

Dual-foraging of Cory's shearwaters in the Azores: feeding locations, behaviour at sea and implications for food provisioning of chicks

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ABSTRACT: Many procellariiform (tube-nosed) seabirds employ a dual-foraging strategy involving repeated alternation of short and long foraging trips. For species breeding at sites around the Southern Ocean, long trips typically extend to areas of enhanced productivity at great distance from the nest. Evidence concerning the use of such areas during dual-foraging in other oceanographic regions is, however, limited. The present study examines the foraging strategy, locations and behaviour at sea of Cory's shearwaters in the Azores, a chain of 9 islands and associated islets in 3 groups straddling the mid-Atlantic ridge (MAR) in the North Atlantic Ocean. Adults used a dual-foraging strategy with an average of 3 short (1 to 4 d) trips followed by a long trip of up to 20 d (average 9 d). Short trips were evenly distributed around breeding sites within an average range of 75 km, whereas long trips without exception headed north of the Azores and extended up to 1800 km from the nest. Core foraging areas for long trips were within apparent regions of enhanced productivity resulting from cold water upwelling along the MAR north of the colony (for birds from the central Azores) or over the western flank of the MAR northwest of the colony (for birds from the western Azores). On long trips from all 3 island groups birds also visited an additional area of enhanced productivity in the region of Flemish Cap, close to the North American continental shelf edge. Birds commuted to and from distant foraging sites relatively quickly (25 km h⁻¹ on average), but individual parents did not co-ordinate their foraging activity to reduce the frequency of nights when chicks were unfed. As a result, chicks experienced much longer intervals between feeds (up to 9 nights) than conspecifics at other North Atlantic islands in the absence of dual-foraging (maximum 4 nights). However, chicks in the Azores received much larger meals when they were fed, and so the overall food provisioning rate (g d⁻¹) was similar to that recorded elsewhere.

KEY WORDS: *Calonectris diomedea* · Wildlife telemetry · Seamounts · Geolocation · Home range · Optimal foraging

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INTRODUCTION

During the breeding season, foraging behaviour forms an essential link between prey availability and predator reproductive success. Flexibility in foraging behaviour may be particularly important when the distribution and abundance of prey is variable or when parents need to travel long distances to access prey resources (Wilson et al. 2005, Hamer et al. 2007). Pelagic seabirds routinely travel long dis-

tances from the nest, making foraging trips of several hours to several days duration and travelling tens to thousands of kilometres from the breeding site on a single trip (Hedd & Gales 2005, Phillips et al. 2005). Advances in remote-sensing technology have provided increasingly detailed information on the foraging locations and behaviour of pelagic seabirds (see Weimerskirch 2007 for recent review) but there is still relatively little information on how distances travelled and behaviour during foraging trips vary in

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relation to trip duration under different environmental conditions or in relation to parental foraging strategies.

Recent studies have shown that many procellariiform (tube-nosed) seabirds employ a dual or bimodal foraging strategy that alternates short foraging trips, used mainly to procure food for the chick, with trips of longer duration during which parents replenish their own nutritional reserves depleted during short trips (Weimerskirch et al. 1994, Stahl & Sagar 2000, Terauds & Gales 2006). For species breeding at sites around the Southern Ocean, long trips typically extend to areas of enhanced productivity associated with continental shelves, shelf slopes or frontal zones at great distance from the nest, in particular the Antarctic Polar Frontal Zone, more than 2000 km from many breeding colonies (Waugh et al. 1999, Catard et al. 2000, Klomp & Schultz 2000). Evidence concerning the use of such areas of enhanced productivity in other oceanographic regions is, however, limited (Hyrenbach et al. 2002). Adults could remain close to the colony but take prey solely for their own use during trips of long duration rather than visiting distant sites (Ropert-Coudert et al. 2004, Congdon et al. 2005), and there is very little information concerning destinations of long trips for regions other than the Southern Ocean (Weimerskirch et al. 2001, Hamer et al. 2006). Indeed, little is known about the prevalence of dual-foraging among Procellariiformes in other regions (see Baduini & Hyrenbach 2003 for recent review).

In the northern hemisphere, Laysan albatrosses *Phoebastria immutabilis* and black-footed albatrosses *P. nigripes* nesting in the Hawaiian Islands employ bimodal foraging-trip strategies, with long trips visiting productive regions associated with frontal zones in colder waters and at higher latitudes (Fernandez et al. 2001, Hyrenbach et al. 2002). However, wedge-tailed shearwaters *Puffinus pacificus* at the same site do not use a dual-foraging strategy and appear to forage mainly in waters close to the colony (Baduini 2002), which casts doubt on whether the findings for albatrosses have general validity for other Procellariiformes. Moreover, whilst wedge-tailed shearwaters do exhibit dual-foraging in NE Australia (Congdon et al. 2005), it is not known whether or not foraging ranges differ between short and long trips in that region.

In the North Atlantic Ocean, there is little evidence of bimodal foraging trips and the marine environments exploited by Procellariiformes are only poorly understood (Mougin & Jouanin 1997, Gray & Hamer 2001, Weimerskirch et al. 2001). Cory's shearwaters *Calonectris diomedea* in the sub-tropical North Atlantic exhibited dual-foraging under conditions of low food availability around the colony in 1997 (Granadeiro et

al. 1998a) but not in other years or at other sites with higher chick-feeding rates (Granadeiro et al. 1998a, Hamer et al. 1999) and the foraging ranges and locations of adults during chick-rearing were again unknown. Thus, further data are needed, particularly for species other than albatrosses, to determine the prevalence of dual-foraging and the locations and behaviour of birds on trips of different duration in oceanographic regions beyond the Southern Ocean.

Large populations of Cory's shearwaters (50 000 to 90 000 pairs, comprising >70% of breeding numbers of the Atlantic subspecies *Calonectris diomedea borealis*; Monteiro et al. 1996) breed in the Azores, a chain of 9 islands and associated islets in 3 groups straddling the mid-Atlantic ridge (MAR) over a distance of about 600 km (see Fig. 1). Marine transects along the MAR have recorded adults of this species foraging in association with dolphin species over 1000 km north of the Azores during the breeding season (Nøttestad & Olsen 2005) and this raises the possibility that adults breeding in the Azores may employ dual-foraging to exploit prey resources in such distant locations. Cory's shearwaters are opportunistic predators, and diets of adults in the eastern Azores differ markedly from those in the central and western islands during chick-rearing (Granadeiro et al. 1998b). However, it is not known to what extent this pattern reflects variation in the marine environments utilized by adults. The present study examines the foraging strategy, locations and behaviour at sea of Cory's shearwaters in the Azores. We test the hypothesis that adults employ dual-foraging to exploit productive regions in waters north of the archipelago and examine how foraging locations and behaviour vary between island groups. Dual-foraging, which involves making both short and long trips, could result in longer average intervals between feeds and lower overall feeding rates of chicks (g d^{-1}) compared to unimodal foraging, but there are few data within individual species to address this issue (Granadeiro et al. 1998a, Terauds & Gales 2006). Hence we also assess the impact of variation in foraging strategy on the food provisioning rates of chicks.

