 2003; but see Vandenabeele et al. 2012), including Cory's shearwaters (Igual et al. 2005). The GPS loggers were attached to feathers in the mantle region with Tesa[®] tape and set to record position (median error of < 10m) every 5 min. Birds were tracked continuously from 1 to 19 days (10.3 ± 4.7 days).

Stable isotope analyses (SIA)

Stable isotope analyses of carbon and nitrogen were performed to estimate and compare trophic niche width among years and between periods (Bearhop et al. 2004, Newsome et al. 2007, Jackson et al. 2011). Carbon stable isotope value ($\delta^{13}\text{C}$) mainly reflects the foraging habitat of consumers, while nitrogen stable isotope value ($\delta^{15}\text{N}$) is mainly used to define trophic position of consumers. Plasma and RBC retain information on diet from a few days prior to sample collection (hence plasma reflects choices made during tracking), up to the previous 3-4 weeks, respectively. Because of the differing turnover rates of plasma and RBC we were able to investigate the effect of short-term consistency in the foraging ecology (Votier et al. 2010, Ceia et al. 2012). We analysed $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) in plasma and RBC from each breeding adult sampled and tracked. For specifications how the samples were prepared for SIA and nitrogen and carbon isotope ratios were determined see Chapter 2.

Breeding success and bird condition status

We determined laying success (number of eggs laid / number of nests) and breeding success (number of fledged birds / number of eggs laid) of Cory's shearwaters, as it should be a good proxy of breeding conditions among years including the accessibility of main food resources. The standard residuals of the relationship between body mass (mean between capture and recapture) and tarsus length ($F_{1,67} = 104.1$, $P < 0.001$, $r = 0.598$) were used to estimate the body mass index (BMI) of all sampled birds, an index primarily reflecting body lipid reserves (Sánchez-Guzmán et al. 2004), to evaluate whether breeding adults were in a similar health state. In addition, the haematocrit was calculated, which in conjunction with other physiological indicators such as body mass index, can be a useful indicator of the current health condition status of the individuals (see Fair et al. 2007 for a review).

Data analysis

GPS data were separated into individual foraging trips by calculating the time from when the birds departed the colony until their return. GPS locations at the colony were excluded from analyses. Then, the relocations (between consecutive tracking points) were filtered on running flight speed; according with Louzao et al. (2009) we only used GPS relocations which exclusively represented the areas where Cory's shearwaters were

searching for food (10 – 15 km h⁻¹) and active feeding (2 - 10 km h⁻¹). Finally, a distance-to-colony filter of 2 km was applied, to remove relocations while flying over the colony before landing.

The nonparametric fixed kernel density (FKD) estimator was used to calculate the 25, 50 and 75% density contour areas (km²), of each bird using functions (“*kernelUD*”, “*getvolumeUD*”, “*getverticeshr*” and “*kernel.area*”) of the *adehabitat* package ($h = 0.18$, $grid = 500$; Calenge 2006) under R 2.15.2 (R Development Core Team 2011). The intra-specific overlap in the estimated foraging range among individuals within each period was assessed following Fieberg and Kochanny (2005). The 25, 50 and 75% FKD overlap were calculated for each bird using the function “*kerneloverlap*” of the *adehabitat* package ($meth = “VI”$; Calenge 2006) under R 2.15.2. We also determined the maximum distance from colony (km) and geographic position at maximum distance from the colony (latitude and longitude) of each bird to investigate the effect of latitude, longitude and foraging range on foraging niche.

To analyse stable isotope data in the context of isotopic niche (i.e. trophic niche) among the periods, we adopted the recent metrics based in a Bayesian framework that allows robust comparison to be made among data sets comprising different sample sizes (Stable Isotope Bayesian Ellipses in R: SIBER; Jackson et al. 2011; but see Syvaranta et al. 2013). The standard ellipse area corrected for small sample sizes (SEAc, an ellipse that has 95% probability of containing a subsequently sampled datum) was adopted to compare among years and between periods (see Jackson et al. 2011 for more details). We used the computational code to calculate the metrics from SIBER using functions (“*standard.ellipse*” and “*convexhull*”) implemented in the package SIAR (stable isotope analyses in R: SIAR; Parnell et al. 2010) under R 2.15.2.

All foraging variables and SIA results were compared among periods using a Kruskal-Wallis test. To test for homogeneity of variances in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, which provides a measure of trophic niche width (see Bearhop et al. 2004 for more details), we used a Levene’s Test. Similarly, a Levene’s Test was used to test for the assumption of equal variances in foraging variables as a measure of variation in foraging patterns. We only used individuals wherein we have collected the essential information (tracking data and SIA simultaneously) to achieve our goals focusing on the variability at individual level and not at the population level. Thus, although the relatively small sample size in each

sampling period could not provide reliable estimates of total home-range area and trophic niche width of the whole population in each period (see Syvaranta et al. 2013; Soanes et al. 2013), it should have a minor influence on the assessment of variability in trophic niche and spatial distribution at sea on the studied individuals in different periods (see Layman et al. 2007), and test whether they are associated.

To obtain an estimate of short-term (within about one month) consistency in carbon source and trophic level, we regressed stable isotope ratios in plasma on those in RBC (Votier et al. 2010, Ceia et al. 2012). Integration of prey isotopes into blood components is a continuous, dynamic process, and the analyses of short-term consistency were performed using the same blood sample, separated into plasma and RBC, which could lead to a temporal overlap in the synthesis of these tissues. To evaluate how the same blood sample could affect short-term consistency (i.e. due to possible high overlap) we collected samples in capture and recapture during the 2010 chick-rearing period and then we regressed stable isotope ratios in plasma from recapture on those in RBC from capture, in an attempt to reduce overlap between the two blood components. Because the results did not show apparent differences, we only took blood samples once at each period to reduce stress on birds. Based on these results we were able to compare short-term consistency in foraging niche (i.e. shifts in trophic level and carbon source) among periods and its relationship with foraging patterns at sea and trophic niche width.

All data were tested for normality and homoscedasticity; foraging area (25, 50 and 75 FKD) and maximum distance from the colony were \log_{10} transformed to assess relationships among the six studied periods, and proportions were arcsine transformed. When transformation did not normalize the data, non-parametric tests were used. Values are presented as means \pm SD.

Results

Spatial distribution at sea

From 2010 to 2012 we obtained a total of 394 foraging trips from 69 individuals. The longest trip recorded in terms of duration was 19 days during the 2012 pre-laying period and the farthest trip distanced 3236 km from the colony (trip length = 7135 km) during the 2011 pre-laying period (Fig. 13).

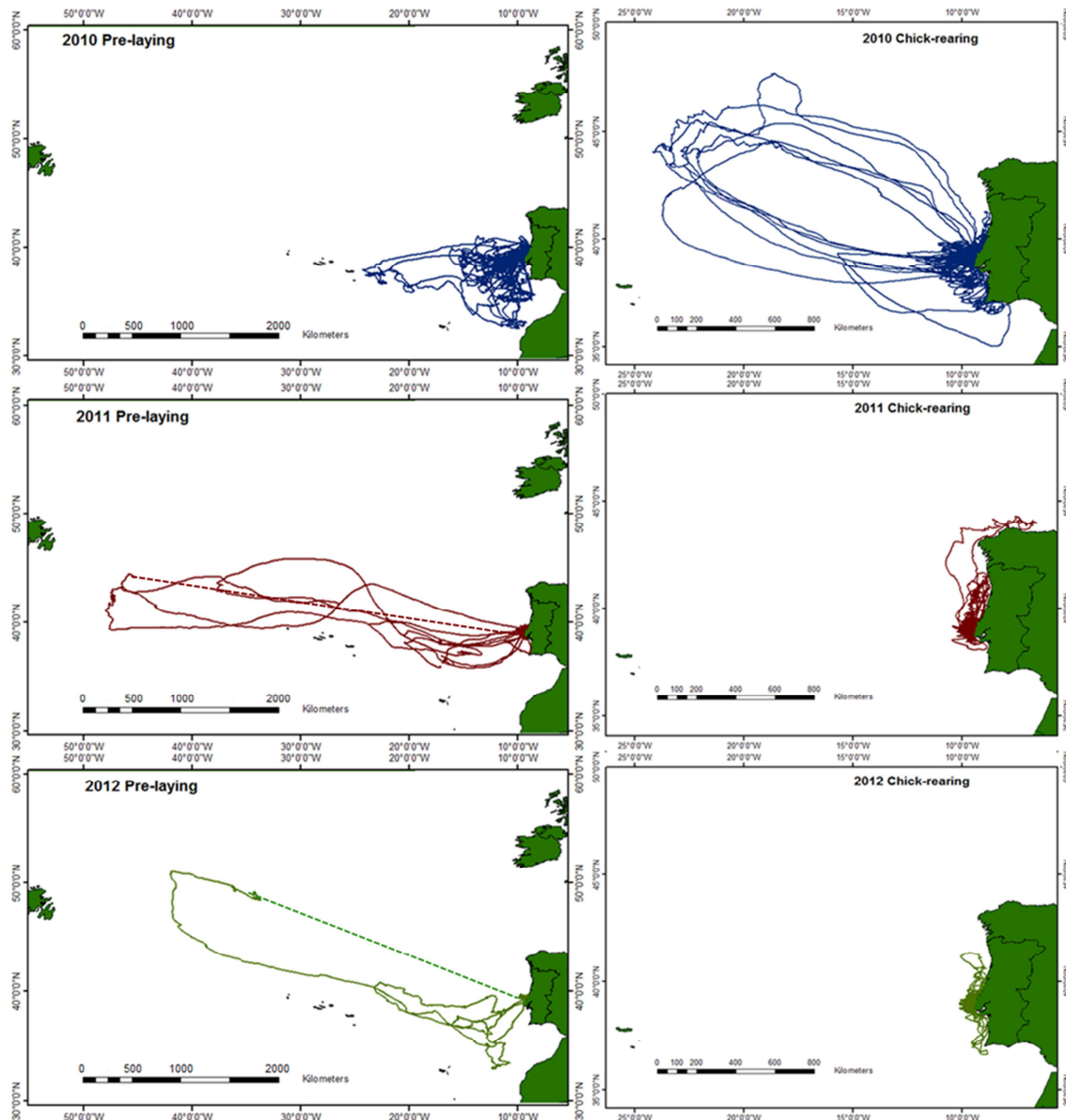


Figure 13. GPS locations showing spatial distribution during foraging trips of Cory's shearwaters (*Calonectris diomedea*) breeding in Berlenga Island during the pre-laying and chick-rearing periods in 2010, 2011 and 2012. The dashed lines connecting the mid-Atlantic Ocean to Berlenga represents part of long foraging trips that were lost due to battery loss.

Although birds explored a larger area (25, 50 and 75% FKD) during the pre-laying period than during the chick-rearing period in both 2011 and 2012 (Table 7), differences among all periods were only significant at 75% FKD (Kruskal-Wallis test: $H_{5,69} = 12.2$, $P = 0.033$). However, highly significant differences in the homogeneity of variance for areas explored among all periods at 25, 50 and 75% FKD (Levene's test: all $P < 0.01$) indicates wide range of variances in the foraging area among the six periods, with a particularly high variance for the 2011 pre-laying period (Table 7). Differences were also found in the overlap in the estimated foraging areas at 25, 50 and 75% FKD among

all periods (Kruskal-Wallis test: all $P < 0.01$); the overlap among birds within each period was greater during the chick-rearing than in the pre-laying period, especially in 2012. Overall, these differences were related with the type of habitat explored (i.e. neritic vs. oceanic), as revealed by highly significant differences in foraging trips at maximum distance from the colony among all periods in longitude, but not in latitude (Table 7).

Trophic niche width

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of Cory's shearwaters' plasma, which provides an indication of recent meals (i.e. during the tracking period), differed significantly among all periods (Kruskal-Wallis test: all $P < 0.01$; Table 8). However, we highlight that Cory's shearwaters exhibited substantial differences among all periods in the homogeneity of variances for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of plasma (Levene's Test: all $P < 0.001$), which provides a measure of trophic niche width (see Bearhop et al. 2004). A wide range of variances in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of plasma and RBC suggest a variable trophic niche width among periods. Specifically, SEAc index indicates a greater isotopic niche area during the 2011 pre-laying period and a lower isotopic niche area in the 2012 chick-rearing period (Fig. 14).

Overall, SIA results matched those of foraging parameters: along the six studied periods we found significant relationships between the trophic niche width and spatial distribution of birds; specifically, SEAc index based on plasma was positive correlated with 50% FKD area ($F_{1,4} = 21.9$, $P = 0.009$, $r^2 = 0.846$), 75% FKD area ($F_{1,4} = 20.6$, $P = 0.010$, $r^2 = 0.838$) and maximum distance from colony ($F_{1,4} = 25.7$, $P = 0.007$, $r^2 = 0.866$). Moreover, positive correlations were found between SEAc and 25, 50 and 75% FKD standard deviations (all $P < 0.05$) with relevance to 50% FKD ($F_{1,4} = 144.7$, $P < 0.001$, $r^2 = 0.973$, Fig. 15), indicating that a higher variation in the area explored among individuals led to trophic niche expansion of the population.

