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Foraging segregation between two closely related shearwaters breeding in sympatry

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Trophic segregation has been proposed as a major mechanism explaining the coexistence of closely related animal taxa. However, how such segregation varies throughout the annual cycle is poorly understood. Here, we examined the feeding ecology of the two subspecies of Cory's shearwater, *Calonectris diomedea diomedea* and *Calonectris diomedea borealis*, breeding in sympatry in a Mediterranean colony. To study trophic segregation at different stages, we combined the analysis of isotope values ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$) in blood obtained during incubation and in feathers moulted during chick-rearing and wintering periods with satellite-tracking data during the chick-rearing period. Satellite-tracking and stable isotope data of the first primary feather revealed that *C. d. borealis* foraged mainly in the Atlantic whereas *C. d. diomedea* foraged exclusively in the Mediterranean. This spatial segregation could reflect the foraging behaviour of the *C. d. borealis* individuals before they arrived at the Mediterranean colony. Alternatively, greater wing loading of *C. d. borealis* individuals may confer the ability to fly across the strong winds occurring at the at the Gibraltar strait. Isotope values of the eighth secondary feather also support segregation in wintering areas between the two forms: *C. d. diomedea* wintered mainly in association with the Canary current, whereas *C. d. borealis* wintered in the South African coast. Overall, our results show that spatial segregation in foraging areas can display substantial variation throughout the annual cycle and is probably a major mechanism facilitating coexistence between closely related taxa.

Keywords: feeding ecology; migration; satellite tracking; seabirds; stable isotopes

1. INTRODUCTION

Competition between similar species exploiting similar niches is expected to lead to ecological divergence or exclusion (Pianka 2000). However, in some cases, closely related species can coexist (Grant 1975). Partitioning of food resources has been proposed as one

of the main mechanisms explaining the coexistence of closely related seabird species (e.g. Weimerskirch *et al.* 1986). Trophic partitioning among seabird species can operate through habitat segregation or prey segregation within the same habitat (Hyrenbach *et al.* 2002). The degree of such foraging or dietary segregation among species can also vary seasonally due to different constraints associated with various components of the annual cycle such as breeding or migration. However, despite the importance of understanding mechanisms driving temporal changes in foraging segregation among species, few studies have addressed this question for sympatric species over the annual cycle (González-Solís *et al.* 2008).

Recent technological developments have provided new tools to study feeding ecology during both breeding and wintering periods. We can currently investigate the foraging ecology of seabirds by using devices to track the movements of birds (e.g. BirdLife International 2004). The analysis of stable isotopes in animal tissues has also been shown to be an effective technique for investigating the feeding habits and trophic segregation among species (Genner *et al.* 1999; Hobson *et al.* 2000). In the marine environment, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are indicators of the foraging area and trophic levels of consumers, respectively (Inger & Bearhop 2008). Their temporal integration largely depends on the growing or turnover period of the selected tissue (Inger & Bearhop 2008). For example, blood allows the study of trophic habits at different stages of the breeding season, and analysing feathers formed in different seasons allows the study of dietary differences throughout the year (Ramos *et al.* in press).

Cory's shearwater (*Calonectris diomedea*) is a migratory seabird genetically and morphologically differentiated into two forms: the Scopoli's, breeding across the Mediterranean and the Atlantic Cory's shearwater, mainly breeding in the northeast Atlantic, although individuals of both forms breed sympatrically in the Mediterranean (Gómez-Díaz *et al.* 2006). Their taxonomic status is currently being debated and some recent studies have suggested that they should be regarded as different species (Gómez-Díaz *et al.* in press). Since this debate is not resolved, we will consider them as subspecies, *Calonectris diomedea diomedea* and *Calonectris diomedea borealis*, respectively. In addition to differences in size (Gómez-Díaz *et al.* 2006), individuals from both subspecies breeding allopatrically in the Mediterranean and Atlantic colonies exhibit different migration patterns (González-Solís *et al.* 2007). Here, we combined analyses of stable isotope in blood obtained during incubation and in feathers moulted during chick-rearing and wintering periods, with satellite-tracking data during the chick-rearing period, to examine the feeding ecology of the two forms of Cory's shearwater breeding in sympatry in a Mediterranean colony. Specifically, our aims were to investigate how the two forms segregate or overlap in their feeding ecology throughout the entire annual cycle.