MATERIALS AND METHODS

Species and study sites. Cory's shearwaters breed throughout the Azores Islands, and the present study was conducted at 3 sites spanning the archipelago (Fig. 1): Corvo Island in the western group (40°N, 31°W), Praia Islet near Graciosa in the central group (39°N, 28°W) and Vila Islet near Santa Maria in the eastern group (37°N, 25°W). Adults in the Azores nest in burrows and lay a single egg, which typically hatches in mid- to late July. Chicks are fed nocturnally

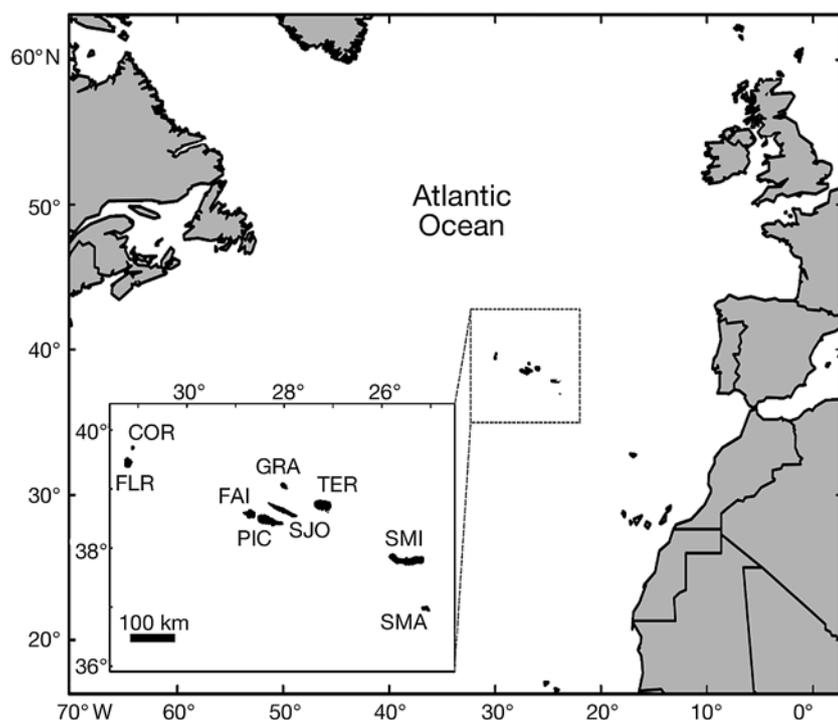


Fig. 1. North Atlantic Ocean showing position of Azores archipelago. Inset shows individual islands. Western Group: COR = Corvo, FLR = Flores; Central Group: GRA = Graciosa, FAI = Faial, PIC = Pico, SJO = São Jorge, TER = Terceira; Eastern Group: SMI = São Miguel, SMA = Santa Maria. Study sites were at Corvo and islets offshore from Graciosa and Santa Maria

by both parents for about 90 d before fledging in mid- to late October. Chicks are fed small meals relatively frequently (>95% of chicks fed each night) for the first 10 d post-hatching and are fed infrequently (<25% of chicks fed each night) prior to fledging, but both meal size and feeding frequency are more or less independent of chick age over the range 10 to 70 d (Hamer & Hill 1993, Ramos et al. 2003).

Field protocol. Fieldwork took place from late July to mid-September 2004 to 2006, and all data were for nests with chicks aged 10 to 60 d (chick ages determined shortly after hatching by calibration of wing-length against growth in birds of known age; Granadeiro 1991). Over the 3 yr of the study, 82 adults were captured at night by hand at nests with hatching dates ± 2 wk from the annual mode ($n = 18$ birds in the western Azores plus 19 birds in the eastern Azores in 2004, 35 in the eastern Azores in 2005, and 10 in the central Azores in 2006). A VHF radio-transmitter (ATS in 2004; Biotrack in 2005) weighing 15 and 10 g, respectively (<2% of body mass in each case) was attached to the back feathers of 59 birds ($n = 10$ in the western Azores plus 19 birds in the eastern Azores in 2004, and 30 in the eastern Azores in 2005) using waterproof tape (Tesa). In addition, a platform terminal

transmitter (PTT; Microwave Telemetry) weighing 30 g (<4% of adult mass) and with a duty-cycle of continuous transmission was attached to 23 birds ($n = 8$ in the western Azores in 2004, 5 in the eastern Azores in 2005, and 10 in the central Azores in 2006) in the same way as for radio-transmitters. A blood sample (less than 0.1 ml) was also taken under licence from the tarsal vein of each bird for DNA sexing following Fridolfsson & Ellegren (1999). Attachment of tags and blood-sampling took <15 min and birds were then returned immediately to the nest.

Trip durations and foraging behaviour

at sea. After release, visits of radio-tagged birds to the colony were recorded for a mean of 44 d ($SD \pm 25$) during chick-rearing each year, using an ATS R4500 scanning receiver attached to an ATS omni-directional antenna located at the colony. Field trials indicated that the range of this system was ca. 1 km, so we were confident that signals received were from birds in the vicinity of their nests and not at sea. Birds carrying PTTs were tracked for a mean of 17 d ($SD \pm 5$) over a period of 38 to 44 d during chick-rearing each year. A recent review of effects of transmitters indicated negligible adverse

effects for tags weighing up to 3% of adult body mass (Phillips et al. 2003), and for Cory's shearwaters, 12 to 15 g data loggers and radio-transmitters had no discernible impacts on foraging, nest attendance or food delivery to chicks (Hamer et al. 1999, Igual et al. 2005). In addition, there was no significant difference in our study between foraging trip durations of birds carrying radio-transmitters (2.8 ± 3.7 d, $n = 940$) and those carrying PTTs (3.2 ± 3.9 d, $n = 100$; generalized linear model, GLM, including island and trip type [long or short; see 'Results'] as fixed effects, and bird identity nested within island as a random effect; $F_{1,985} = 0.1$, $p = 0.7$). Data were collected over a period of 3 yr but there was no difference between trip durations of birds in the eastern Azores in 2004 and 2005 (GLM; $F_{1,189.7} = 1.9$, $p = 0.2$), suggesting that foraging behaviour did not vary from year to year.