Table 7. Comparison of foraging parameters of Cory's shearwaters (*Calonectris diomedea*) breeding in Berlenga Island during the pre-laying and chick-rearing periods in 2010, 2011 and 2012. Values are means \pm SD. PL = Pre-laying period, CR = chick rearing period. Significant results are in bold.

h=0.18	2010		2011		2012		Kruskal-Wallis test		Levene's test	
	PL (n=10)	CR (n=19)	PL (n=8)	CR (n=11)	PL (n=12)	CR (n=9)	H _(5,69)	P	F _(5,63)	P
Mean 25% FKD (km ²)	2189 \pm 2275	2414 \pm 1450	2424 \pm 2136	1759 \pm 716	1914 \pm 2161	1379 \pm 685	7.4	0.19	3.6	0.007
Mean 50% FKD (km ²)	6331 \pm 6565	6898 \pm 4536	11062 \pm 10652	4650 \pm 1905	6031 \pm 7653	3981 \pm 2877	9.7	0.08	5.4	<0.001
Mean 75% FKD (km ²)	15830 \pm 16722	15724 \pm 11331	39882 \pm 46963	9898 \pm 4080	13433 \pm 18554	8708 \pm 6754	12.2	0.033	4.6	0.001
25% FKD overlap (%)	4.5 \pm 3.2	5.3 \pm 2.3	3.2 \pm 2.5	3.7 \pm 2.2	3.7 \pm 2.8	9.7 \pm 3.3	18.8	0.002	1.2	0.34
50% FKD overlap (%)	13.3 \pm 7.5	13.3 \pm 3.7	9.8 \pm 6.1	12.4 \pm 5.8	11.7 \pm 7.6	24.7 \pm 4.8	22.2	<0.001	3.5	0.008
75% FKD overlap (%)	22.2 \pm 11.5	22.2 \pm 5.2	15.5 \pm 9.0	26.2 \pm 10.5	22.0 \pm 13.3	41.8 \pm 6.3	27.2	<0.001	3.7	0.006
Mean max distance from colony (km)	341.4 \pm 380.7	455.9 \pm 478.8	1510.2 \pm 1233.7	202.4 \pm 136.0	423.2 \pm 836.4	147.2 \pm 86.2	16.0	0.007	10.2	<0.001
Latitude ($^{\circ}$ at max distance)	38.3 \pm 1.5	40.0 \pm 2.4	39.9 \pm 2.3	40.3 \pm 2.0	39.8 \pm 4.0	38.3 \pm 1.1	8.9	0.11	0.9	0.47
Longitude ($^{\circ}$ at max distance)	-12.4 \pm 4.6	-13.7 \pm 5.9	-26.8 \pm 15.3	-9.1 \pm 0.6	-13.6 \pm 9.7	-9.4 \pm 0.3	22.1	<0.001	10.8	<0.001

Table 8. Stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in plasma and red blood cells (RBC) of Cory's shearwaters (*Calonectris diomedea*) breeding in Berlenga Island during the pre-laying (PL) and chick-rearing (CR) periods in 2010, 2011 and 2012. The area of the standard ellipse (SEAc) and the layman metric of convex hull area (TA) are also shown (see Jackson et al. 2011 for more details on these metrics of isotopic niche width). Values are means \pm SD. Significant results are in bold.

	2010		2011		2012		Kruskal-Wallis test		Levene's test	
	PL (n=10)	CR (n=19)	PL (n=8)	CR (n=11)	PL (n=12)	CR (n=9)	$H_{(5,69)}$	P	$F_{(5,63)}$	P
Plasma										
$\delta^{13}\text{C}$ (‰)	-19.5 \pm 1.2	-18.1 \pm 0.6	-18.9 \pm 0.8	-18.2 \pm 0.3	-19.2 \pm 0.4	-18.4 \pm 0.2	30.3	<0.001	13.3	<0.001
$\delta^{15}\text{N}$ (‰)	13.8 \pm 0.8	13.4 \pm 0.6	13.6 \pm 1.4	14.3 \pm 0.4	13.6 \pm 1.1	12.8 \pm 0.2	17.3	0.004	8.1	<0.001
SEAc	1.37	0.85	2.34	0.26	1.50	0.12				
TA	1.95	2.25	3.44	0.41	2.57	0.20				
RBC										
$\delta^{13}\text{C}$ (‰)	-18.3 \pm 0.7	-18.8 \pm 0.5	-18.5 \pm 0.6	-18.5 \pm 0.2	-18.5 \pm 0.4	-18.6 \pm 0.2	5.7	0.34	5.3	<0.001
$\delta^{15}\text{N}$ (‰)	12.6 \pm 0.8	12.8 \pm 0.5	12.5 \pm 0.9	13.5 \pm 0.2	13.0 \pm 0.8	12.4 \pm 0.2	20.5	0.001	4.1	0.003
SEAc	1.11	0.46	1.48	0.13	0.71	0.16				
TA	1.88	0.46	2.25	0.26	1.59	0.23				

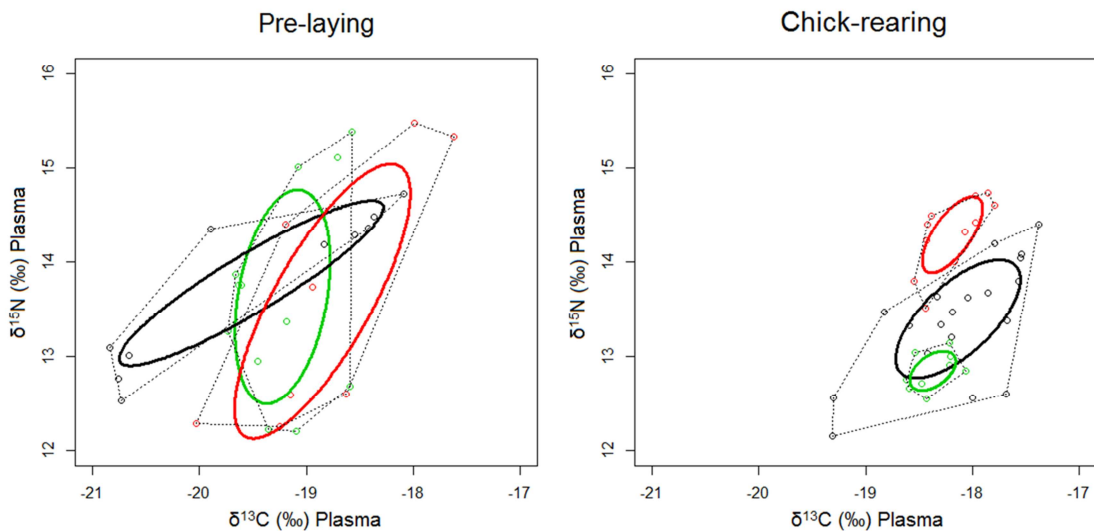


Figure 14. Isotopic niche area based on stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in plasma of Cory's shearwaters (*Calonectris diomedea*) breeding in Berlenga Island during the pre-laying and chick-rearing periods in 2010 (black), 2011 (red) and 2012 (green). The area of the standard ellipses (SEAc, 95% credible interval) were represented by the solid bold lines (ellipses) and the layman metric of convex hull area (TA) by black dotted lines (see Jackson et al. 2011 for more details on these metrics of isotopic niche width).

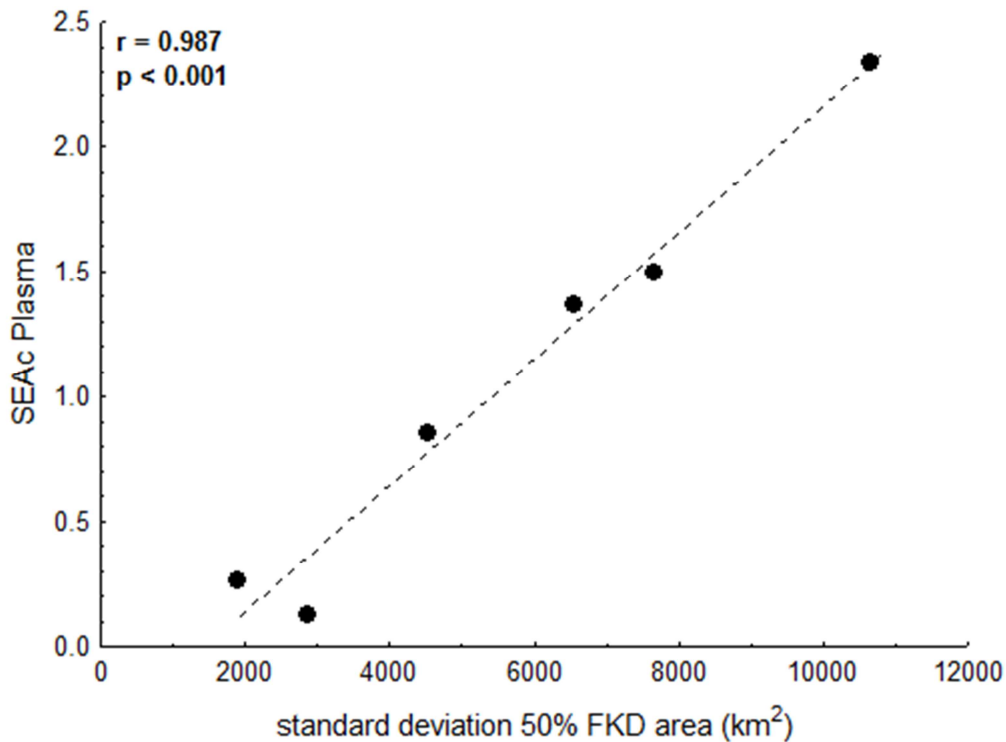


Figure 15. Relationship between 50% FKD (fixed kernel density, km²) standard deviation and area of the standard ellipse (SEAc) based on plasma for the six sampling periods of Cory's shearwaters (*Calonectris diomedea*) breeding in Berlenga Island.

Short-term consistency in the foraging niche

Dissimilar patterns in short-term consistency in the foraging niche of Cory's shearwaters were detected among years and between periods. Although, significant positive relationships were found in $\delta^{15}\text{N}$ and in $\delta^{13}\text{C}$ between RBC and plasma of individual adults during both the pre-laying and chick-rearing periods (Fig. 16), indicating short-term foraging consistency during specific periods where relationships were detected, some differences were detected among the six sampling periods. Specifically, significant positive relationships were found in $\delta^{15}\text{N}$ and in $\delta^{13}\text{C}$ during the pre-laying period in 2010 and 2012 (except for $\delta^{13}\text{C}$), but not in 2011. On the other hand, during the chick-rearing period these relationships were not detected in 2012 for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$.

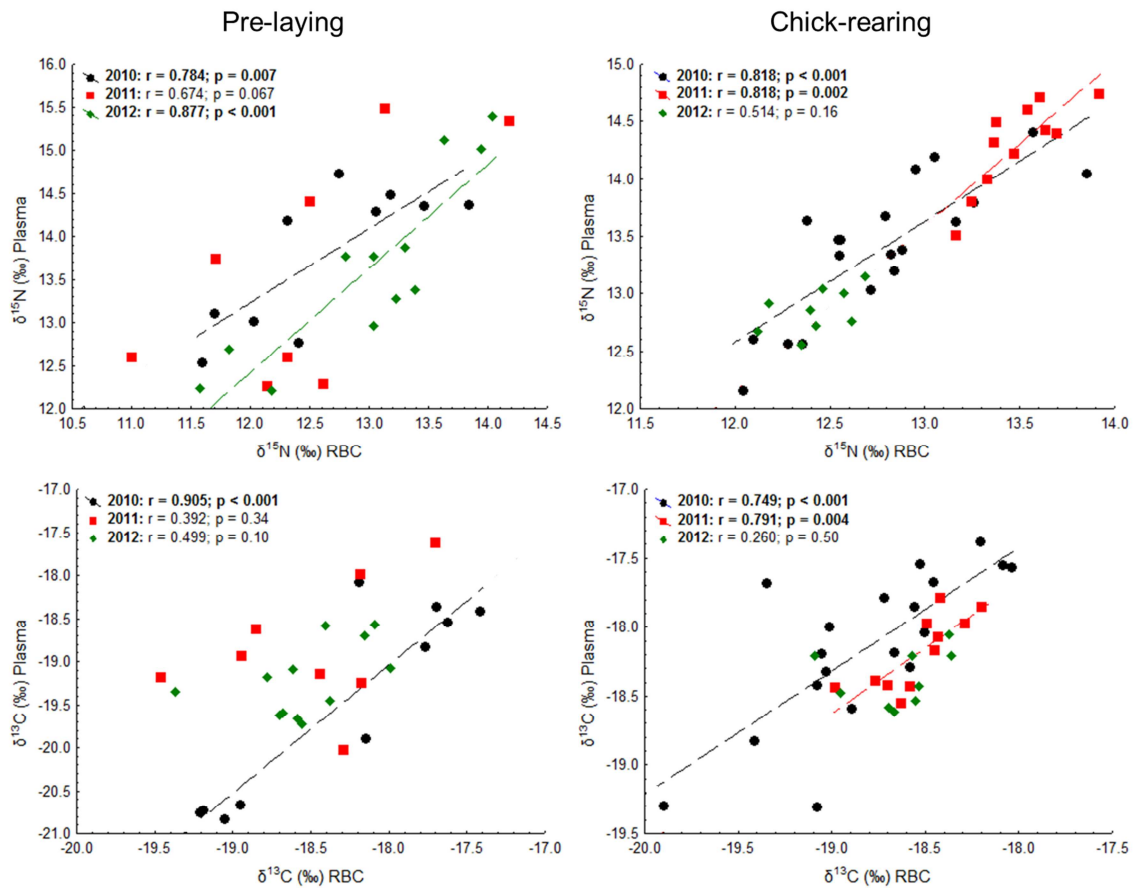


Figure 16. Relationships in $\delta^{15}\text{N}$ (upper panel) and $\delta^{13}\text{C}$ (lower panel) between red blood cells (RBC) and plasma of Cory's shearwaters (*Calonectris diomedea*) breeding in Berlenga Island during the pre-laying (left panel) and chick-rearing (right panel) periods in 2010, 2011 and 2012.