2. MATERIAL AND METHODS

(a) Fieldwork

We conducted this study in the Chafarinas archipelago (35°11' N; 2°26' W, southwest-Mediterranean; figure 1) where both subspecies

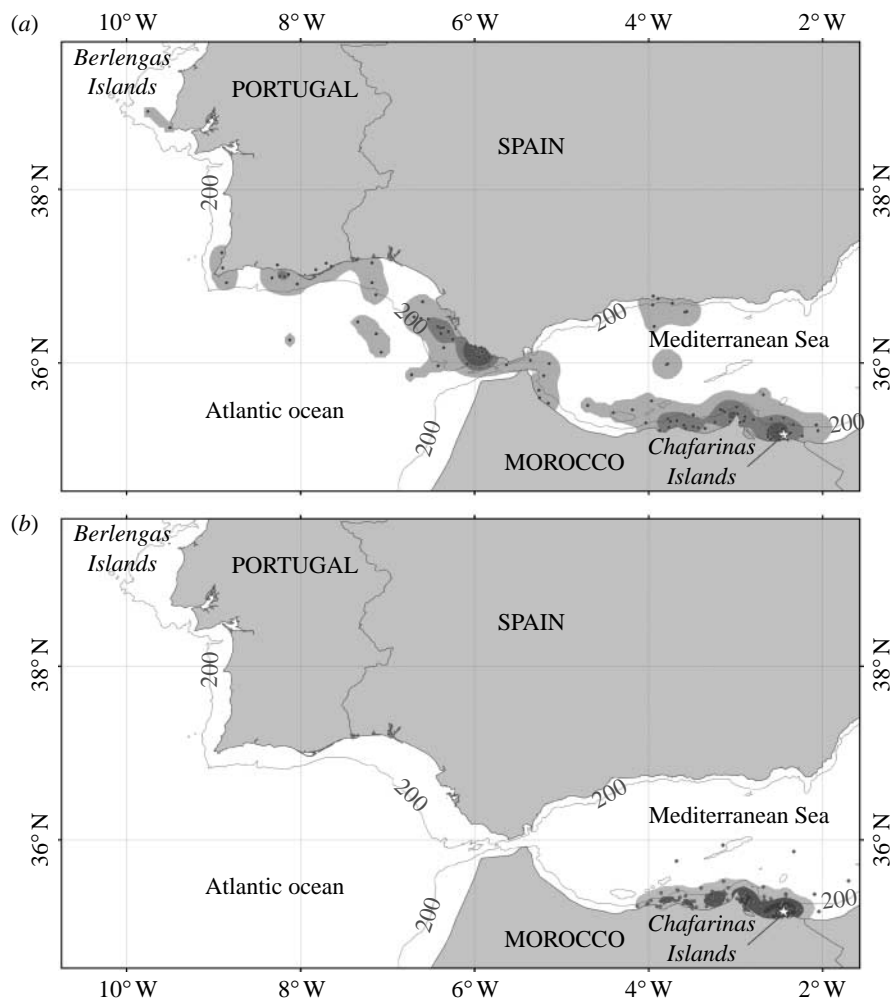


Figure 1. Location of the foraging areas that encompassed the 50, 75 and 95% satellite-tracking locations of (a) three *C. d. borealis* (dots, foraging locations; black, kernel 50%; dark grey, kernel 75%; light grey, kernel 95%) and (b) four *C. d. diomedea* during chick-rearing in 2007 (dots, foraging locations; black, kernel 50%; dark grey, kernel 75%; light grey, kernel 95%).

breed in sympatry (Gómez-Díaz *et al.* in press). During the incubation period of 2001, we took 0.2 ml of blood from 82 individuals for molecular sexing and for stable isotope analyses (trophic habits during incubation period). We also took two feathers from each individual according to its moulting period (Ramos *et al.* 2009) to analyse $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, the innermost primary (P1) moulted during the previous chick-rearing period and the eighth secondary (S8) mostly moulted during migration. Moreover, we equipped four *C. d. diomedea* and three *C. d. borealis* with 18 g platform terminal transmitters (PTTs) during the chick-rearing period of 2007 (North Star Technology, USA). The high consistency in the foraging behaviour shown for Cory's shearwater (Navarro & González-Solis 2009) suggests that although the number of tracked birds was low, the results were robust and replicable. Subspecies classification of each bird was evaluated using a cluster analysis based on biometric data (see Gómez-Díaz & González-Solis 2007).

(b) Stable isotope and statistical analyses

Stable isotopes of homogenized blood and feathers were analysed by a continuous-flow isotope ratio mass technique using a Europe 20:20 mass spectrometer (Europe Scientific, UK). All isotope abundances are expressed in δ -notation as parts per thousand (‰) deviation from standards.