Data provided by PTTs were processed using the Advanced Research and Global Observation Satellite (ARGOS) facility in France (Centre National d'Etudes Spatiales, CNES). Following previous authors (e.g. Hedd et al. 2001, Hamer et al. 2007), we used only data of Class A or better (average of 13.3 locations $\text{bird}^{-1} \text{d}^{-1}$) to examine foraging locations at sea, giving us a maximum SD on each location of <10 km, which was

small in comparison to distances travelled by birds (see Table 1). Locations of birds at sea were examined in Arc-View GIS and the scale of movements each year was compared using fixed kernel density (FKD) estimates with least-squares cross-validation (Worton 1989, Beisiegel & Mantovani 2006). Following previous authors (e.g. Iversen & Esler 2006, Hamer et al. 2007) we considered the 95% and 50% FKD estimates to represent the area of active use and the core area of foraging activity, respectively.

To examine individual foraging trips in more detail, we used the furthest recorded location from the colony during each trip to provide information on trip destinations and we also calculated total distance travelled as the sum of distances between consecutive locations at sea. The average speed of travel during trips was then calculated as (total distance/duration), and the directness of travel was estimated by calculating the maximum range as a percentage of the total distance travelled.

In order to examine movements over shorter intervals within the total foraging ranges of birds, we estimated travel speeds during short sections of each trip as the distance between consecutive pairs of locations divided by the time elapsed between them. The time between locations influenced the estimated speeds of travel, with increasing underestimates resulting from locations spaced further apart ($F_{4,4451} = 64.4$, $p < 0.001$). Specifically, estimates from locations separated by ≤ 2 h (21.7 ± 19.2 km h⁻¹, $n = 3547$) were significantly greater than those at all longer temporal resolutions (2–4 h, 12.1 ± 4.0 km h⁻¹, $n = 707$; 4–6 h, 7.8 ± 4.1 km h⁻¹, $n = 137$; 6–8 h, 7.3 ± 4.6 km h⁻¹, $n = 33$; 8–10 h, 7.8 ± 4.8 km h⁻¹, $n = 32$; Tukey's HSD, $p < 0.01$). We therefore limited further analysis of travel speeds to locations spaced by ≤ 2 h ($n = 3547$).

Food delivery to the nest. Parental food provisioning can be partitioned into the probability that a chick is fed overnight (derived from feeding frequency) and the mass of food delivered when fed (here termed feed size). To quantify feed sizes and feeding frequencies of chicks at each island, a sample of chicks aged 10 to 60 d ($n = 14$ in the western, 17 in the central, and 46 in the eastern Azores) was weighed to the nearest 5 g using a Pesola spring balance at 20:00 h (before the first parents returned overnight) each day from 29 July to 6 September 2004 (39 d) in the western Azores, from 3 August to 17 September 2006 (45 d) in the central Azores and from 4 August to 7 September 2005 (34 d) in the eastern Azores (range of ages: western Azores, 10–52 d, mean = 29.2 ± 11.2 d; central Azores, 10–59 d, mean = 32.9 ± 13.5 d; eastern Azores, 10–50 d, mean = 26.5 ± 9.7 d). Chicks were also weighed at 01:00 h and 06:00 h (after the last parents had departed each morning) on up to 10 nights at each colony. Feed size was

calculated from the sum of positive mass increments recorded overnight, using equations in Hamer et al. (1999) to correct for the mass lost through digestion, respiration and excretion between weighings. Feeding frequency was then estimated from net daily mass changes calibrated against overnight feeding, following Hamer & Hill (1997).

Data analysis. In many cases we recorded more than 1 foraging trip per bird. To examine individual variation in foraging and food provisioning behaviour and to take account of potential pseudoreplication of data, we therefore used generalized linear models (GLMs), or generalized linear mixed models (GLMMs) for non-normal data, with island included as a fixed effect and bird identity included as a random effect nested within island. Means are given ± 1 SD unless otherwise stated.

RESULTS

Foraging trip durations and time spent foraging

We recorded the duration of 1040 trips of 82 birds at 3 colonies (134 trips of 18 birds in the western Azores in 2004; 855 trips of 54 birds in the eastern Azores in 2004 and 2005; 51 trips of 10 birds in the central Azores in 2006). Trips lasted up to 20 d but the majority of trips (71%) were a single day (Fig. 2). The frequency distribution of trip durations was bimodal with 2 separate peaks in abundance at durations of 1 d and 10 d (Fig. 2a), indicating a clear separation between short and long trips. The proportion of time at sea spent on trips of different duration showed a similar pattern, with trips lasting 4 to 5 d being less frequent and taking up less of the birds' time than either shorter or longer trips (Fig. 2b). Classifying trips of 1 to 4 d as short trips (ST) and those of ≥ 5 d as long trips (LT), birds spent $35.5 \pm 16.3\%$ of their time on STs (mean duration = 1.1 ± 0.4 d, $n = 836$) and $64.5 \pm 16.3\%$ of their time on LTs (mean = 9.8 ± 3.1 d, $n = 204$), with no difference between islands in the distribution of STs and LTs (Fig. 2c). Each bird visited the nest on $36.7 \pm 15.4\%$ of nights (Table 1) with no difference in this proportion among islands or between males and females (analysis of variance using arcsine-transformed data; $F_{2,71} = 0.7$, $p = 0.5$ and $F_{1,71} = 0.02$, $p = 0.9$, respectively). On average, each bird made 3 STs between consecutive LTs (mean = 2.98 ± 2.7 , $n = 124$, range = 0 to 12), with the duration of LTs significantly positively related to the number of consecutive preceding STs (GLM; $F_{1,77} = 6.5$, $p = 0.01$). There was no difference in the slope or elevation of this relationship among islands, between males and females or among birds at each island ($p > 0.1$ in all cases).