Overall, these results suggest a principally high short-term consistency in the foraging niche within the population, but with exceptions such as those during the 2011 pre-laying and 2012 chick-rearing periods. Interestingly, the lack of consistency in these two periods matched the highest and lowest values of isotopic niche area, spatial distribution at sea and overlap in the estimated foraging range.

Body mass index, condition status and breeding success

No significant differences were detected in BMI and haematocrit values of Cory's shearwaters among the six periods (Table 9). However, laying success and breeding success of Cory's shearwaters on Berlenga showed significant differences among years (Table 9), which were mostly attributed to a higher laying and breeding success in 2012 than in the other two years.

Table 9. Comparison of body mass index (BMI) and haematocrit of Cory’s shearwaters (*Calonectris diomedea*) breeding in Berlenga Island during the pre-laying and chick-rearing periods in 2010, 2011 and 2012 and inter-annual comparison of laying success and breeding success. Values are means \pm SD (sample size).

	2010		2011		2012		Statistical comparison
	PL	CR	PL	CR	PL	CR	
BMI	-0.25 \pm 1.03 (10)	-0.08 \pm 1.12 (19)	0.36 \pm 0.82 (8)	-0.61 \pm 0.91 (11)	0.46 \pm 0.45 (12)	0.26 \pm 1.15 (9)	$F_{(5,63)} = 2.0$ $P = 0.10$
Hematocrit	0.45 \pm 0.16 (10)	0.49 \pm 0.11 (19)	0.49 \pm 0.07 (8)	0.49 \pm 0.05 (11)	0.50 \pm 0.09 (12)	0.48 \pm 0.04 (9)	$F_{(5,63)} = 0.3$ $P = 0.91$
Laying success (%)	47.7 (65)		49.2 (65)		80.0 (65)		$X^2_{(2)} = 17.9$ $P < 0.001$
Breeding success (%)	77.4 (31)		50.0 (32)		96.2 (52)		$X^2_{(2)} = 33.1$ $P < 0.001$

Discussion

Our results provide evidence that an increased variation in the foraging patterns of pelagic seabird species, namely in the spatial distribution at sea, can lead to trophic niche expansion (Fig. 15) supporting the ‘niche variation hypothesis’ (Van Valen 1965). Moreover, our findings suggest that short-term consistency in the foraging niche of Cory’s shearwaters, and possibly related pelagic species, is an intrinsic trait affecting the foraging ecology of the population that could disappear due to sporadic and extraordinary extrinsic factors (e.g. variability in available food resources).

During the present study, Cory’s shearwaters presented a great foraging plasticity among periods, particularly between pre-laying and chick-rearing periods, as expected and demonstrated before in other studies (Navarro et al. 2007, Paiva, Geraldes, Ramírez, Meirinho, et al. 2010a). However, the variability in foraging patterns also varied within periods and was greater in the 2011 pre-laying period and minor in the 2012 chick-rearing period. Interestingly, among other very long trips, we recorded an extraordinary trip that distanced 3236 km from the colony in the 2011 pre-laying period. Such long trips are expected from populations breeding in oceanic islands (e.g. Magalhães et al. (2008) documented a mean maximum distance from the colony of 1570 km during long trips of birds breeding in the eastern Azores, North Atlantic), but

to our knowledge this was the Cory's shearwaters' farthest trip ever recorded during the breeding season, and particularly relevant because this is a neritic environment. The dramatic variation in the distribution and foraging behaviour of Cory's shearwaters during the 2011 pre-laying period (in relation to the other studied periods) could be derived to low abundance of their pelagic fish prey along the Portuguese neritic system (Paiva et al. 2013).

According to our expectations, our results showed that a wide-ranging foraging area led to a wider trophic niche of this pelagic seabird population. Accordingly, when birds foraged farther from the colony the trophic niche also tended to expand as suggested by the positive significant relationship between maximum distance from colony and SEAc. However, we highlight the strong relationship of variation in the foraging area among individuals with their trophic niche along the six periods, which is less influenced than previous parameters by sample size; low standard deviations values in the area explored (25, 50 and 75% FKD) strongly suggest more even distribution of trophic niches (SEAc values). These results are in line with community-wide metrics of trophic structure described by Layman et al. (2007), that relate wider trophic niche occupied to a greater amount of trophic diversity among individuals. For instance, Bolnick et al. (2007) confirmed across a diverse set of taxa, that more generalized populations also tend to be more ecologically heterogeneous due to higher diet variation than more specialized populations, in accordance to Van Valen (1965) hypothesis. However, our study suggests that a given population with more variability in spatial distribution at sea among its members show wider trophic niche than the same population with less variability in foraging areas, corroborating that foraging niche variation apparently is a widespread phenomenon within the same population, which is related with their diet, and ultimately with variation in foraging areas among individuals, supporting Van Valen (1965) hypothesis.

Niche variation among individuals may have several implications affecting whole population dynamics (Bolnick et al. 2011), including the individual specialization in the specific resources used (Svanbäck and Bolnick 2007, this study). Our results showed that short-term consistency in the foraging niche of Cory's shearwaters was relatively high along the study, highlighting individual preferences among birds (Fig. 16); interestingly, however, in two periods short-term consistency in the foraging niche was not verified. During the 2011 pre-laying period and the 2012 chick-rearing period, no

relationships were detected either in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ between RBC and plasma of individual adults, indicating greater variation within individuals than among individuals. Bolnick et al. (2010) found that individual and population niche widths are decoupled; in fact, our results suggested that variation within individuals was greater than variation among individuals when population niche was highest (2011 pre-laying period) and smallest (2012 chick-rearing period). Most probably, in the 2011 pre-laying period birds that performed very long trips did not show short-term consistency because previous trips were presumably not in the same area due to anomalies at very large scales. On the other hand, in the 2012 chick-rearing period birds performed shorter trips with high overlap in foraging areas among birds, resulting in less variance among individuals. Because they probably preyed on the same presumably few but superabundant resources during the 2012 chick-rearing period, the population niche tended to be narrower than if they preyed on a broad spectrum of items (Bearhop et al. 2004). Therefore, when all individuals use similar resources, typical from low-competition environments (Svanbäck & Bolnick 2007), the variances in SIA may be too small or hidden from the effects of selection on resource use required to detect consistency and, thus, variation within individuals may be higher than variation among individuals.

To our knowledge, this is the first study to address consistency in the foraging niche across several years in a seabird population. Our results suggest that birds varied their individual foraging strategies according to extrinsic factors, particularly between the 2011 pre-laying period and the 2012 chick-rearing period. In fact, our data showed a small breeding participation in 2011, in opposition to 2012, suggesting contrasting breeding conditions that could be derived by food availability. We found no evidence that condition status of birds was affected among years and periods; however, it is believed that shearwaters present a fixed investment maintained body condition by reducing parental investment and consequently reducing breeding success (Navarro & González-Solís 2007). Apparently birds preferred to forage farther in the 2011 pre-laying period because of lack of resources around the colony in contrast with the 2012 chick-rearing period, when birds preferred to forage in adjacent areas to colony. Intra-specific competition should favour niche width expansion of a single population via greater between-individual variation (Svanbäck & Bolnick 2007, Bolnick et al. 2010). Our results matched with this hypothesis because the Cory's shearwater niche width was smaller in the 2012 chick-rearing period where supposedly intra-specific

competition was smaller (corroborated with a higher overlap in the foraging area) possibly attributed to high abundance of food resources, in contrast with the 2011 pre-laying period. Interestingly, foraging niche consistency (i.e. greater variation among individuals than within individuals) in Cory's shearwaters was relatively high and persistent along all other periods, suggesting that this trait may play an important role among members of a pelagic seabird population by reducing intra-specific competition during periods of typical average food resource conditions. In this case, birds may have a narrow foraging niche (i.e. individuals use a subset of their population's niche) helping to reduce intra-specific competition as demonstrated in other seabird species such as northern gannets *Morus bassanus* (Votier et al. 2010) and wandering albatrosses *Diomedea exulans* (Ceia et al. 2012).

Conclusions

Our results confirm a strong positive relationship between spatial distribution at sea and trophic niche width of a pelagic seabird population. This relationship is particularly relevant considering variation in spatial distribution at sea among individuals, i.e. low standard deviations values correspond to a more even distribution of trophic niches and vice-versa. Therefore, our results support the 'niche variation hypothesis' (Van Valen 1965) in the foraging ecology point of view. We also found that short-term consistency in the foraging niche is an intrinsic trait of Cory's shearwaters; apparently, the advantages of such trait may relate with an attempt to reduce intra-specific competition among individuals. However, our results showed that consistency was not verified in circumstances of very small variation in the spatial distributions and small trophic niche width. Interestingly, consistency was also not verified in the opposite extreme patterns. Thus, consistency in foraging niche (i.e. individual preferences) appears to be an individual's trait that should drive the dynamics of Cory's shearwater foraging ecology, and possibly related pelagic species; it seems to occur only under determined environmental conditions that we defined as typical food availability conditions, but further studies must be conducted to validate this hypothesis.

Acknowledgments

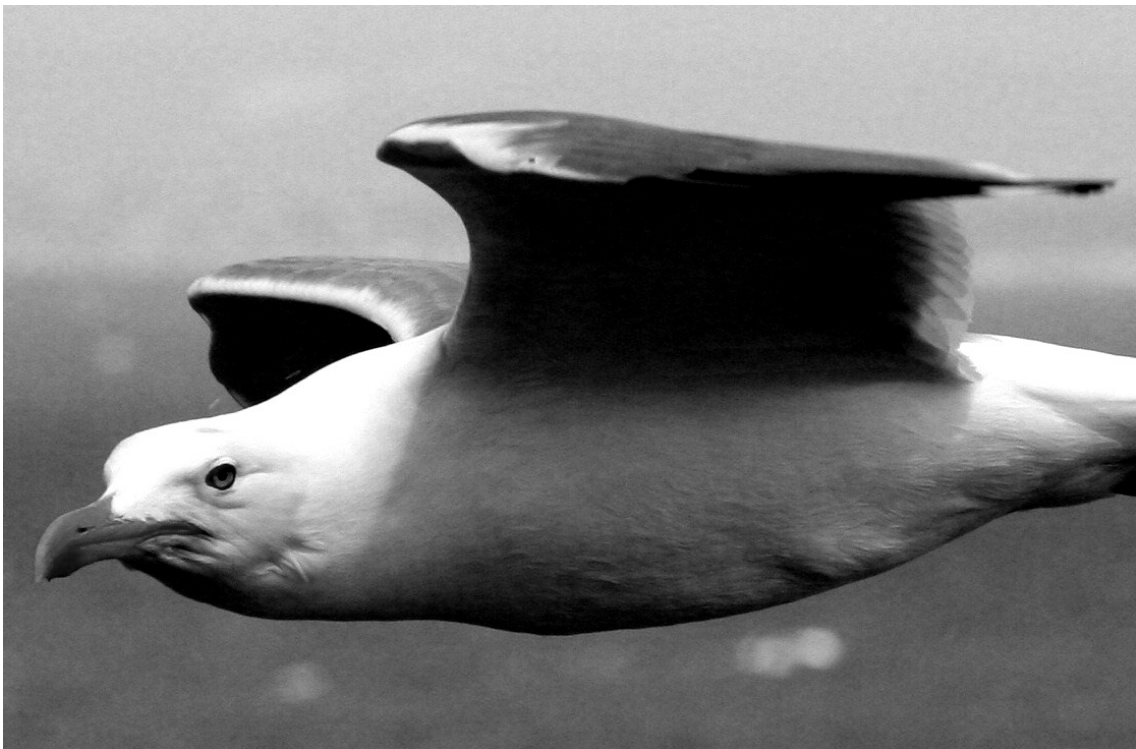
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Chapter 4

Annual and seasonal consistency in the feeding ecology of an opportunistic species, the yellow-legged gull *Larus michahellis*

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Abstract

This study investigated the extent to which the plasticity of a generalist and opportunistic species allows individuals to shift their feeding ecology and foraging behaviour throughout the annual cycle and between two years of contrasting food availability during the breeding season. The spatio-temporal variations in the foraging niche of an overpopulated and problematic gull species at Berlenga Island (Portugal), the yellow-legged gull *Larus michahellis*, were assessed using blood (plasma and cells) and different feathers for stable isotope analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) from 52 breeding adults in two consecutive years (2011 and 2012). In addition, Global Positioning System (GPS) loggers were deployed on 11 individuals and removed after several foraging trips, to infer the foraging behaviour of the species. Results suggest inter-annual differences in the feeding ecology and foraging behaviour of birds during the breeding season that were associated with the availability of food resources around the colony. These differences in food availability apparently had an impact on the body condition. Despite the high feeding plasticity and opportunistic behaviour of yellow-legged gulls, individual birds exhibited short- and long-term consistency in the feeding ecology, with exception of the period between the winter and pre-laying. Therefore, our results support the hypothesis that individual feeding preferences throughout most of the annual cycle are an intrinsic characteristic of this population and potentially of related opportunistic and generalist species.

