

Foraging behavior and habitat use by the Southern Giant Petrel on the Patagonian Shelf

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Abstract We explored the at-sea behavior and marine habitat use of the Southern Giant Petrel breeding in Patagonia, Argentina by means of satellite telemetry. Adult breeders showed a wide distribution over the Patagonian Shelf, using 74% of its surface. The maximum distance traveled from the colonies was 683 km, but on average birds moved no more than 200 km further away from their colony. Important marine areas were located in the shelf break, middle shelf and coastal waters. Areas of activity by sex overlap between 35 and 94%. Females foraged primarily away from the coast and males mainly on coastal areas. Both sexes were capable of flying up to 4,000 km but most of the foraging trips were of less than 200 km. Our results emphasize the importance of the Patagonian Shelf as foraging habitat for pelagic seabirds and contribute to international efforts to identify and protect a network of marine sites.

Introduction

Albatrosses and giant petrels are among the most pelagic seabird species, traveling vast distances from their breeding sites to foraging areas (see review Shealer 2002). During the breeding season, foraging behavior at sea is crucial, since both parents must maximize the energy acquisition in

order to satisfy both their own and their chick’s requirements (Stearns 1992). Each sex feeding in different areas during this period is a relatively common characteristic of procellariiformes (Birdlife-International 2004; Phillips et al. 2004; González-Solís et al. 2008) and may have implications for conservation (e.g. sex-specific overlap with fisheries). Accurate knowledge of the at-sea behavior of albatrosses and petrels (i.e. distances traveled to foraging areas, preferred paths, trip duration, foraging time, etc.) is important to understanding their energy requirements, relationship with environmental conditions, and susceptibility to changes in the marine environment. Spatial and behavioral data are also crucial for several management aspects such as to support the implementation of precautionary ecosystem-based approaches, allow for sustainable use of marine resources and to contribute to the design of coastal and pelagic marine protected areas as an essential step for the conservation of marine species and their habitat. Approaches to these kinds of questions have been extensively addressed during the last decade by the extended use of electronic devices such as geolocator systems (GLSs), satellite transmitters (PTTs) and more recently, global position systems (GPSs) (see review Wilson et al. 2002; Ropert-Coudert and Wilson 2005).

The Southern Giant Petrel (SGP, *Macronectes giganteus*) is a wide ranging procellariiform with a circumpolar breeding distribution (Carboneras 1992) and one of the dominant scavengers of the Southern Atlantic Ocean (Hunter 1983; Hunter and Brooke 1992). In Patagonia, Argentina, the SGP breeds at four colonies (with the exception of Malvinas/Falklands colonies), two of which are localized in Chubut Province (Isla Arce and Isla Gran Robredo) and the other two in Tierra del Fuego—Isla de los Estados (Isla Observatorio and Península López; Quintana et al. 2005, 2006; Copello and Quintana 2009a).

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Located in the wide marine ecosystem of the Patagonian Shelf, the Argentinean colonies are surrounded by temperate waters. In contrast, most of the remaining worldwide colonies are situated in the cold Antarctic and sub Antarctic waters. Recent satellite and geolocation data indicate that the Patagonian Shelf is extensively used as a migration and foraging area by several seabird and marine mammal species breeding either in temperate or sub Antarctic waters (Campagna et al. 2001; Pütz et al. 2003, 2006; Birdlife-International 2004; Wilson et al. 2005).

In Argentina, former studies of the SGP addressed general aspects of the population status (Quintana et al. 2006), biology (Quintana et al. 2005; Copello et al. 2006, Copello and Quintana 2009a), health (Uhart et al. 2003), diet (Copello and Quintana 2003; Copello et al. 2008), spatial interaction with fisheries (Copello and Quintana 2009b), post-fledging dispersal (Copello et al. 2009) and foraging movements of a few Southern Giant Petrel individuals from northern Patagonian colonies (Quintana and Dell' Arciprete 2002). However, basic aspects of the space use remain to be explored for the Patagonian aggregations. Moreover, the current knowledge on the pelagic ecology of SGP (and albatrosses) is considered insufficient in terms of the recent Agreement on the Conservation of Albatrosses and Petrels (ACAP) (<http://www.acap.aq/>). Here, we examine the at-sea behavior and marine habitat use of the SGP breeding in the Patagonian colonies of Argentina by means of satellite telemetry. Research was orientated to: (1) assess foraging at-sea distribution, (2) analyze foraging behavior (in terms of frequency, duration and distances of foraging trips), (3) examine gender and nesting site differences in feeding areas and foraging behavior, and (4) delineate marine important areas for SGP over the Patagonian Shelf.