Foraging locations

The maximum distance of STs was 588 km from the colony in the western Azores, 214 km in the central Azores and 107 km in the eastern Azores (Fig. 3). The duration of STs from the western Azores were more than 50 % longer on average than those from the other island groups (Table 1; GLMM; $\chi^2_2 = 14.3$, $p < 0.01$), maximum range (GLM; $F_{2,21.2} = 4.5$, $p < 0.05$) and total distance travelled ($F_{2,20.4} = 3.7$, $p < 0.05$), with no significant difference between males and females or among birds at each island ($p > 0.5$ in each case). Destinations of STs were mainly over the MAR and were widely spaced, with a similar frequency of trips north and south at all 3 islands (Fig. 3; western Azores, 7 north, 12 south, $\chi^2_1 = 0.7$, $p = 0.5$; central Azores, 29 north, 12 south, $\chi^2_1 = 3.7$, $p = 0.1$; eastern Azores, 10 north, 5 south, $\chi^2_1 = 0.9$, $p = 0.5$).

In the central and eastern Azores, trips north and south were similar in terms of duration, range and distance travelled ($p > 0.1$ in all cases). In the western Azores, however, trips north were much longer than trips south in terms of duration (2.1 ± 0.9 d and 1.1 ± 0.3 d, respectively; $F_{1,13.3} = 10.7$, $p < 0.01$), maximum range (270.3 ± 214.1 km and 38.6 ± 28.3 km, respectively; $F_{1,14.9} = 10.2$, $p < 0.01$) and total distance travelled (711.4 ± 502.6 km and 186.7 ± 106.1 km respectively; $F_{1,14.4} = 8.5$, $p = 0.01$). This was because trips south mainly stayed close to the coasts of Corvo and Flores (the 2 western islands; Figs. 1 & 3), whereas some trips north headed across deep water (>3000 m) west of the MAR (Fig. 3). FGD estimates indicated that the area used for foraging (95 % FGD) was largest in the western Azores; 5.2 times larger than in the central Azores and 9.4 times larger than in the eastern Azores (Table 1), with no overlap between islands in areas used (Fig. 3). The core foraging area (50 % FGD) was also largest in the western Azores; 4.7 times larger than in the central Azores and 9.2 times larger than in the eastern Azores. Despite these differences between islands in terms of distances travelled on STs, the core foraging area was a similar proportion of the total area used in each case (14.0% in the western, 15.4% in the central Azores, and 14.3% in the eastern Azores; calculated from data in Table 1).

LTs without exception headed north of the Azores, to a maximum range of 1315 km for birds nesting in the western Azores, 1528 km for the central Azores and 1819 km for the eastern Azores (Fig. 4). Trips from the central Azores almost all headed along the MAR, with maximum ranges mainly at 45 to 48°N but with some trips extending as far as the Charlie Gibbs Fracture Zone at 52°N (Fig. 4). Trips from the western Azores nearly all headed NW of the colony, with maximum ranges mostly along the western edge of the MAR but with some trips heading across deeper water (>3000 m; Fig. 4). Foraging tracks of birds from the

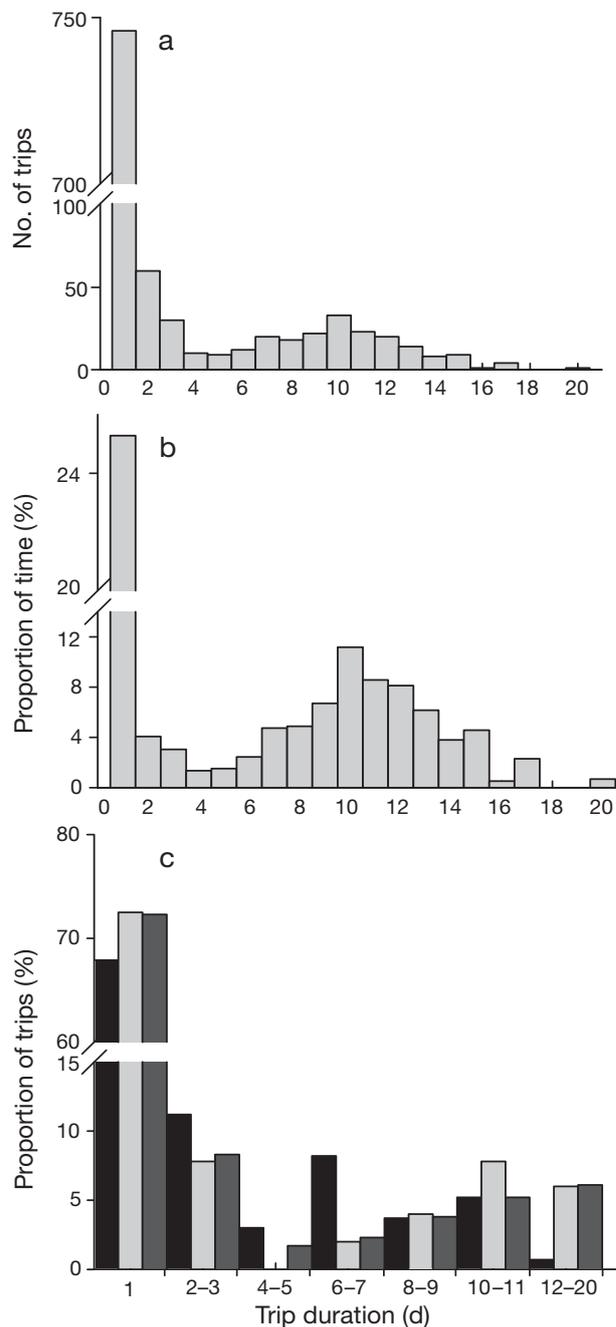


Fig. 2. *Calonectris diomedea*. (a) Durations of foraging trips by adults raising chicks at colonies in the Azores; (b) proportion of time spent on trips of different durations; (c) proportions of trips of different durations in the western Azores (black), central Azores (light grey) and eastern Azores (dark grey)

eastern Azores were more variable, with destinations both east and west of the MAR, from 15 to 44°W. At least 1 LT from each island took birds close to the North American continental shelf east of Newfoundland at Flemish Cap (Fig. 4). There was extensive overlap in the foraging paths and total foraging areas (95 % FGDs) of birds from different islands, both along the MAR and

Table 1. *Calonectris diomedea*. Characteristics of foraging trips made by adults rearing chicks at different islands in the Azores. Attendance at nest and trip durations based on 134 trips (106 short, 28 long) of 18 birds in the western Azores; 51 trips (41 short, 10 long) of 10 birds in the central Azores; 855 trips (689 short, 166 long) of 54 birds in the eastern Azores. All other data from satellite telemetry of 30 trips (19 short, 11 long) of 8 birds in the western Azores, 51 trips (41 short, 10 long) of 10 birds in the central Azores, 19 trips (15 short, 4 long) of 5 birds in the eastern Azores. FKD: fixed kernel density