Key-words: activity patterns, generalist seabirds, foraging specialization, habitat use, GPS tracking, stable isotopes

Introduction

The distribution and size of colonies and the distribution of seabirds at sea is typically correlated with hydrographic features (e.g. oceanic fronts and upwelling areas) and marine productivity, but also with the activity of fishing vessels. However, foraging strategies of species can differ substantially and vary according to factors such as foraging behaviour, morphology, and bioenergetics, resulting in the exploitation of different niches. Among all seabird species, gulls (*Larus* spp.) are some of the most plastic, exploiting different habitats/resources (e.g. marine, coastal and terrestrial) and

combining diet items of different origins (e.g. natural and anthropogenic sources) as demonstrated by several studies (e.g. Schwemmer & Garthe 2008; Moreno et al. 2009; Ramos et al. 2011). The generalist and opportunistic behaviour of most gull species allow individuals to modify relatively easily their foraging strategies (i.e. exploited habitat/resource, diet and spatial or temporal distribution) according, for instance, to the reproductive role or to the competition for food (Ramos et al. 2011, Ramírez et al. 2012). Some research into how inter-annual and seasonal variation of resources influence foraging and fitness of generalist and opportunistic species, such as gulls and skuas, have been performed, but particular incidence on individual specialization over time (individual consistency) is currently scarce (but see Watanuki 1992, Votier et al. 2004, Sanz-Aguilar et al. 2009).

To determine the major factors contributing to population change, one needs to understand the variation in foraging patterns within and among individuals (see Bolnick et al. 2003 for a review) as well as the foods used. Techniques such as data-loggers and stable isotope analysis (SIA) are very useful to detect spatio-temporal variations in the ecological niche of target populations likely associated with changes in the availability of resources. Opportunistic species may owe their success to the fact that diet can change very quickly according to resource availability or to their nutrient requirements (Rutz & Bijlsma 2006; Ramírez et al. 2012), and therefore may have implications for the consistency of their diet and exploited habitat, among seasons or contrasting years.

Flexibility in foraging is particularly relevant for populations of yellow-legged gull *Larus michahellis*, which have increased dramatically throughout Europe in recent decades, with several ecological and social impacts. This increase has been mainly attributed to the great ability of gulls to adapt to human-altered environments by opportunistically exploiting both terrestrial (e.g. refuse dumps) and marine (e.g. fishery discards) resources (Ramos, Ramírez, et al. 2009a, Moreno et al. 2009). Previous studies used diet (e.g. Munilla 1997; Ramos et al. 2009b; Matias & Catry 2010) and SIA (e.g. Ramos et al. 2009a, 2011; Moreno et al. 2009) to infer the feeding ecology of this species. However, to our knowledge this is the first study to address individual foraging consistency and to provide tracking data for the yellow-legged gull.

Here, we tested for foraging consistency and investigated the foraging behaviour of yellow-legged gull breeding adults from Berlenga (the largest breeding colony of this

species in Portugal), in two consecutive years (2011 and 2012) with markedly different baseline diet and oceanographic conditions. Together with conventional dietary sampling and individual movement data, multiple tissues with different turnover rates were sampled for SIA to test for spatio-temporal variation of resource exploitation along seasons and between years. By determining the isotopic composition ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of blood, separated into plasma and cells, and feathers formerly grown during the summer and wintering seasons, we characterized feeding ecology during different periods of the annual cycle of the yellow-legged gull (Quillfeldt et al. 2010, Ramos et al. 2011). We evaluated short- (during breeding) and long-term (along seasons) consistency in the feeding ecology (trophic level and habitat/resource use) of yellow-legged gull individuals (Bearhop et al. 2006, Votier et al. 2010, Ceia et al. 2012). We expected low consistency in their feeding ecology, since they are very plastic and able to rapidly switch diet and habitat/resource use. Specifically, we predict that seasonal and inter-annual variation in resources drive (1) the foraging niche and feeding ecology of population, (2) short- and long-term consistency in the feeding ecology of individuals, (3) foraging behaviour and effort, and (4) condition status of birds. Our goal was to investigate the extent to which the extreme plasticity of yellow-legged gulls allows individuals to react to seasonal and, eventually, inter-annual variations during breeding and non-breeding periods.

Materials and methods

Study area and study species

Fieldwork was carried out during the incubation period of yellow-legged gulls during 2011 and 2012 at Berlenga Island, Portugal (39°24'N, 009°30'W). A large population of about 8500 pairs of yellow-legged gull is estimated to breed in Berlenga Island, a small neritic island of ca. 78.8 ha about 11 km off the western Portugal coast. This island is situated within a large continental shelf characterized by shallow waters and high marine productivity due to coastal upwelling (Sousa et al. 2008). We selected Chlorophyll *a* concentration (Chl *a*, mg m^{-3}) and Sea Surface Temperature (SST, °C) variables to characterize marine environment used by yellow-legged gulls between years. Both environmental predictors were downloaded for a spatial resolution of 0.04° (approx. 4 km) of Aqua-MODIS mapped products from <http://coastwatch.pfeg.noaa.gov/coastwatch/CWBrowserWW180.jsp>. Mean composites

of remote sensing data up to 100 km around the colony, from January to June in 2011 and 2012 (spatial and temporal scale that have been found to relevant to characterize marine habitats based on the longest trip recorded and the temporal dynamism of these variables), were used to detect differences between years in the marine environment used by the individuals during pre-laying and incubation periods. Chl *a* was \log_{10} transformed to better fit a normal distribution. Both variables were compared by month between years using a t-test followed by a Bonferroni correction.

Sample collection

In May-June, 52 breeding adults (26 each year) with three egg clutches were caught on the nest and sampled. Blood samples (0.5-1 ml from the tarsal vein) were collected from each bird using 27G needles and, within 2-3 h, separated into plasma and red blood cells (RBC) using a centrifuge (15 min at 3000 rpm). Haematocrit was recorded and samples were stored frozen until preparation for SIA. The sampling scheme involved collecting 4-5 randomly selected breast feathers and the tips of the 1st primary (P1) and 8th secondary (S8), which were stored in sealed plastic bags for later SIA. Additionally, a GPS logger was deployed on 11 birds (four in 2011 and seven in 2012) and removed after 3 to 25 foraging trips at sea (details of the devices below). Stomach contents were collected from 19 sampled individuals (five in 2011 and 14 in 2012) by water-offloading, following Wilson (1984). Captured birds were weighed and wing length was measured. Deployment or retrieval of devices and collection of samples took 10-15 min. per bird.

Diet sampling and stable isotope analysis

All regurgitates came from breeding individuals. Each component (fish, crustaceans, refuse and terrestrial invertebrates) was sorted and individual prey items identified to species-level whenever possible. The prey species identified in regurgitates collected from gulls were the fish species Atlantic horse mackerel *Trachurus trachurus* and blue whiting *Micromesistius poutassou*, and the pelagic crab species Henslow's swimming crab *Polybius henslowii*. Refuse was represented to a large extent by meat (chicken, beef scraps and organs from unknown species). We also found occasional terrestrial prey (terrestrial invertebrates) namely insects (bees and ants), spiders and snails. Fresh crustaceans (*P. henslowii*), fish (*T. trachurus*, with otoliths attached; we were not able

to collect fresh *M. poutassou*), refuse and terrestrial invertebrates were stored frozen for SIA.

Different tissues have different turnover rates and therefore can reflect temporal changes in trophic position and habitat/resource use (i.e., a change in isotopic niche; reviewed in Newsome et al. 2007). Carbon stable isotope value ($\delta^{13}\text{C}$) mainly reflects the habitat/resource use of consumers, while nitrogen stable isotope value ($\delta^{15}\text{N}$) is mainly used to define trophic position of consumers. Specifically, we analysed $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) in plasma, RBC, S8, P1 and breast feathers from each breeding adult sampled. Plasma and RBC retain information on diet from a few days prior to sample collection, up to the previous 3-4 weeks, as representative tissues of incubation and pre-laying period, respectively (Hobson & Clark 1993, Votier et al. 2010). On the other hand, analyses on specific feathers provide unique isotopic information of a spatiotemporal period, unrelated with the sampling period (Quillfeldt et al. 2010, Ramos et al. 2011). We collected P1 and S8 to represent the preceding summer and wintering seasons, respectively (Ramos et al. 2011). We assumed that breast feathers represented the overall diet during the non-breeding season, because body feathers moult throughout the non-breeding season (Arcos et al. 2002). In addition, we analysed $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) of fresh prey items obtained from stomach contents to create a basis for the interpretation of the isotopic signatures of tissues and further construction of mixing models.

Samples (plasma, RBC and prey items) were freeze-dried and homogenized prior to SIA. Because high lipid concentrations in plasma and in flesh from prey items can lead to depleted $\delta^{13}\text{C}$ values, lipids were removed using successive rinses in a 2:1 chloroform-methanol solution (Cherel et al. 2005). Prior to SIA, feathers were cleaned of surface contaminants using successive rinses in a 2:1 chloroform-methanol solution, dried at 60°C for 24 h and then homogenized. For specifications how nitrogen and carbon isotope ratios were determined see Chapter 2.

GPS tracking

During the two years study, 11 breeding adults were fitted with a GPS logger (CatTraq GT-120, Perthold Engineering LLC). The plastic case was removed and replaced by a 7 cm long thermo-retractile rubber sleeve reducing the total weight to 17 g. The total mass of the device was below 3% of adult mass (1.6–2.3%), as recommended by Phillips et

al. (2003). The GPS loggers were attached to feathers in the mantle region with Tesa[®] tape and set to record position (median error of < 10m) every 2 min, to have a detailed report of the behaviour of gulls. We tracked birds continuously from 2 to 8 days (median = 5 days), the data from which were used to determine seven foraging behaviour and effort parameters (see data analysis below).

Bird condition status

We used the standard residuals of the relationship between body mass and wing length ($F_{1,50} = 104.1$, $P < 0.001$, $r = 0.822$) to estimate the body mass index (BMI) of all sampled birds, an index primarily reflecting body lipid reserves (Sánchez-Guzmán et al. 2004). We used the haematocrit value that in conjunction with other physiological indicators, such as BMI, can be a useful indicator of the current health condition status or energy expenditure of individuals (see Fair et al. 2007 for a review).

Data analysis

To estimate contributions for each dietary source to the diet of each individual, we adopted a Bayesian multi-source stable isotope mixing model (stable isotope analyses in R: SIAR; Parnell et al. 2010) under R 2.15.2 (R Development Core Team 2011). All possible combinations of each source contribution were examined using both isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) from plasma (corresponded to the incubation period, when birds were tracked) for each bird, and the mean and standard deviation of each of the four food sources collected from regurgitates (*T. trachurus*, *P. henslowii*, refuse and terrestrial invertebrates). Isotopic data of *T. trachurus* were pooled, since no differences were found between 2011 and 2012 ($\delta^{13}\text{C}$: $F_{1,3} = 2.5$, $P = 0.21$; $\delta^{15}\text{N}$: $F_{1,3} = 0.8$, $P = 0.43$). For *P. henslowii* we used the values from samples collected in 2012, because no crustaceans were found in the diet of gulls in 2011 (see results). Finally, we combined all items composed by refuse in a single category and the terrestrial invertebrates in a distinct food source. There are no diet-blood fractionation factors available for yellow-legged gulls; hence, we used the average values of fractionation between prey and whole blood of four seabird species, from controlled experiments, available in the literature: 0.30 and 2.85‰ enrichment for carbon and nitrogen, respectively (Hobson & Clark 1992, Bearhop et al. 2002, Cherel, Hobson, & Hassani 2005). A standard deviation of $\pm 1.0\%$ was adopted, considering potential differences in fractionation factors among species. SIA results were compared between years using an ANOVA or a

Mann-Whitney U Test. To test the homogeneity of variances in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, which provides a measure of niche width (see Bearhop et al. 2004 for more details), we used a Levene's Test. However, to analyse stable isotope data in the context of isotopic niche width between years and among seasons and periods, we adopted the recent metrics based in a Bayesian framework (Stable Isotope Bayesian Ellipses in R: SIBER; Jackson et al. 2011), which allows for robust statistical comparisons. The area of the standard ellipse (SEAc, an ellipse that has 95% probability of containing a subsequently sampled datum) was adopted to compare between years and their overlap in relation to the total niche width (both years combined), and a Bayesian estimate of the standard ellipse and its area (SEAB) to test whether group 1 is smaller than group 2 (i.e. p , the proportion of ellipses in 2011 that were lower than 2012; see Jackson et al. 2011 for more details). We used the computational code to calculate the metrics from SIBER using functions ("*standard.ellipse*", "*convexhull*" and "*siber.ellipses*") implemented in the package SIAR (Parnell et al. 2010) under R 2.15.2.