Methods

Satellite telemetry

The at-sea movements of breeding SGP were studied using satellite telemetry. A total of 16 adult breeding SGP (7 males and 9 females) from the northern colonies of Isla Arce and Isla Gran Robredo and southern colony of Isla Observatorio (see Table 1; Fig. 1) were instrumented with satellite transmitters (PTTs-100, “Platform Terminal Transmitters”, Microwave Telemetry, Columbia, Maryland, USA) during four breeding seasons (1998, 1999, 2001 and 2003). The transmitters weighed 45 g, representing less than 2% of the bird's body weight (see Copello et al. 2006). Fourteen birds were instrumented during the early chick rearing period and the remaining two were instrumented during the late incubation period (see Table 1).

Instrumented birds were sexed by morphometric measurements and/or by molecular techniques (Copello et al. 2006). PTTs were attached to the mid-dorsal mantle feathers using Tesa Tape (Wilson et al. 1997) and were programmed to transmit data every 60 s. We observed non-deleterious effect on the instrumented birds. All individuals equipped with devices showed no signs of discomfort due to the attachment of the device and continued breeding normally during the study period. Data on the geographic position of the instrumented animals were obtained from the ARGOS service provider (CLS, Toulouse, France). Each one of the obtained positions was automatically classified according to its estimated error [Type 0: >1,000 m, Type 1: 350–1,000 m, Type 2: 150–350 m, Type 3: 0–150 m and Type A or B: without an estimated error (ARGOS 2006)].

Analysis of satellite tracks

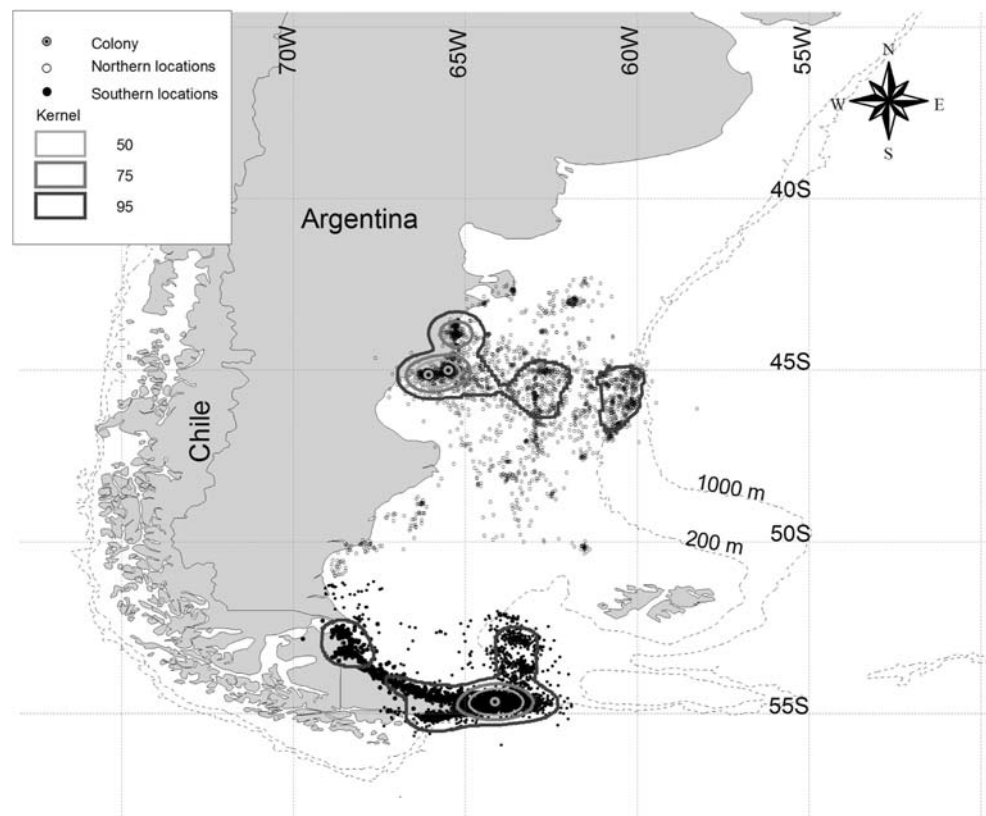
All positions obtained by the ARGOS system were filtered following the iterative procedure used by the “Global Procellariiform Tracking Database” (Birdlife-International 2004) and McConnell et al. (1992). Such procedure takes into consideration the position quality (determined by ARGOS) and the horizontal flying speed between each location fix. Positions with a quality of 0, A or B and a flying speed higher than 100 km h⁻¹ were eliminated. Validated positions were mapped using Arcview GIS 3.2. Filtered positions were then re-sampled every hour following the procedure of Birdlife-International (2004).