To explore whether subspecies segregated with respect to their stable isotope values throughout the annual cycle (chick rearing, wintering and incubation), we performed generalized linear mixed models for each isotope. Individual identity was treated as a random term using GLIMMIX in the SAS program, and main effect of subspecies and period of the annual cycle (i.e. indicated by blood and different feathers) and their interaction were tested.

PTTs positions were obtained from the ARGOS system and were filtered following BirdLife International (2004) recommendations; trip distance covered, trip duration and foraging range were

calculated. Foraging ground was defined using kernels of 50, 75 and 95 per cent of positions. Effect of subspecies status on trip descriptors was tested by general linear models.

3. RESULTS

(a) Stable isotopes

From the 82 sampled individuals, 64 were classified as *C. d. diomedea* and 18 as *C. d. borealis* according to their morphology. Considering $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values as explanatory variables, we obtained two models that included the significant effect of period of the year ($\delta^{15}\text{N}$: $F_{2,137}=93.52$, $p<0.0001$; $\delta^{13}\text{C}$: $F_{2,137}=154.12$, $p<0.0001$) and the interaction between period of the year and subspecies ($\delta^{15}\text{N}$: $F_{2,137}=6.81$, $p=0.001$; $\delta^{13}\text{C}$: $F_{2,137}=6.42$, $p=0.002$), after controlling for the random effect of individual identity ($\delta^{15}\text{N}$: $Z=0.9$; $p=0.18$; $\delta^{13}\text{C}$: $Z=1.77$, $p=0.04$). These models explained 65.1 and 76.3 per cent of the initial deviance for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, respectively. Individuals of both subspecies showed similar blood $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values during incubation (ANOVA, all $p>0.4$). During the chick-rearing period (P1), *C. d. borealis* individuals had higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values than individuals classified as *C. d. diomedea*, but these differences were significant only for $\delta^{15}\text{N}$ ($F_{1,82}=8.1$, $p=0.006$). Both subspecies differed in

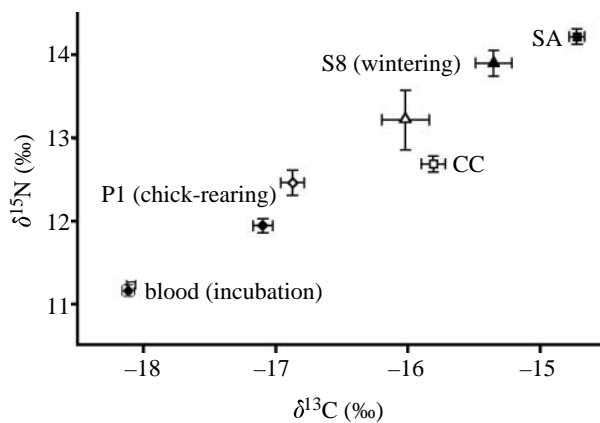


Figure 2. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (\pm s.e.) for 64 *C. d. diomedea* (white symbols) and 18 *C. d. borealis* (black symbols) individuals through the annual period; blood (incubation period of 2001). P1, first primary feather moulted at the end of the chick-rearing period of 2000; S8, eighth secondary feather moulted during the wintering period of 2000–2001. SA corresponds to Cape gannets foraging in the South Africa coast (Jaquetmet & McQuaid 2008). CC corresponds to Cape Verde shearwaters foraging in the Southern Canary Current (Gómez-Díaz & González 2007).

their $\delta^{15}\text{N}$ ($F_{1,81}=6.3$, $p=0.05$, not significant; figure 2) and $\delta^{13}\text{C}$ ($F_{1,82}=6.2$, $p=0.01$; figure 2) values during wintering (S8).

(b) Foraging movements

The three satellite-tracked *C. d. borealis* foraged mainly in the Atlantic, crossing the Gibraltar Strait. By contrast, the four satellite-tracked *C. d. diomedea* foraged exclusively in the Mediterranean, close to the breeding colony (figure 1). Trips conducted by *C. d. borealis* were longer, although differences were not significant (*C. d. diomedea* = 3.17 ± 2.55 days, *C. d. borealis* = 6.43 ± 2.81 days; $F_{1,8}=4.0$, $p=0.08$). However, *C. d. borealis* showed a higher foraging range (*C. d. diomedea* = 73.96 ± 55.96 km, *C. d. borealis* = 440.66 ± 316.47 km; $F_{1,8}=5.8$, $p=0.04$) and the trip distance covered (*C. d. diomedea* = 249.98 ± 201.73 km, *C. d. borealis* = 1102.77 ± 633.22 km; $F_{1,8}=8.3$, $p=0.02$).