To obtain an estimate of short-term consistency (between pre-laying and incubation periods) in carbon source and trophic level, we regressed stable isotope ratios in plasma on those in RBC. For long-term consistency, we regressed stable isotope ratios in RBC on those in S8 (between wintering season and pre-laying period), RBC in P1 (between summer season and pre-laying period) and S8 in P1 (between summer and wintering seasons). Since $\delta^{13}\text{C}$ has a trophic component, we used the residuals of the relationships with $\delta^{15}\text{N}$ in the same tissue categorised by year (2011 and 2012: plasma, RBC, S8 and P1; P all < 0.05) to determine the degree of repeatability in $\delta^{13}\text{C}$, independently of trophic effects (Bearhop et al. 2006, Votier et al. 2010, Ceia et al. 2012). The analyses of short-term consistency were performed using plasma and RBC, which could lead to a temporal overlap in the synthesis of these tissues as integration of prey isotopes into body tissues is a continuous, dynamic process. On the other hand, overlap between samples in the analyses of longer-term (i.e. with feathers) will be negligible as the selected feathers for this analysis were synthesized in different seasons. Two outliers that had a significant influence on the results for residual $\delta^{13}\text{C}$ in S8 and P1 in 2011 (-1.7 and -2.6, respectively) were excluded from these analyses. Based on these results we were able to compare the consistency in foraging tactics of yellow-legged gulls between years and among seasons and periods.

The nonparametric fixed kernel density (FKD) estimator was used to calculate the 25, 50, 75 and 95% density contour areas of each trip using functions (“*kernelUD*”, “*getvolumeUD*”, “*getverticeshr*” and “*kernel.area*”) of the *adehabitat* package ($h = 0.05$, $grid = 500$; Calenge 2006) under R 2.15.2. GPS data-points at the colony were excluded from analyses and we defined foraging trips from the time when the birds departed from the colony until their return. The overlap with land in the estimated foraging range was calculated based on the FKD.

Our measurements of foraging behaviour and effort comprised: (1) geographic position at maximum distance from the colony (latitude and longitude); (2) trip duration (days); (3) maximum distance from colony (km); (4) trip length (km); (5) area covered (95% FKD; km^2); (6) number of trips per day; and (7) proportion of trips where birds exclusively foraged at sea. Variables (1) to (5) were calculated for each trip and compared between years creating variance components for ANOVA designs with random effects (mixed-ANOVA). The year was included as a fixed factor and bird identity as a random effect to control for pseudoreplication, because more than one foraging trip per individual was recorded. Variables (6) and (7) were calculated per individual and compared between years with a Mann-Whitney U Test. All data were tested for normality and homoscedasticity; trip duration was \log_{10} transformed, maximum distance, trip length and area covered were square root transformed and proportions were arcsine transformed.

Results

Diet and stable isotope analysis

In 2011 and 2012 combined, we obtained four food sources collected in regurgitates from gulls: fish, crustaceans, refuse and terrestrial invertebrates. The crustaceans (represented by *P. henslowii*) were not found in regurgitates of yellow-legged gulls in 2011, but occurred in 58.3% of the gulls sampled that contained food in 2012. Moreover, in 2011 we did not observe *P. henslowii* in gull pellets present in the colony, nor during several boat trips around the island, suggesting that *P. henslowii* was not available during the incubation period of 2011. In contrast, during 2012 this species was extremely common in the pellets and in the sea around the colony during the same period. This pattern matched with monthly differences in the patterns in Chl *a* and SST, between 2011 and 2012, up to 100 km around the colony (t-test, Bonferroni correction:

all $P < 0.01$; Fig. 17). The significantly lower value of Chl *a* in May 2011 and its abrupt decline in 2011 contrasted to 2012 (Fig. 17b) when the *P. henslowii* were abundant.

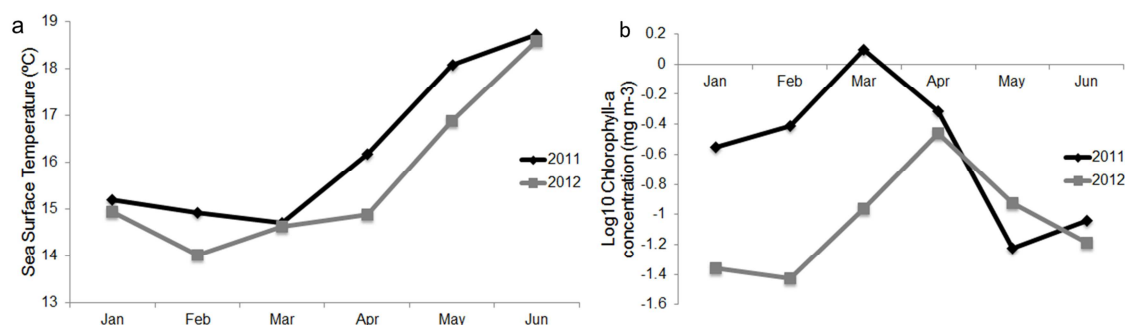


Figure 17. Mean mensal composites of (a) Sea Surface Temperature (SST) and (b) \log_{10} Chlorophyll *a* concentration (Chl *a*) up to 100 km around the Berlenga Island, from January to June in 2011 and 2012.

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the four food sources differed significantly (Kruskal-Wallis Test; $\delta^{13}\text{C}$: $H_{3,18} = 9.6$, $P = 0.022$; $\delta^{15}\text{N}$: $H_{3,18} = 13.0$, $P = 0.005$) in at least one of the isotopes, with exception of *P. henslowii* and refuse (Table 10). However, differences were found in the homogeneity of their variances in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Levene's Test; $\delta^{13}\text{C}$: $F_{1,7} = 6.1$, $P = 0.042$; $\delta^{15}\text{N}$: $F_{1,7} = 52.4$, $P < 0.001$); the high variances in refuse indicated the wide isotopic spectrum of items ingested.

Table 10. Stable isotopic signature of carbon and nitrogen (mean \pm SD) of the four food sources recorded in regurgitates collected from yellow-legged gulls (*Larus michahellis*) breeding in Berlenga Island during the incubation period. Terrestrial invertebrates were included insects, spiders and snails.

Prey source	<i>n</i>	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>T. trachurus</i>	5	-18.6 ± 0.6	11.9 ± 0.6
<i>P. henslowii</i>	4	-17.8 ± 0.6	6.2 ± 0.2
Refuse	5	-17.1 ± 1.1	6.9 ± 4.3
Terrestrial invertebrates	4	-23.7 ± 4.0	15.2 ± 3.2

SIAR mixing model outputs revealed significant differences between 2011 and 2012 in the relative proportion of food sources ingested ($F_{3,48} = 4.6$, $P = 0.007$), particularly in the consumption of *P. henslowii* ($F_{1,50} = 8.0$, $P = 0.007$), which was the most consumed item in 2012 (Fig. 18). *T. trachurus* was ingested in similar proportions in both years

(33.9% in 2011 and 34.4% in 2012), but there was a strong difference in the ingestion of *P. henslowii* (28.5 and 39.9%), refuse (19.2 and 12.3%) and terrestrial invertebrates (18.4 and 13.4%). These differences are based on a conservative estimation, i.e. considering *P. henslowii* similarly available during both years. Assuming that *P. henslowii* was not consumed by birds during the incubation period of 2011 (as our data indicates), the estimated percentages of *T. trachurus*, refuse and terrestrial invertebrates for 2011 were 45.1, 38.2 and 16.7%, respectively.

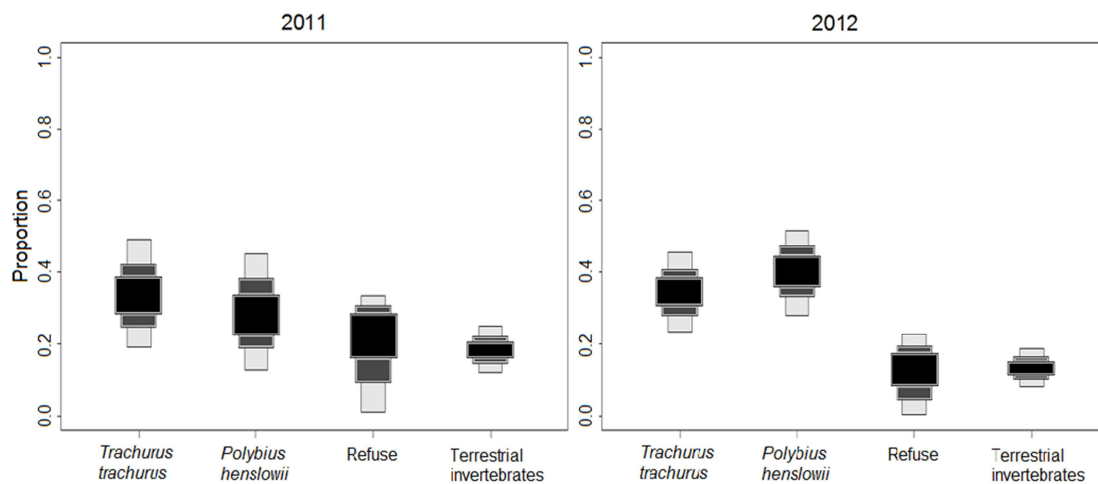


Figure 18. Range of possible proportions of the four main food sources in the diet of yellow-legged gulls (*Larus michahellis*) breeding in Berlenga Island during the incubation period (based on C and N isotopic signatures of plasma) in 2011 and 2012. Terrestrial invertebrates were composed of insects, spiders and snails. Decreasing bar widths represent 50, 75 and 95% Bayesian credibility intervals computed by Stable Isotope Analysis in R (SIAR; Parnell et al. 2010).

Inter-annual consistency in feeding ecology at the population level

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of yellow-legged gulls' plasma, which provides an indication of recent meals (i.e. during the incubation period), did not differ significantly between 2011 and 2012 (Mann-Whitney U Test; $\delta^{13}\text{C}$: $Z = -0.4$, $P = 0.65$; $\delta^{15}\text{N}$: $Z = 1.6$, $P = 0.11$). However, gulls exhibited substantial inter-annual differences in the homogeneity of variances in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Levene's Test; $\delta^{13}\text{C}$: $F_{1,50} = 5.0$, $P = 0.030$; $\delta^{15}\text{N}$: $F_{1,50} = 7.8$, $P = 0.007$), which provides a measure of niche width (see Bearhop et al. 2004). In fact, SIBER analysis revealed that yellow-legged gulls occupied an isotopic niche area two times higher in 2011 than in 2012 (SEA_B ; $p = 0.014$; Fig. 19a; Table 11), with a 28.6% overlap in niche width between the two years.

Significant differences were found for RBC (i.e. representing the pre-laying period) between years in $\delta^{15}\text{N}$ ($F_{1,50} = 14.6$, $P < 0.001$), but not in $\delta^{13}\text{C}$ ($F_{1,50} = 1.0$, $P = 0.33$); in 2011 birds showed enrichment in $\delta^{15}\text{N}$, suggesting inter-annual differences in the consumption of food sources from different trophic levels. These differences were revealed in the occupancy of the isotopic niche area, in which the inter-annual overlap was only 1.3% during the pre-laying period, although no differences were found in the area (SEAB ; $p = 0.093$; Fig. 19b; Table 11).

No differences were found for S8 (i.e. winter diet) between years in both $\delta^{13}\text{C}$ ($F_{1,50} = 0.2$, $P = 0.63$) and $\delta^{15}\text{N}$ ($F_{1,50} = 3.1$, $P = 0.08$). The isotopic niche area was similar between years (SEAB ; $p = 0.547$; Fig. 19c; Table 11), with an overlap of 44.9%. These results suggest inter-annual consistency in the feeding ecology of this population during winter.

On the other hand, there were significant differences for P1 (i.e. summer diet) between years in $\delta^{13}\text{C}$ ($F_{1,50} = 9.1$, $P = 0.004$), but not in $\delta^{15}\text{N}$ ($F_{1,50} = 0.1$, $P = 0.81$); birds showed depleted $\delta^{13}\text{C}$ values in the summer season of 2010, suggesting inter-annual differences (between 2010 and 2011) in habitat/resource use. In fact, the summer isotopic niche overlap between these two years was only 16.7%, although the area was similar (SEAB ; $p = 0.746$; Fig. 19d; Table 11).