Island group and trip	Prop. nights birds at nest		Trip duration (d)		Max. distance (km)		Total distance (km)		95 % FKD (km ²)	50 % FKD (km ²)	Speed ^a (km d ⁻¹)		Speed ^b (km d ⁻¹)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD			Mean	SD	Mean	SD
Western	0.34	0.14												
Short			1.53	0.80	133.7	177.7	406.2	413.9	15922	2226	125.0	48.5	222.6	58.8
Long			7.09	1.92	758.4	294.2	2487.3	926.7	562457	57654	214.4	56.7	348.9	72.1
Central	0.33	0.18												
Short			1.15	0.48	55.9	41.3	230.2	160.4	3039	469	86.0	38.5	193.5	69.7
Long			10.60	2.68	1233.5	204.6	4209.5	481.9	778266	73029	241.4	81.7	409.0	99.7
Eastern	0.38	0.15												
Short			1.07	0.27	54.4	31.9	234.7	120.3	1690	242	99.1	38.1	206.4	62.3
Long			9.76	3.56	1570.3	220.6	5573.8	827.1	1286950	94172	209.5	19.5	371.2	33.6

^aCalculated using maximum distance from the colony; ^bCalculated using total distance travelled

in the vicinity of the North American continental shelf. However the core foraging areas (50 % FKDs) were widely separated and non-overlapping (Fig. 5).

Together with differences in core foraging areas, LTs from the western Azores were 40 to 50 % shorter on average than those elsewhere in terms of duration (Table 1; GLM; $F_{2,20.6} = 18.3$, $p < 0.001$) maximum range from the colony ($F_{2,19.7} = 15.5$, $p < 0.001$) and total distance travelled ($F_{2,20.2} = 24.9$, $p < 0.001$), with no significant difference between sexes or among birds at each island ($p > 0.3$ in each case). The area used for foraging (95 % FKD) in the western Azores was 0.72 times that in the central Azores and 0.44 times that in the eastern Azores, whilst the core foraging area (50 % FKD) was 0.79 times that in the central Azores and 0.61 times that in the eastern Azores (Fig. 5). As with STs, the core foraging area was a similar proportion of the total area used around each island (10.3 % in the western, 9.4 % in the central, and 7.3 % in the eastern Azores; from data in Table 1). The total area encompassed by STs and LTs from all 3 islands was ca 1.8 million km² (Figs. 3 & 4).

Average speeds of travel over complete trips

Across all foraging trips, there was a positive linear relationship between trip duration and both maximum range from the colony (GLM excluding intercept; $F_{1,73} = 33.6$, $p < 0.001$, $R^2 = 0.93$) and total distance travelled ($F_{1,73} = 48.2$, $p < 0.001$, $R^2 = 0.96$). The slopes of these relationships were significantly higher for LTs than for STs (for maximum range, $F_{1,73} = 4.7$, $p < 0.05$; for total distance travelled, $F_{1,73} = 7.8$, $p < 0.01$), indicating a higher rate of travel during LTs, according to the following relationships for STs:

$$\begin{aligned} \text{Maximum distance (km)} = \\ 69.5 \text{ (SE } \pm 6.8) \text{ trip duration (d)} \end{aligned} \quad (1)$$

$$\begin{aligned} \text{Total distance (km)} = \\ 232.0 \text{ (SE } \pm 17.1) \text{ trip duration (d)} \end{aligned} \quad (2)$$

and for LTs:

$$\begin{aligned} \text{Maximum distance (km)} = \\ 107.6 \text{ (SE } \pm 5.1) \text{ trip duration (d)} \end{aligned} \quad (3)$$

$$\begin{aligned} \text{Total distance (km)} = \\ 371.8 \text{ (SE } \pm 13.1) \text{ trip duration (d)} \end{aligned} \quad (4)$$

Average speed during these trips was thus estimated as 139 (SE ± 14) km d⁻¹ during STs and 215 (SE ± 10) km d⁻¹ during LTs (twice the slope of Eqs. 1 and 3, respectively) using maximum range from the colony, and as 232 (SE ± 17) km day⁻¹ during STs and 372 (SE ± 13) km day⁻¹ during LTs (the slopes of Eqs. 2 and 4, respectively) using total distance travelled. GLMs indicated no difference between islands in the slopes of these relationships ($p > 0.1$ in both cases) and this was confirmed by comparison among islands of the mean travel speeds for individual birds (Table 1; 1-way ANOVA using a single value for each bird; from maximum range from the colony, $F_{2,15} = 1.6$, $p = 0.2$ and $F_{2,18} = 0.5$, $p = 0.6$ for ST and LT, respectively; from total distance travelled, $F_{2,15} = 0.4$, $p = 0.7$ and $F_{2,18} = 1.2$, $p = 0.3$ for ST and LT, respectively). The maximum range comprised $29.6 \pm 3.5\%$ ($n = 25$) of the total distance travelled during LTs, significantly more than during STs ($25.0 \pm 9.9\%$ ($n = 75$; GLM using arcsine-transformed data; $F_{1,74} = 10.5$, $p = 0.002$), suggesting that birds travelled to foraging areas and back more directly during LTs. Directness of travel also varied significantly among individuals at each island ($F_{19,74} = 3.0$, $p < 0.001$) but did not differ between islands ($F_{2,26.5} = 0.2$, $p = 0.8$).