Habitat use analysis

A Kernel analysis (“fixed kernel method”, Worton 1989) was employed to analyze the habitat use and the amount of time spent at different marine areas. We used the “Animal Movement Program” package of ArcView 2.0 (Hooge et al. 1999) with a smoothing parameter h of 40 km to determine the areas where animals spent 95, 75 and 50% of their foraging time. Even though validated positions from the same trip are not independent, kernel density procedures do not require independence of data (De Solla et al. 1999). The total area covered by the Southern Giant Petrel at sea was estimated using the Minimum Convex Polygon Analysis (MCP, Worton 1987), which provides an acceptable measure of the minimum area covered by the birds taking into account all their positions at sea. To evaluate the spatial overlap of foraging birds of different sexes, we calculated the proportion of the kernel areas (50, 75 and 95%) for one sex being overlapped by those of the other sex (González-Solís et al. 2000; Hyrenbach et al. 2002).

Table 1 Summary of satellite telemetry data obtained from instrumented Southern Giant Petrels from Patagonian colonies during the breeding period

Individual	Sex	Colony	Breeding season	Timing of breeding	Start tracking	End tracking	Total days recorded	Hours of tracking
Northern colonies								
5,609	M	Gran Robredo	1998	Chick rearing	09/01/1999	31/01/1999	22	528
5,819	F	Gran Robredo	1998	Chick rearing	09/01/1999	22/02/1999	43	1,054
25,135	F	Gran Robredo	1999	Late incubation/chick rearing	26/11/1999	23/01/2000	57	1,393
25,138	M	Gran Robredo	1999	Late incubation/chick rearing	27/11/1999	20/01/2000	53	1,299
10,100	M	Arce	2001	Chick rearing	03/01/2002	22/02/2002	49	1,197
10,101	F	Arce	2001	Chick rearing	04/01/2002	24/02/2002	50	1,247
10,102	M	Arce	2001	Chick rearing	03/01/2002	28/02/2002	55	1,258
10,103	M	Arce	2001	Chick rearing	04/01/2002	06/01/2002	2	58
10,104	M	Arce	2001	Chick rearing	06/01/2002	16/01/2002	10	250
Southern colony								
44,281	M	Observatorio	2003	Chick rearing	06/01/2004	10/03/2004	64	1,386
44,282	F	Observatorio	2003	Chick rearing	06/01/2004	11/01/2004	5	124
39,792	F	Observatorio	2003	Chick rearing	06/01/2004	12/01/2004	6	137
39,791	F	Observatorio	2003	Chick rearing	06/01/2004	09/01/2004	3	69
39,793	F	Observatorio	2003	Chick rearing	09/01/2004	08/03/2004	59	1,399
39,794	F	Observatorio	2003	Chick rearing	12/01/2004	02/03/2004	50	1,197
44,283	F	Observatorio	2003	Chick rearing	12/01/2004	04/02/2004	22	546

Fig. 1 At-sea distribution and marine areas (95, 75 and 50% kernel contours) used by tracked Southern Giant Petrel from Patagonian colonies during the breeding period, 1998–2003

Foraging behavior

Following (Stahl and Sagar 2006), we considered the beginning of a foraging trip to commence once the first three or more successive fixes were recorded outside of a 3-km radius around the colony. Our analysis of foraging excursions only included those tracks starting and ending at the colony. During the whole instrumentation period we monitored the nests to confirm departures and arrivals of the instrumented birds. The foraging trips of the individuals #25135 and #25138 ($n = 13$ for both birds) carried out during the late incubation period (see Table 1) were not included in the analysis because, as it has been previously observed in other albatross and petrel species (Huin 2002; Phillips et al. 2004), differences were found in the total distance covered between these trips and the ones performed during the chick rearing period (for our data: $U = 3$, $P < 0.05$).