Table 11. Stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in plasma, red blood cells (RBC), 8th secondary (S8), 1st primary (P1) and breast feathers of yellow-legged gulls (*Larus michahellis*) breeding in Berlenga Island in 2011 ($n = 26$) and 2012 ($n = 26$). The area of the standard ellipse (SEAc) and the layman metric of convex hull area (TA) are also shown (see Jackson et al. 2011 for more details on these metrics of isotopic niche width). Values are means \pm SD.

Tissue type	$\delta^{13}\text{C}$ (‰)		$\delta^{15}\text{N}$ (‰)		SEAc		TA	
	2011	2012	2011	2012	2011	2012	2011	2012
Plasma	-18.9 ± 0.8	-18.7 ± 0.5	12.9 ± 1.5	12.2 ± 1.0	3.03	1.51	8.09	4.60
RBC	-19.3 ± 0.7	-19.2 ± 0.6	12.7 ± 1.4	11.4 ± 1.1	2.18	1.39	7.28	4.69
8 th secondary	-17.2 ± 0.5	-17.1 ± 0.7	13.2 ± 1.6	14.0 ± 1.7	2.43	2.41	8.06	10.75
1 st primary	-17.7 ± 0.9	-17.0 ± 0.8	14.0 ± 1.1	13.9 ± 1.8	2.59	2.99	8.25	11.91
Breast feathers	-17.4 ± 0.4	-17.2 ± 0.6	13.0 ± 1.2	13.3 ± 1.0	1.52	1.45	4.51	4.44

No differences were found between years in $\delta^{13}\text{C}$ (Mann-Whitney U Test; $Z = -1.8$, $P = 0.08$) and $\delta^{15}\text{N}$ ($F_{1,50} = 1.1$, $P = 0.29$) of yellow-legged gulls' breast feathers, which provides an average picture of the diet along the non-breeding season. SIBER indicated that the isotopic niche area was similar between years (SEA_B ; $p = 0.461$; Fig. 19e; Table 11). Moreover, the overlap between the two years (2010/2011 and 2011/2012) was 47.8%, which suggests inter-annual consistency in the feeding ecology of this population during the non-breeding season.

Short- and long-term consistency in feeding ecology within a year

Similar patterns in short- and long-term consistency in feeding ecology of yellow-legged gulls were detected in both years. Strong significant positive relationships were found in $\delta^{15}\text{N}$ and in residual $\delta^{13}\text{C}$ (hereafter $\delta^{13}\text{C}$) between RBC and plasma of individual breeding adults in both years (Fig. 20ab). These results suggest short-term foraging consistency (along the pre-laying and incubation periods) within individuals in relation to both the use of the same habitat/resource and trophic level. In relation to longer-term consistency, significant relationships were found between P1 and RBC in $\delta^{15}\text{N}$ in both years (Fig. 20c), but not in $\delta^{13}\text{C}$, which suggests consistency in trophic level between the summer season and the pre-laying period. On the other hand, significant relationships were found between P1 and S8 in $\delta^{13}\text{C}$ in both years (Fig. 20d), but not in $\delta^{15}\text{N}$, which suggests consistency in habitat/resource use between the summer and the wintering seasons. Interestingly, no significant relationships were found in either $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ between S8 and RBC, for any of the two years, which means greater variation within individuals than among individuals. Hence, birds apparently became less consistent between the winter season and the pre-laying period, where they probably begin to exploit different food sources and habitats.

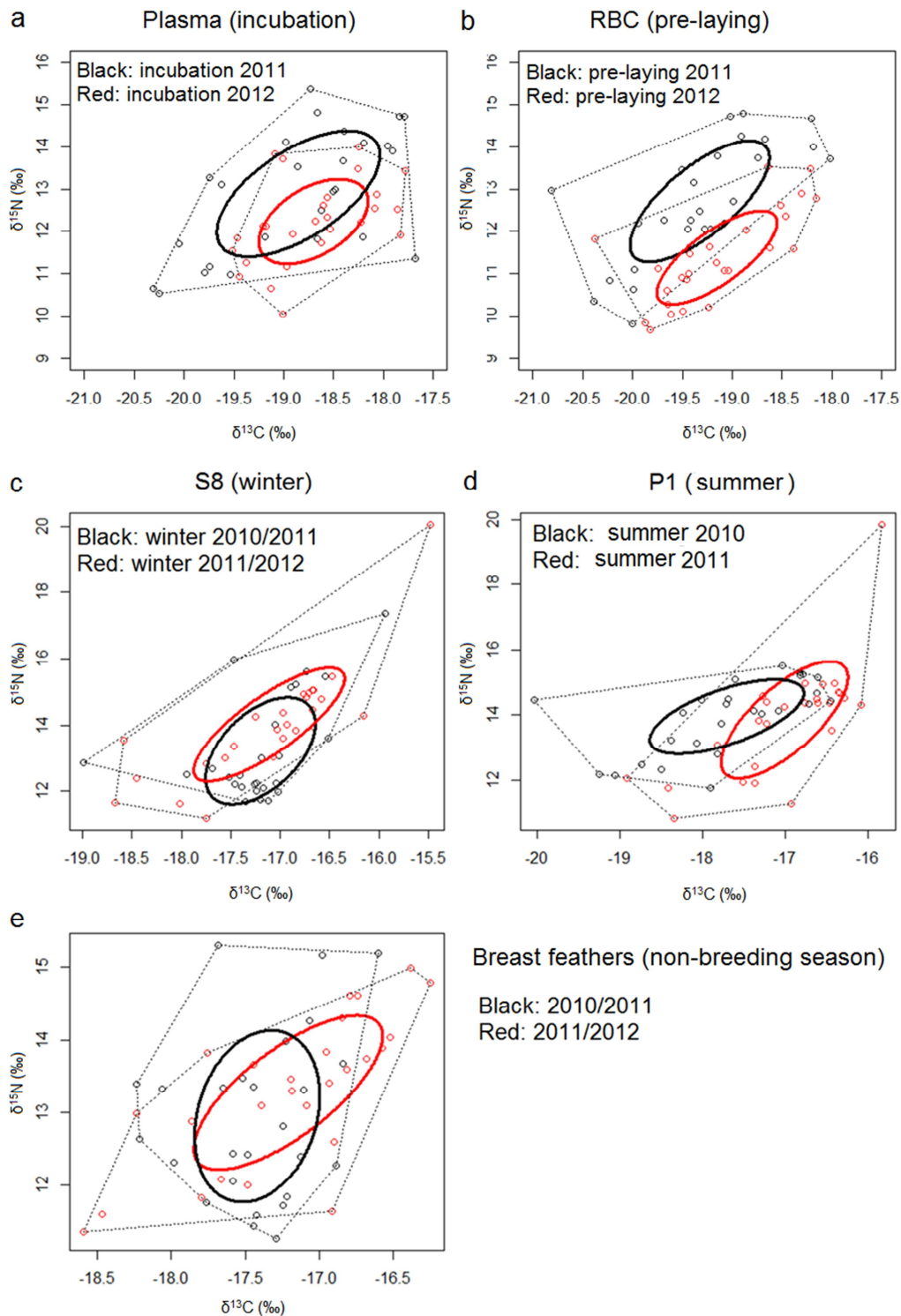


Figure 19. Stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in (a) plasma, (b) red blood cells (RBC), (c) 8th secondary (S8), (d) 1st primary (P1) and (e) breast feathers of yellow-legged gulls (*Larus michahellis*) breeding in Berlenga Island in 2011 (black) and 2012 (red). The area of the standard ellipses (SEAc, 95% credible interval) were represented by the solid bold lines (ellipses) and the layman metric of convex hull area (TA) by black dotted lines (see Jackson et al. 2011 for more details on these metrics of isotopic niche width). ($n = 26$ in each year).

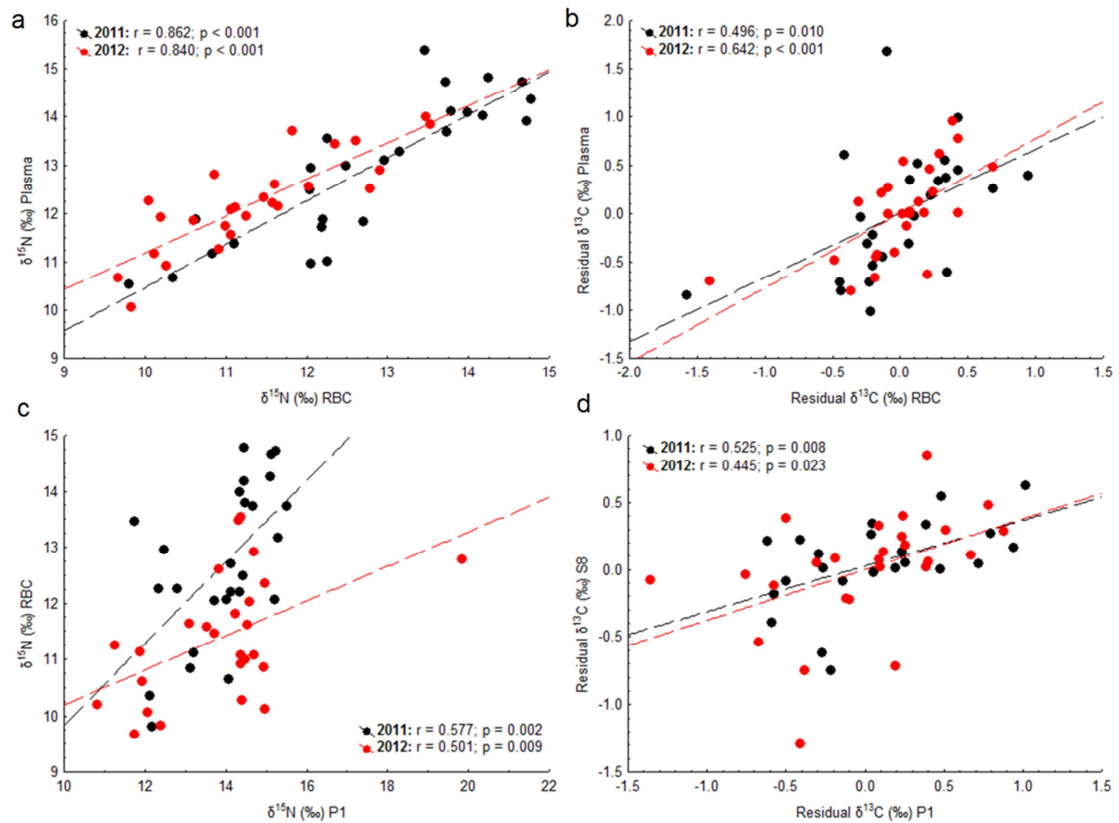


Figure 20. Relationships between (a) $\delta^{15}\text{N}$ values in red blood cells (RBC) and plasma, (b) residual $\delta^{13}\text{C}$ values in RBC and plasma, (c) $\delta^{15}\text{N}$ values in 1st primary (P1) and RBC and (d) residual $\delta^{13}\text{C}$ values in P1 and 8th secondary (S8) of yellow-legged gulls (*Larus michahellis*) breeding in Berlenga Island in 2011 (blue) and 2012 (red).

Habitat selection and foraging behaviour

We obtained 103 foraging trips from 11 individuals (2011: 25 trips from four individuals; 2012: 78 trips from seven individuals). In both years, birds showed a unimodal distribution in trip duration; although the mode class (< 0.2 days for both years) was much higher in 2012 (86%) than in 2011 (48%). However, in terms of maximum distance from the colony (= 98 km), birds showed a dual foraging strategy in both years with modal classes of 0-10 (83%) and 40-50 km (9%) in 2012 and 0-10 (36%) and 60-70 km (12%) in 2011, which means that foraging effort was higher in 2011.

The spatial patterns of foraging habitat selection differed markedly between 2011 and 2012. In 2012 birds preferred to forage at sea whereas in 2011 they preferred to forage inland. In fact, the maximum longitude during trips was significantly different between years, but not latitude (see Table 12), denoting inter-annual spatial segregation based on the type of habitat explored (marine vs. terrestrial). Although birds used terrestrial and

coastal habitats to forage in both years, such as refuse dumps (e.g. Leiria, Vilar, Azambuja and Rio Maior) and fisheries leftovers (e.g. Peniche harbour and Costa da Caparica seashore), they did it more frequently in 2011 than in 2012; 25% FGD showed that the overlap with terrestrial habitat was 35.3% in 2011 and only 0.8% in 2012 (i.e. the overlap with Berlenga Island), which corresponded to the two feeding areas identified based on 25% FGD: (1) the area adjacent to the city of Peniche in 2011 (14 km from the colony; Fig. 21a), and (2) the marine area adjacent to the colony in 2012 (Fig. 21b).