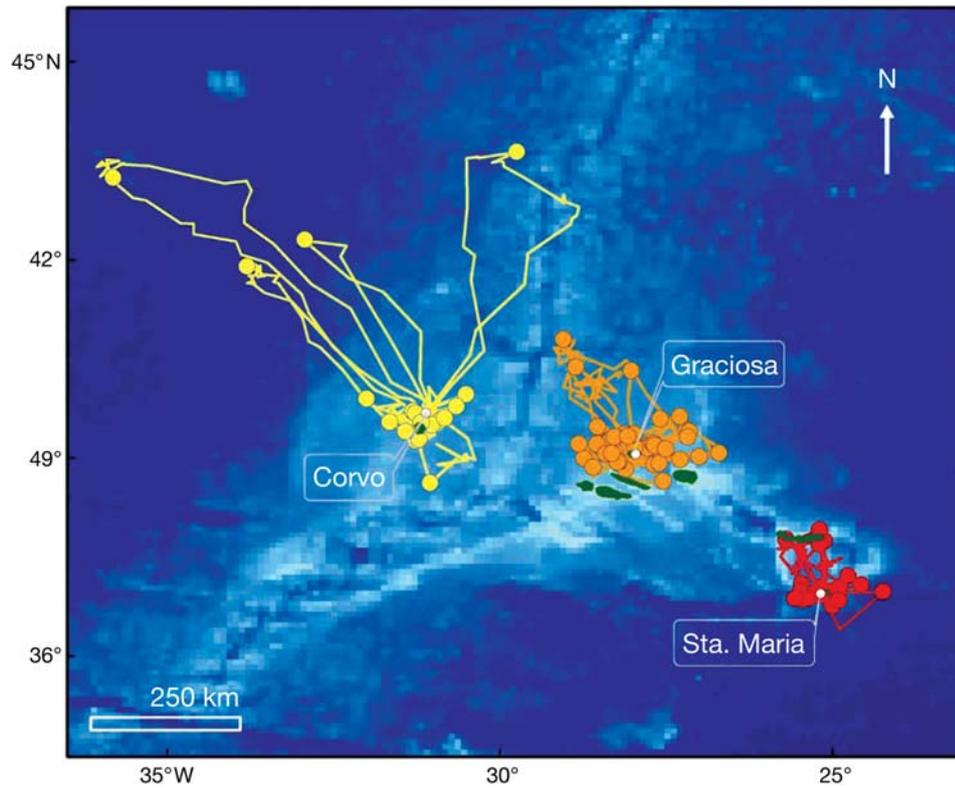


Fig. 3. *Calonectris diomedea*. Foraging ranges and destinations of short trips (1 to 4 d) from 3 islands in the western (yellow), central (orange) and eastern (red) Azores. Circles mark maximum ranges for individual foraging trips. Palest blue indicates depths below 1000 m and darkest blue depths above 3000 m

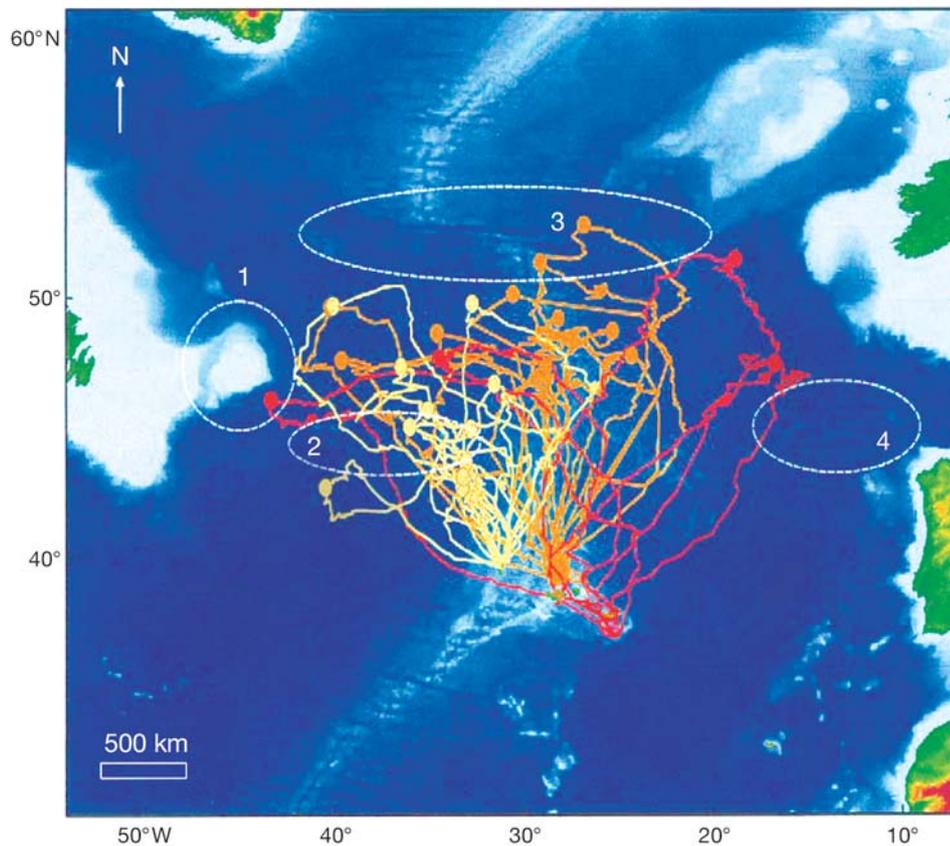


Fig. 4. *Calonectris diomedea*. Foraging ranges and destinations of long trips (5 to 18 d) from 3 islands in the western (yellow), central (orange) and eastern (red) Azores. Circles mark maximum ranges for individual foraging trips. Oceanographic features: 1 = Flemish Cap; 2 = Milne seamounts; 3 = Charlie Gibbs Fracture Zone; 4 = Charcot seamounts. Palest blue indicates depths below 1000 m and darkest blue depths above 3000 m

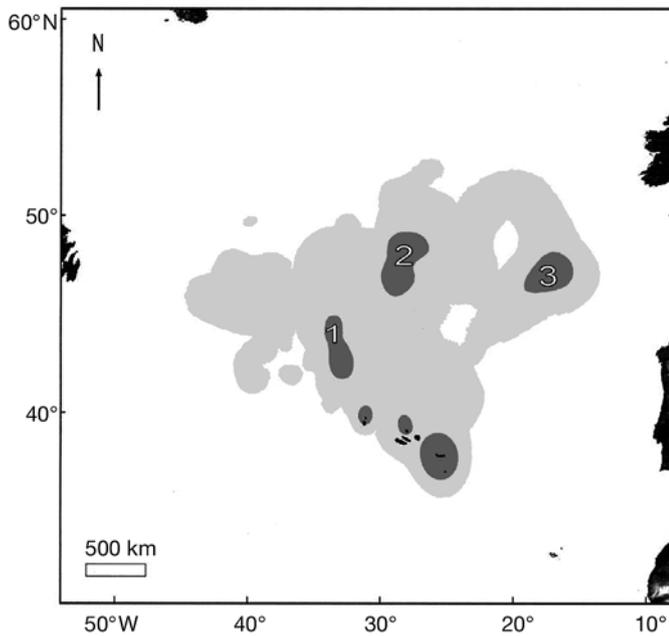


Fig. 5. *Calonectris diomedea*. Kernels encompassing 50% (dark grey) and 95% (light grey) of locations at sea during long trips from 3 islands in the Azores. Areas encompassing 95% of foraging locations for birds from different islands overlapped extensively, but those encompassing 50% of locations were non-overlapping (numbered 1, 2 and 3 for the western, central and eastern Azores respectively)