4. DISCUSSION

Although breeding in sympatry, segregation in feeding ecology between the two seabird subspecies, *C. d. diomedea* and *C. d. borealis*, occurred during the chick-rearing and wintering periods. By contrast, similar blood $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values during the incubation period reported between both Cory's shearwater subspecies suggested similar feeding habits through this period. Since the incubation routine in petrels depends on relief by the partner, males and females of both subspecies need to forage relatively close to the breeding colony (Warham 1990). During the chick-rearing period, both satellite-tracking data and stable isotope values from the P1 (moulted during chick-rearing period, Ramos *et al.* 2009) revealed a spatial segregation in foraging areas between subspecies. We found that all satellite-tracked individuals of *C. d. diomedea* foraged exclusively in proximity to the breeding colony in the Mediterranean waters, whereas satellite-tracked

individuals of *C. d. borealis* mainly foraged in the Atlantic waters. Similarly, greater $\delta^{15}\text{N}$ signatures in P1 of *C. d. borealis* probably reflected the greater $\delta^{15}\text{N}$ signatures at the base of the Atlantic food web compared with lower values of the Mediterranean food web (Pantoja *et al.* 2002).

So, what mechanism leads to the spatial segregation in foraging during chick rearing? Two complementary explanations could explain this behaviour. Cory's shearwaters, similar to other pelagic seabirds, learn where and when their pelagic prey are distributed within their foraging range and may return consistently to specific feeding areas (Weimerskirch 2007; Navarro & González-Solis 2009). Individuals of *C. d. borealis* could have arrived in the Mediterranean Sea from the nearby Atlantic colonies, where they probably foraged in the Atlantic waters. After moving to the Chafarinas Islands, they may have remained faithful to their previous foraging area. Supporting this hypothesis, one satellite-tracked *C. d. borealis* foraged close to a potential population source: Berlengas Island, where about 250 pairs breed (figure 1, Granadeiro 1991). Alternatively, foraging movements of shearwaters may have been mediated by the strength and direction of winds, since seabirds with greater wing loading can cope with stronger winds (Suryan *et al.* 2009). *Calonectris diomedea borealis* are larger (Gómez-Díaz *et al.* 2006) and show greater wing loading compared with *C. d. diomedea* (J. Navarro 2008, unpublished data), and therefore are probably better prepared to fly into the strong winds flowing across the Gibraltar strait.

Similarly to P1, we found a significant difference between subspecies in the isotopic values in S8 (moulted during migration, Ramos *et al.* 2009), also suggesting spatial segregation between the subspecies in winter. It is known that, while both subspecies winter on the South African coast, *C. d. diomedea* also winters associated with the Canary current (González-Solis *et al.* 2007). Consequently, the observed differences in the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of the S8 between both subspecies probably indicate this spatial segregation in the winter areas (Ramos *et al.* in press). Indeed, feather signatures of Cape gannets (*Morus capensis*) breeding in South Africa are similar to those of *C. d. borealis*, whereas signatures from Cape Verde shearwaters (*Calonectris edwardsii*) in the P1, moulted on the southern Canary current, are similar to the values of *C. d. diomedea* (figure 2). However, the S8 signatures from *C. d. diomedea* showed more variability than *C. d. borealis* probably because a few *C. d. diomedea* also used the South Africa coast as a secondary wintering area (González-Solis *et al.* 2007).

In summary, this study reveals for the first time, to our knowledge, the segregation in the feeding ecology and foraging areas during chick-rearing and wintering periods between two closely related shearwaters, *C. d. diomedea* and *C. d. borealis*, breeding sympatrically in the Mediterranean. Our results are in line with other studies on feeding segregation in different species inhabiting freshwater (e.g. closely related fish species living sympatrically in continental lakes, Genner *et al.* 1999; and terrestrial, e.g. bear species inhabiting colder regions, Hobson *et al.* 2000) environments. This therefore highlights the value of stable isotope

analyses to address feeding segregation and coexistence of closely related taxa breeding sympatrically. More investigations are now required to improve our knowledge of the consequences of the use of different wintering or foraging areas for adult and chick survival.

All methodology was conducted following the ethical rules from the Spanish Government.

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