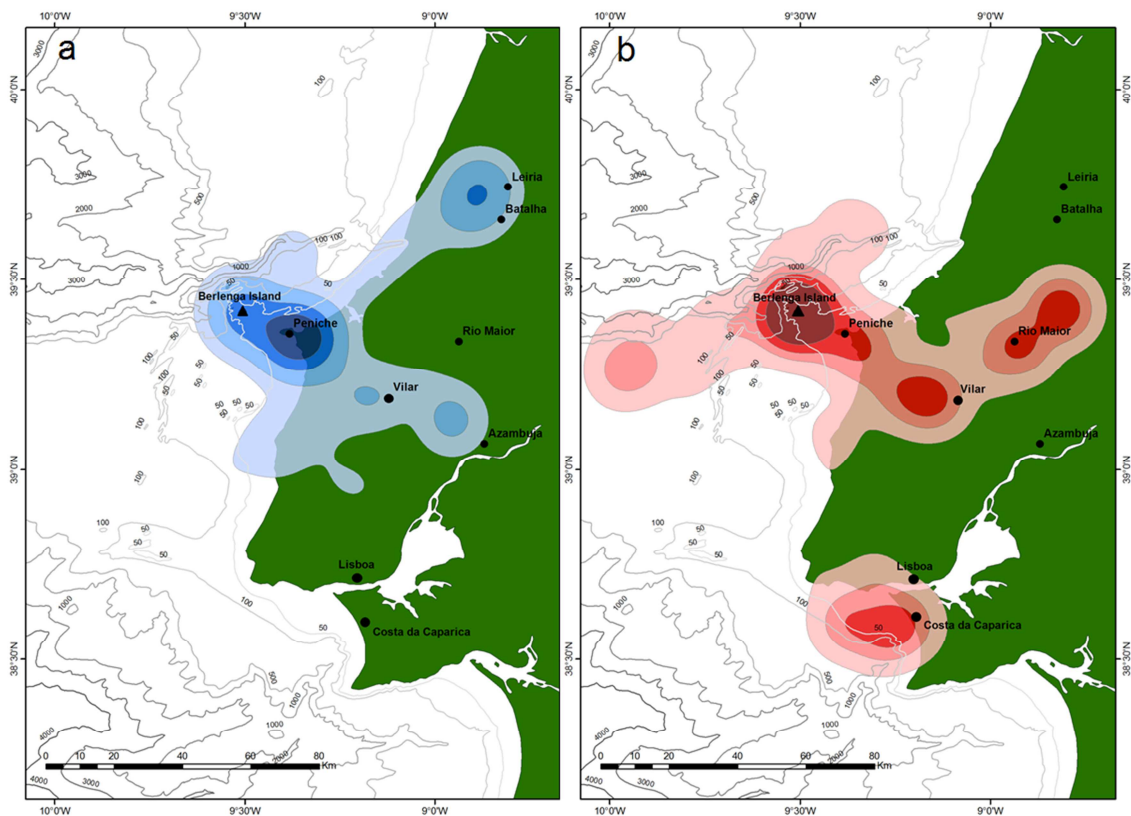


Figure 21. Foraging distributions of yellow-legged gulls (*Larus michahellis*) breeding in Berlenga Island during the incubation period in (a) 2011 and (b) 2012. Decreasing kernel polygon shades represent 25, 50, 75 and 95% foraging home ranges.

Differences in the foraging behaviour and foraging effort of birds between 2011 and 2012 (Table 12) were even more obvious than differences in the spatial patterns. Specifically, the foraging trips were shorter (spatially and temporally), and the area covered by birds during foraging trips was significantly smaller in 2012 than in 2011. Differences were also found in the mean number of trips per day and in trips where individuals forage exclusively at sea; both were significantly greater in 2012 than in 2011.

Table 12. Comparison of foraging trip parameters performed by yellow-legged gulls (*Larus michahellis*) breeding in Berlenga Island during the incubation period in 2011 (25 foraging trips from four birds) and 2012 (78 foraging trips from seven birds). Values are means \pm SD per individual, but statistical comparison was performed per trip (with year as a fixed effect and bird identity as a random effect), with the exception of trips per day and trips to the sea, in which values per individual were compared between years with a Mann-Whitney U-test. Significant results are in bold.

	2011	2012	Statistical comparison
Maximum latitude	39.35 \pm 0.13	39.38 \pm 0.03	$F_{1,9} = 0.2, P = 0.704$
Maximum longitude	-9.33 \pm 0.06	-9.47 \pm 0.11	$F_{1,9} = 8.8, P = 0.016$
Trip duration (days)	0.29 \pm 0.06	0.15 \pm 0.11	$F_{1,9} = 6.7, P = 0.030$
Maximum distance (km)	22.1 \pm 7.2	11.7 \pm 9.4	$F_{1,9} = 8.4, P = 0.019$
Trip length (km)	67.5 \pm 17.9	37.0 \pm 31.9	$F_{1,9} = 6.9, P = 0.029$
95% FKD area (km ²)	751 \pm 119	337 \pm 314	$F_{1,9} = 9.6, P = 0.013$
Trips per day	1.1 \pm 0.2	2.6 \pm 2.3	$Z = -2.3, P = 0.023$
Trips to the sea (%)	22.9 \pm 20.8	75.2 \pm 35.7	$Z = -2.0, P = 0.047$

Bird condition status

BMI and haematocrit values of yellow-legged gulls differed significantly between 2011 and 2012: individuals presented greater BMI and lower haematocrit (lower proportion of RBC) in 2012 than in 2011 (Table 13). Positive significant relationships were found between the consumption of *P. henslowii* estimated with the SIAR model and BMI ($F_{1,50} = 5.2, P = 0.027, r = 0.307$), and between trip duration and haematocrit ($F_{1,9} = 7.5, P = 0.023, r = 0.675$). These relationships suggest a higher BMI in birds that consume more *P. henslowii* and lower haematocrit values in birds that performed shorter trips.

Table 13. Comparison of body mass index (BMI) and haematocrit of yellow-legged gulls (*Larus michahellis*) breeding in Berlenga Island during the incubation period in 2011 and 2012. Values are means \pm SD (sample size).

	2011	2012	Statistical comparison
BMI	-0.45 \pm 0.82 (26)	0.45 \pm 0.96 (26)	$F_{1,50} = 13.1, P < 0.001$
Haematocrit (%)	0.46 \pm 0.05 (26)	0.42 \pm 0.05 (26)	$F_{1,50} = 10.3, P = 0.002$

Discussion

We used yellow-legged gull as a model of a generalist and opportunistic species to infer the consistency in feeding ecology at the population and individual levels in a small North Atlantic neritic island. Contrary to our expectations, our results show a high level of short- and long-term consistency in the feeding ecology of yellow-legged gulls at both the individual and population levels, in particular between some stages of their annual cycle (see below). The foraging behaviour, effort and niche width of yellow-legged gulls differed markedly between 2011 and 2012, matching the strong variation in oceanographic conditions and in the availability of the main prey species, *P. henslowii*, between years. Such differences between years had no major consequences for the overall patterns of short- and long-term consistency in the feeding ecology of individuals, but had a significant influence on bird condition status.

It is well documented that the pelagic crab *P. henslowii* is an important component of the diet of the yellow-legged gull (Moreno et al. 2009), which, despite its spatial and temporal unpredictability (Munilla 1997), may be the most important marine prey in Iberian Atlantic waters during the breeding season. Signa et al. (2008) suggested that the spatial structure of *P. henslowii* populations during the adult pelagic phase in coastal and surface waters in Galicia (Spain), as it gathers in shoals at high densities, is related with their feeding behaviour and oceanographic characteristics; the density of *P. henslowii* was positively correlated with Chl *a* and should be influenced by outwelling, upwelling and downwelling regimes. Our results suggest that *P. henslowii* was not commonly available during the 2011 incubation period of the yellow-legged gulls at Berlenga, in contrast with 2012, most probably due to the different oceanographic conditions recorded between both years (particularly Chl *a*, which was significantly lower in May 2011, i.e. during the incubation period). Even when considering that *P. henslowii* was equally available in both years during the incubation period, the SIAR mixing model revealed a higher significant consumption in 2012. Because *P. henslowii* and refuse lacked differences in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, SIAR could not precisely differentiate their relative proportions. We were not able to perform sulphur stable isotope analyses, as its inclusion in SIAR could improve this analysis by giving more discriminating power to differentiate refuse and *P. henslowii* (Moreno et al. 2009, Ramos et al. 2011). However, due to its distinct origin and importance to the yellow-

legged gulls' diet, both food sources were considered independently as their homogeneity of variances differed significantly in both isotope ratios.

Yellow-legged gulls showed inter-annual differences in the feeding ecology during both the incubation and pre-laying periods. A significant higher isotopic niche area in 2011 than 2012 (twice higher) during the incubation period and inter-annual differences in the homogeneity of variances in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in plasma were detected. The broad spectrum of trophic levels in refuse and the small variances in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of *P. henslowii* appeared to be the basis of the differences found, because populations where individuals mostly consume prey over a narrow spectrum of trophic levels will tend to show less isotopic variance than those which feed on a broad spectrum of items from different trophic levels (Bearhop et al. 2004). With *P. henslowii* largely available in 2012, birds concentrated their foraging effort around the colony, consuming easily obtained crabs, in contrast with 2011 where birds preferred to forage farther inland, consuming more refuse, as SIAR and tracking data corroborated. During the pre-laying period, inter-annual differences were found in the occupancy of the isotopic niche area, mainly driven by greater significant $\delta^{15}\text{N}$ values in 2011. We have no data to corroborate the availability of *P. henslowii* during this period. However, the trace availability of *P. henslowii* in 2011 during the pre-laying and chick-rearing periods (i.e. during the breeding season) in contrast to 2012 was reported by another on-going study based on pellets and chick regurgitates in Berlenga Island (Hany Alonso, pers. comm.) and by local fishermen (Rui Filipe, pers. comm.). The unavailability of a very accessible resource such as *P. henslowii* apparently motivated the birds to consume items from higher trophic levels, in order to satisfy energetic or nutritional demands (Schwemmer & Garthe 2008). On the other hand, no differences were found in the feeding ecology of yellow-legged gulls during the non-breeding season between years. Inter-annual differences in habitat/resource use, but not in trophic level, were detected at the population level during the summer season (i.e. in P1; Ramos et al. 2011). However, these differences vanished throughout the non-breeding season, and in the winter season yellow-legged gulls exhibited a similar foraging niche between years. Since birds are confined to a limited foraging area around the colony during the breeding season, foraging opportunities should be more limited during the breeding than during the non-breeding season (Ramos et al. 2011). Thus, the differences in prey availability during the breeding season between years, particularly in the consumption of *P. henslowii*, may

be the cause of such inter-annual differences in the isotopic niche of yellow-legged gulls during the pre-laying and incubation periods.

Correlations in stable isotope ratios between different tissues can highlight particular details of seabird ecology, such as the degree of foraging specialization (Bearhop et al. 2006, Votier et al. 2010, Ceia et al. 2012). The yellow-legged gull is widely considered to be a generalist top predator species in its respective ecosystem, but our results document short- and long-term consistency in feeding ecology within individuals along seasons in two consecutive years at Berlenga. Furthermore, a similar pattern in the consistency levels was found although both years showed markedly different patterns in prey availability and oceanographic conditions during the breeding season. Specifically, we detected (1) a high level of short-term consistency within individuals in the feeding ecology (i.e. in habitat/resource use and in trophic level) between the pre-laying and the incubation periods; (2) long-term consistency in trophic level between the summer season and the pre-laying period; and (3) long-term consistency in habitat/resource use between the summer and the wintering seasons. These results suggest individual preferences in both habitat/resource use and in trophic level of this highly opportunistic and generalist species at specific stages of its annual cycle. Therefore, this characteristic may be widespread in this population and related species and could be driven mostly by traits affecting the individual (e.g. individual specialization, intra-specific competition) rather than by traits affecting the whole population (e.g. environmental conditions), as demonstrated in other species such as penguins (e.g. Cherel et al. 2007), albatrosses (e.g. Ceia et al. 2012), guillemots (e.g. Woo et al. 2008), gannets (e.g. Votier et al. 2010) and skuas (e.g. Anderson et al. 2009). However, greater variation within individuals than among individuals from the winter season to the pre-laying period, as no relationships were found between S8 and RBC for any of the two years, strongly suggests that the general feeding pattern changed within the population. These results are in accordance with Ramos et al. (2011) which reported a change in dietary preferences between breeding and non-breeding seasons on the same species in the Mediterranean. However, our study suggests that strong changes in feeding ecology of the whole breeding population occur from the winter season to the pre-laying period.

Although the sample size of tracked birds was relatively low in both years, our results suggested substantial inter-annual variation in foraging behaviour and effort of yellow-legged gulls during the incubation period in Berlenga Island. There were differences in

both spatial and temporal patterns of the trips and in its frequency. Apparently, this variability was strongly related to the availability of *P. henslowii*, which differed markedly between the two years. The unavailability of this food resource in 2011 induced birds to make longer trips to find food, particularly to the city of Peniche and its harbour, most probably to scavenge on fishery leftovers and refuse waste as our SIAR model indicates. On the other hand, in 2012 birds made smaller and more frequent at-sea trips around the colony due to the high densities of *P. henslowii*. Therefore, our results suggest that foraging behaviour of this opportunistic species is influenced to a large extent by prey conditions (namely availability of *P. henslowii*) around the colony. Similarly, Schwemmer et al. (2013) found that foraging behaviour of lesser black-backed gulls *Larus fuscus* was influenced by the availability of swimming crabs *Liocarcinus* spp. near from their colony in the North Sea; besides, inter-annual variation in foraging tactics determined by prey availability was demonstrated by Garthe et al. (2011) for a more specialized species, the northern gannet *Morus bassanus*.