Variation in travel speeds during trips

Speeds of travel over intervals ≤ 2 h within trips (see 'Materials and methods') were significantly higher during the day (mean per trip = 16.8 ± 6.6 km h⁻¹, n = 100 trips) than at night (10.2 ± 6.7 km h⁻¹, n = 100; paired *t*-test; $t_{99} = 8.7$, $p < 0.001$). This difference was apparent during both STs (14.7 ± 5.8 km h⁻¹, n = 75 by day, 9.2 ± 6.9 km h⁻¹, n = 75 at night; paired $t_{74} = 5.9$, $p < 0.001$) and LTs (23.2 ± 4.5 km h⁻¹, n = 25 by day, 13.1 ± 5.1 km h⁻¹, n = 25 at night; paired $t_{24} = 9.4$, $p < 0.001$). For LTs, we used the total distance travelled over the first and final 2 d of the trip to estimate average speed during the outward and return sections of the trip, respectively. Birds travelled out from the colony and returned at similar speeds (23.8 ± 8.0 km

h⁻¹, n = 25 and 25.7 ± 8.0 km h⁻¹, n = 25 respectively), about 50% faster than during the middle section of the trip (17.5 ± 4.7 km h⁻¹, n = 25). Similarly, the straight-line distance between locations at the beginning and end of each section comprised a much greater proportion of the total distance travelled during outward and return legs ($67.1 \pm 13.7\%$, n = 25 and $74.3 \pm 13.5\%$, n = 25, respectively) than during the middle section of the trip ($29.4 \pm 17.0\%$, n = 25), indicating much less sinuous flight-paths on the outward and return legs.

Food provisioning rates of chicks

Over the period 10 to 60 d post-hatching, when food provisioning rate is independent of chick age (Ramos et al. 2003), each chick was fed on $59.3 \pm 9.7\%$ of nights (n = 77 chicks), with no difference in this proportion between islands (Table 2; 1-way ANOVA of arcsine-transformed data with a single mean value for each chick; $F_{2,74} = 2.6$, $p = 0.1$). Intervals between meals delivered to chicks ranged from 1 to 9 d (Fig. 6), with an average interval of 1.69 ± 1.2 d (n = 77 chicks) and no difference in intervals between islands (Table 2; Kruskal-Wallis $\chi^2_2 = 1.69$, $p = 0.4$). When fed, chicks received 127.2 ± 42.1 g of food overnight (Table 2) with no difference between islands in mean feed size per chick ($F_{2,74} = 0.6$, $p = 0.5$). Chicks at all 3 islands received significantly larger feeds when tagged parents returned from LTs (mean = 154.9 ± 53.5 g, n = 28) than from STs (mean = 113.5 ± 62.1 g, n = 152; GLMM; for difference between LTs and STs, $F_{1,144} = 13.2$, $p < 0.001$; for difference between islands, $F_{2,144} = 0.9$, $p = 0.5$). The overall food provisioning rate was 75.8 ± 27.1 g night⁻¹ (Table 2) and the mean mass growth rate of chicks was 14.1 ± 3.7 g d⁻¹ (Table 2), with no difference between islands in either case ($F_{2,74} = 0.9$, $p = 0.9$ and $F_{2,74} = 3.0$, $p = 0.1$, respectively).

DISCUSSION

Cory's shearwaters breeding in the Azores employed dual-foraging to exploit feeding areas up to 1800 km from the nest (average range = 1107 km; from data in

Table 2. *Calonectris diomedea*. Food provisioning and growth rates of chicks. Based on 14 chicks in the western Azores, 17 in the central Azores and 46 in the eastern Azores

Island group	Proportion of nights chick fed		Interval between feeds (d)		Feed size (g)		Provisioning rate (g night ⁻¹)		Mass growth rate (g d ⁻¹)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Western	0.61	0.10	1.62	1.01	115.9	28.3	72.8	24.1	14.2	3.7
Central	0.63	0.11	1.64	1.17	121.0	29.7	77.7	22.3	15.9	3.3
Eastern	0.58	0.10	1.74	1.27	130.5	47.5	75.8	25.9	13.4	3.7

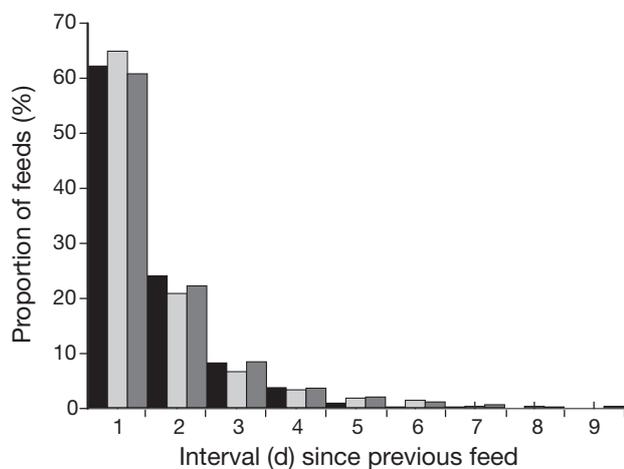


Fig. 6. *Calonectris diomedea*. Intervals between successive feeds for chicks at 3 islands in the Azores (black: western Azores; light grey: central Azores; dark grey: eastern Azores)

Table 1). This supports the notion that dual-foraging among Procellariiformes to exploit sites at great distance from the nest is not confined to the Southern Ocean or to albatrosses in other oceanographic regions. Dual-foraging was not recorded, however, in Cory's shearwaters breeding in the Berlengas Islands off the west coast of Portugal or in most years studied in the Selvagens Islands, 1400 km SE of the Azores in the North Atlantic Ocean (Hamer & Hill 1993, Granadeiro et al. 1998a, Hamer et al. 1999). Thus, foraging strategies of individual species of Procellariiformes may vary both spatially and temporally, presumably in relation to variation in the distribution and abundance of pelagic prey resources around different breeding sites (Baduini & Hyrenbach 2003, Congdon et al. 2005). The consistent presence of dual-foraging in this study suggests that prey availability close to land may be lower on average in the Azores than at other North Atlantic colonies of this species.

STs from all 3 island groups in the Azores tended to remain close to the MAR, with only trips from the western Azores heading away from the ridge across deep water, the longest short trip extending to a small cluster of seamounts at the eastern extremity of the Milne seamount chain west of the MAR (Figs. 3 & 4). In contrast to studies in other oceanographic regions (e.g. Catard et al. 2000), STs in the Azores were widely spaced and not restricted to a narrow range of locations, presumably indicating a more even distribution of prey resources around breeding colonies in the Azores. There was a clear distinction between STs and LTs in the central and eastern Azores, but less so in the western Azores, where the destination of the longest ST was beyond the core foraging area during LTs (Figs. 3 & 5).

Core foraging areas of LTs from the central and western Azores were over the MAR north of the colony and

over the western flank of the MAR northwest of the colony, respectively (Figs. 4 & 5). The MAR north of the Azores is a likely area of enhanced productivity resulting from cold water upwelling and eddies, particularly in the vicinity of seamounts (Haney et al. 1995, Haury et al. 2000, Morato et al. 2008a,b), which have their highest density between the Azores and the Charlie Gibbs Fracture Zone at 52°N (Epp & Smoot 1989, Gubbay 2003). The density of seamounts along the MAR declines markedly north of this zone, and this was the most northerly location of foraging birds during the study (Fig. 4). In addition, at least 1 LT from all 3 island groups extended as far as Flemish Cap east of Newfoundland (Fig. 4), which is an offshore seamount in a region of high productivity associated with the mixing of cold waters of the Labrador Current with warm sub-tropical waters. Thus, as with other species in different oceanographic regions (Baduini & Hyrenbach 2003), LTs of Cory's shearwaters in the Azores appeared to give birds access to regions of enhanced productivity at long distances from the nest. Birds from the eastern Azores had more variable foraging paths, but LTs of 2 birds included concentrated foraging activity in a region of variable depth at the edge of deep water (>3000 m) to the north and west of the Charcot seamounts NW of Portugal and SW of Ireland (Fig. 4), which may also be a region of enhanced productivity.

Despite marked differences between islands in trip durations, foraging ranges and total distances travelled, the behaviour of birds during foraging trips was very similar in each case. Birds travelled faster and more directly during LTs than during STs but there was no difference between islands in the average speed of travel over STs or LTs and the relationship between distance to destination and total distance travelled was also very similar in each case, as was the proportion of the total foraging area (95% FKD) that comprised the core foraging area (Table 1). These data strongly suggest that birds did not alter their overall search strategy or sinuosity of foraging paths (i.e. the extent of deviation from a straight-line course) between islands in relation to trip duration or foraging range. There was no difference between sexes in behaviour at sea but birds travelled more slowly by night than by day, as also found in some other species of Procellariiformes (e.g. Hedd et al. 2001), probably resulting from birds spending a greater proportion of time resting on the sea surface at night. Average rates of travel to and from distant foraging sites (24 km h⁻¹ and 26 km h⁻¹, respectively) were similar to those recorded in white-chinned petrels *Procellaria aequinoctalis* (Catard et al. 2000) and close to the estimated flight speed for Cory's shearwaters (30 km h⁻¹; Dallantonia et al. 1995), suggesting that birds spent most of their time in flight along a more or less direct path when commuting, as

also suggested by the low sinuosity of flight-paths during outward and return legs (see 'Results: Variation in travel speeds during trips').

LTs lasting up to 20 d could result in chicks being unfed for long periods if both parents departed on LTs simultaneously, but this problem could be reduced if the 2 parents co-ordinated their provisioning, as found in wedge-tailed shearwaters (Congdon et al. 2005). In our study, assuming the 2 parents returned independently of each other, the expected percentage of chicks fed each night (from a binomial distribution based on each parent returning on 37% of nights) would be 60% ($1 - (1 - 0.37)^2$), which was very close to the percentage observed (59%) and corresponds with previous data from the Azores (50 to 70% of chicks fed per night; Klomp & Furness 1992, Ramos et al. 2003). These data strongly suggest that the 2 parents did not co-ordinate their activity to reduce the number of nights when chicks were unfed. As a result, the maximum interval between feeds in the Azores (9 nights; Fig. 6) was much longer than previously recorded in the absence of dual-foraging (4 nights; Hamer & Hill 1993, Granadeiro et al. 1998a, Hamer et al. 1999). In common with other Procellariiformes, Cory's shearwaters accumulate large quantities of body fat as nestlings (Hamer & Hill 1993) and maximum intervals between feeds were previously considered too short to explain the sizes of fat stores accumulated. Chicks may, however, require such large stores to survive longer intervals resulting from a dual-foraging strategy among parents, as previously suggested for short-tailed shearwaters *Puffinus tenuirostris* in the Southern Ocean (Schultz & Klomp 2000).

Despite long intervals between feeds, the overall provisioning rate of chicks in the Azores (76 g night⁻¹; Table 2) was very similar to that recorded elsewhere in the absence of dual-foraging (e.g. mean of 3 yr in the Selvagens Islands = 74 g night⁻¹; data from Table 1 in Hamer et al. 1999). Mass growth rates of chicks in this study (14 g day⁻¹ on average) were also similar to those recorded previously in the Azores and elsewhere for chicks of similar age (Hamer & Hill 1993, Ramos et al. 2003). The similarity in provisioning and growth rates of chicks under unimodal and dual foraging was probably because the mean mass of food delivered when chicks were fed was higher in the Azores (127 g; Table 2) than elsewhere (96 g; Hamer et al. 1999), reflecting larger meals delivered by parents after LTs (see 'Results: Food provisioning rates of chicks'; Granadeiro et al. 1998a, Weimerskirch & Cherel 1998). Despite shorter LTs in the western Azores than elsewhere (Table 1), there was no difference between islands in either the proportion of nights each adult returned or the proportion of nights each chick was fed, because shorter LTs in the western Azores were accompanied by longer STs (Table 1).

Cory's shearwaters are opportunistic predators (Granadeiro et al. 1998b) and concern has been expressed over incidental mortality of adults in long-line fisheries in the Mediterranean and Macaronesia (Cooper et al. 2003, Gonz ales-Sol s et al. 2007). Our data suggest that breeding adults from the Azores could potentially be affected by interactions with fisheries over a much larger area of ocean than previously recognized, paralleling recent findings for the overwintering and migration periods (Gonz ales-Sol s et al. 2007).

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