Although an increase of food availability enhances breeding performance whereas adult survival is not normally affected (Pons & Migot 1995, Oro et al. 1999), our results suggest that a change in food supply and foraging behaviour, but not in individual food preferences, of yellow-legged gulls influenced the condition status and energy demand of birds. The greater BMI in 2012 than in 2011 and its positive significant relationship with the consumption of *P. henslowii* estimated by the SIAR model, clearly suggest an increase of body condition when this resource was commonly available, highlighting its importance in the diet of the yellow legged gull (Munilla 1997; this study). Although changes in haematocrit could be caused by a number of different natural factors (see Fair et al. 2007 for a review), the significant lower haematocrit value (together with greater BMI) in 2012 than in 2011, and its positive relationship with trip duration, suggest differences in physiological performance of birds related to foraging effort and energy expenditure. Similarly, other studies have reported greater haematocrit values in birds when the work load was experimentally increased during reproduction as a response to raised oxygen demands due to experimentally induced effort (Hörak et al. 1998, Fargallo et al. 2001).

Conclusions

As expected, our study confirms that opportunistic and generalist behaviour of yellow-legged gulls permits individuals to react to seasonal and inter-annual variations in resources, during the breeding and non-breeding seasons, by exploiting different foraging niches. Inter-annual changes in prey availability around the colony during the breeding season influenced variation in niche width and foraging behaviour on the population of yellow-legged gulls. This variability was strongly related with the prey crab *P. henslowii* that, when present around the colony, appears to act as a key-species for yellow-legged gulls by improving their condition status and reducing foraging effort. Results suggest that birds changed gradually their feeding behaviour throughout the year according to extrinsic factors, such as the resources available, and intrinsic factors, such as individual preferences and energy requirements. However, they showed an abrupt change in the feeding ecology at the population level between winter and the pre-laying period, suggesting this last period as the most susceptible in their annual cycle. Yellow-legged gulls showed high short-term consistency in the feeding ecology during the breeding season and long-term consistency in trophic level and habitat/resource use along seasons. Similar patterns of individual consistency were found in both years, thus highlighting individual feeding preferences in the ecological role of this opportunistic species.

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General Discussion



“The saddest aspect of life right now is that science gathers knowledge faster than society gathers wisdom.”

Isaac Asimov

The present study focused on understanding the ecology of top predators at the individual level, an area in which the knowledge is scarce for the general diversity of taxa and particularly for seabirds. Existing studies suggest that individual specialization is a widespread phenomenon across a diverse set of taxa that poses many important but unanswered questions, and the ecological implications of such trait are not well understood (see Bolnick et al. 2003 for a review). In this context, seabirds are good model species to test hypotheses concerning trophic interactions and niche variation. Here, I used three seabird species with different characteristics, exploiting four different marine habitats, to document the existence of individual variation in resource use throughout time, and demonstrate the role of individual specialization in such variation. In this study, specialization is not limited to a diet consisting of a single prey item, but the observed specialization results from a consistent mixture of resource use over time, i.e. prey consumption and habitat use. This was the first study to estimate the proportion of individuals that are consistent in their foraging niche within a population of wandering albatross (chapter 1), evidencing that this characteristic may be widespread in other seabird species. In fact, it was shown that individual foraging consistency is also an important characteristic of Cory's shearwater, a pelagic seabird species breeding in a neritic temperate region (chapter 3), and, surprisingly, also in a generalist and opportunistic species, the yellow-legged gull (chapter 4). This study also demonstrates that a wide-ranging species, the Cory's shearwater, breeding in very close sub-colonies in an oceanic temperate region exhibited colony-specific foraging areas and, consequently, a high spatial foraging segregation between individuals of the two sub-colonies during short foraging trips around the colony (chapter 2). Overall, this study demonstrates that inter-individual variation in resource use occurs within all the studied populations and species, which is necessary for natural selection and hence adaptation. By extension, individual specialization may play an important role in the foraging dynamic of the populations by reducing intra-specific competition, but further investigation is required in order to understand how ecological implications at individual level may relate to improvements in several traits such as reproductive success, body condition or foraging effort. Such implications could vary according to the species and spatio-temporal variation of the populations and respective incidence of individual specialization.

This study provides an overall picture of three different seabird species exploiting four different marine environments. Trophic relationships may differ depending on the exploited habitat and its respective food webs, translating into different resources used by individuals and, ultimately, in variation of their isotopic niche due to changes in trophic levels and baseline nitrogen and carbon signatures owing to an isotopic gradient (e.g. oceanic/neritic, pelagic/benthic, latitudinal) (Newsome et al. 2007). Responses of the seabird populations to changes in food availability within species with lower ability to switch diet (wandering albatross and Cory's shearwater) compared to more opportunistic species (yellow-legged gull) emphasized their higher vulnerability. However, vulnerability may also be higher in species with smaller foraging ranges such as terns and gulls (*Sterna* spp. and *Larus* spp.), when compared with less range-restricted species (Catry et al. 2013). In fact, the present study highlights that inter-annual changes in marine prey availability around the colony during the breeding season influenced variation in niche width and foraging behaviour of a more range-restricted species, the yellow-legged gull, which apparently had an effect on the body condition of birds. Notwithstanding, inter-annual differences in prey availability also influenced niche width and spatial distribution at sea of Cory's shearwater with apparent consequences in breeding success of birds, but no evidences were found that condition status of birds was affected. No relationships were found between foraging variables and bird condition status (body mass index and haematocrit values) of either Cory's shearwater or wandering albatross. On the other hand, concerning yellow-legged gulls, positive relationships were found between body mass index and the consumption of *Polybius henslowii* (the main prey at Berlenga Island), and between trip duration and haematocrit. Therefore, this study supports the idea that Cory's shearwaters, and possibly other procellariiform species such as the wandering albatross, invest on maintaining body condition disregarding parental investment and, consequently, reducing breeding success (Navarro & González-Solís 2007).

Our knowledge on the distribution of marine species is normally provided by ship-based surveys, which are often logistically constrained, particularly concerning pelagic species patchily distributed over vast ocean areas (e.g. Hampton 1992). This study provides important clues for the use of each studied species as indicator of changes in marine environments. For instance, consistency in habitat use tended to be greater in males than in females of wandering albatrosses over long periods (i.e. during breeding and non-

breeding seasons), thus males can reflect more reliable information on marine environment around the colonies along years. However, we must be cautious in the selection of breeding locations when using birds as indicators, because small-scale differences in breeding location could potentially lead to differences in the spatial distribution of birds at sea, even in wide-ranging species such as Cory's shearwater. The strong positive relationship between spatial distribution at sea and niche width of Cory's shearwater found in the present study supports the 'niche variation hypothesis' (Van Valen 1965) in the context of foraging ecology; this is an important finding as it confirmed that trophic niche expansion occurs via increased variation in spatial distribution at sea among individuals, and future studies may better assess each of these variables. This is the first study (to my knowledge) to provide tracking data for the yellow-legged gull, an opportunistic species usually exploiting both terrestrial and marine anthropogenic resources; data showed here, demonstrated that foraging behaviour of yellow-legged gulls during the breeding season is strongly associated with the availability of natural marine resources around the colony and, consequently, this species could be used as an indicator of marine changes at a local scale. Along with the potential use of studied species as bioindicators of marine environments, the relevance of this work for its management and conservation must be also highlighted.

Some degree of individual foraging specialization was previously documented in a large range of marine taxa, such as invertebrates (e.g. Burrows and Hughes 1991), fishes (e.g. Matich et al. 2010), sea turtles (Thomson et al. 2012), marine mammals (e.g. Tinker, Bentall & Estes 2008) and seabirds. Among the latter, individual specialization over time on foraging strategies, locations or niches have been described (e.g. Votier et al. 2010; Woo et al. 2008; this study), but remains unclear why there are such a high number of specialized and consistent individuals within seabird populations. Woo et al. (2008) suggest that the answer may be related to temporal changes in the predictability of resources and Svanbäck & Persson (2004) showed that individual specialization may fluctuate with population density through feedback mechanisms via resource levels. This study agrees with the hypothesis that individual variation in resources use may fluctuate over time (i.e. among years and periods) in a population of Cory's shearwaters depending on resources availability; individual consistency in Cory's shearwaters was higher during periods with a regular availability of food resources and lower when food availability was either abundant or scarce (chapter 3). However, no evidences of such

oscillations were found in the patterns of individual consistency of yellow-legged gulls between two years of contrasting food availability and oceanographic conditions (chapter 4). Fluctuations in individual consistency in resource use may occur depending if a seabird species/population is more or less specialized. Opportunist and generalist seabird species, like yellow-legged gulls, may present a more stable individual consistency due to the high plasticity of individual birds, which allows individual feeding preferences and adjustments to seasonal and inter-annual variations in resources by exploiting different foraging niches, as an exemplification of a type B generalization (see general introduction). On the other hand, in more specialized species like Cory's shearwaters, fluctuations on consistency may be related to temporal changes in the availability and predictability of resources and thus, more vulnerable to extrinsic factors, as suggested by Woo et al. (2008) and Svanbäck & Persson (2004). Results also suggest that birds were more specialized over short periods of time than over long periods of time, presumably because prey distributions were more predictable over short time-scales (Weimerskirch 2007). Therefore, this study supports the hypothesis that many seabirds concentrate their efforts on persistent, predictable food sources and habitats, particularly over small temporal scales (Weimerskirch et al. 2005, Weimerskirch 2007). This was more evident in wandering albatrosses and less evident in yellow-legged gulls; in species such as wandering albatrosses this may have a greater impact because they are totally dependent on resources that they can find at sea, contrasting with yellow-legged gulls' individual feeding preferences that may perpetuate over longer periods due to the exploitation of stable resources such as refuse dumps.

The ecological implications of individual specialization at individual level remain unclear. Similarly to other studies of specialization in seabirds (Votier et al. 2004; Woo et al. 2008), no evidences were found that individual specialization over time confers an advantage in terms of birds' condition status and breeding success. However, Votier et al. (2004) found some differences in the foraging effort and breeding performance (i.e. hatching dates) associated to dietary specialization of great skuas, a generalist species. The present study shows that individual consistency was high and stable across two years of contrasting food availability in yellow-legged gulls, although birds differed in foraging behaviour and body condition status. This suggests that the ecological implications of individual specialization at individual level could be more conspicuous

in generalist species (type B generalization) than in more specialized species, making them more suitable to study this issue. The rationale is because inter-individual variance is supposedly higher in a generalist population type B than in a generalist population type A or a specialist population, leading to possible improvements in several ecological traits due to substantial advantages in specialization on certain resources (e.g. higher energetic content, lower foraging effort). Nevertheless, whatever are the ecological implications at the individual level, it was shown that individual specialization plays an important role in the foraging dynamic of seabird populations. Similarly to other studies (Svanbäck & Bolnick 2007, Matich et al. 2010, Vander Zanden et al. 2010), this study emphasises the increasing evidence that individual specialization may contribute to reduce intra-specific competition among individuals, particularly on seabird species.

Future research

As one validated hypothesis leads to many other hypotheses to be tested, this study raises an important number of specific hypotheses that deserve further investigation along with those that were tested and validated but require more support. The most prominent result is that many seabird populations may present a high number of specialized and consistent individuals that could not be stable across space or time, but it remains unclear which are the ecological implications at the individual and population level. This study supports the idea that individual specialization within a seabird's population has an important role on its ecology, foraging behaviour and dynamics, namely in contributing to reduce intra-specific competition among individuals. However, I agree with Furness and Birkhead (1984) and Lewis et al. (2001) that this hypothesis is difficult to demonstrate in seabirds, because they are presumably not territorial at sea, and hence it requires further investigation.

Following raised hypothesis is related with the dissimilar inter-annual patterns of individual consistency found in Cory's shearwaters, but not in yellow-legged gulls. As previously discussed, individual consistency may fluctuate less in more generalist seabird species/populations than in more specialized species, but further studies must be conducted to validate this hypothesis. Another key-issue highlighted in this study is 'which conjecture is responsible for the fluctuation of individual consistency within a population?' This study agrees that it could be the predictability of resources as suggested by Woo et al. (2008) and Svanbäck & Persson (2004), but specifically

suggests that individual consistency could be lower or absent when food resources are either very abundant or scarce around the colonies of more specialized populations, although this hypothesis also needs validation and requires further investigation.

Together with the hypotheses raised in this study, many other unanswered ecological questions require future research as trophic interactions among individual conspecifics and their relationships with the marine environment are particularly complex. Examining the degree of individual specialization within seabirds' populations provides a better understand of such relationships. As well as documenting the existence of individual specialization, further studies should explore the timescale at which an individual's specialization is consistent, investigate the relative incidence in different populations, species and communities, and, finally, identify the mechanisms that generate inter-individual variation. Given the long history of diet analyses in seabird ecology, there are a substantial number of appropriate data sets waiting to be analyzed in conjunction with recent powerful techniques such as stable isotope analyses, logger devices and software that would permit a wide range of theoretical hypotheses for niche variation to be tested and validated.

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