For each foraging trip, we derived the following information: (1) total distance traveled; (2) maximum foraging range; (3) trip duration; (4) the horizontal flying speed calculated as an average of the speed between consecutive fixes; and (5) the relationship between the maximum linear distance reached from colony and the total covered distance as an estimation of the directness of the tracks (Nel et al. 2000; Hedd et al. 2001). Birds were treated individually because differences between birds were significant (oneway ANOVA, $P < 0.05$). Means of foraging parameters were determined for each individual and then pooled to calculate overall mean values. The use of non-independent observations is valid if the replicates are pooled to estimate a mean value (Hurlbert 1984).

Results

Analysis of satellite tracks and habitat use

Birds were instrumented, on average, during 31 days (SD = 24 days, range 2–64 days; Table 1). From a total of 9,966 fixes (68.3% classified as Types 0, A or B and the rest as Types 1 to 3), available 3.5% were rejected by the filtering procedure. The mean (\pm SD) number of fixes obtained per bird per day was 18 ± 6 (range 7–25).

During late incubation and chick-rearing periods, giant petrels from the three colonies were widely distributed over the Patagonian Shelf using approximately 74% (MCP = 738,832 km²) of its area. The at-sea distribution of foraging birds occurred mostly onto the shelf, between 42° and 56° S and from coastal to the shelf break areas (Fig. 1). The total marine area used by birds from the northern colonies was almost three times greater than that used by giant petrels from the southern colonies (MCP

545,790 vs. 193,042 km², respectively) (Fig. 1). A clear spatial segregation was observed between the foraging areas of birds from the northern and southern nesting sites (Fig. 1). In general, individuals from both areas moved both to the south and to the north from their respective colonies. However, southern birds spent a higher proportion of their time in waters located to the north of the colony. The maximum distance traveled from the nesting sites was 683 km but, on average, birds from the northern site moved further away from their colonies (450 ± 211 vs. 246 ± 167 km) ($U = 13$, $P < 0.05$).

Main utilization areas of adult breeders from both northern and southern nesting sites were estimated as kernel probability contours of 50, 75 and 95% (Fig. 1). Three important marine areas (as defined by the kernel contour 95%) were identified for giant petrels from the northern colonies: two pelagic (shelf break and middle shelf waters) and one coastal (Fig. 1). Pelagic areas were located between 45° and 47° S and 64° and 60° W, at 357–463 and 150–292 km. from the colonies. The coastal area extended from northern San Jorge gulf to 43° S as the northern limit at approximately 200 km from the colonies (Fig. 1). Two important marine areas (Kernel contour 95%) were identified for giant petrels from the southern colony. One situated in the vicinity of Isla de los Estados at a maximum distance of 243 km from Isla Observatorio and the other in a coastal sector, North of the Isla Grande de Tierra del Fuego, at approximately 290–397 km from the colony (Fig. 1).

Breeding adults from both nesting sites spent 50–75% of their time at sea in the vicinities of their breeding colonies. These areas of activity were in waters inside the San Jorge gulf and coastal areas to the north, and coastal waters of Isla de los Estados and Le Maire Strait, for birds from the north and south colonies, respectively (Fig. 1).

Sexual habitat segregation

Females from northern colonies foraged mainly away from the coast, but also visited coastal areas close to the colonies (Fig. 2). These females prospected an area of exclusive use at the shelf break, centered at about 46° S and 60° W (Fig. 2a). In contrast, males from the northern colonies mainly explored coastal areas and two areas located at the middle shelf (Fig. 2b). One of these areas (between 44.7°–46.4° S and 63.4°–61.9° W) was also visited by females, while the other one was located further south at about 51° S and 69° W (Fig. 2b). Southern females foraged in open waters of the middle shelf and the shelf break at the northeast and southwest of the colony (Fig. 2a). In contrast, the only instrumented male from Isla Observatorio foraged exclusively in coastal waters to the northwest of the colony and in the shelf break area south of Isla de los Estados (Fig. 2b).

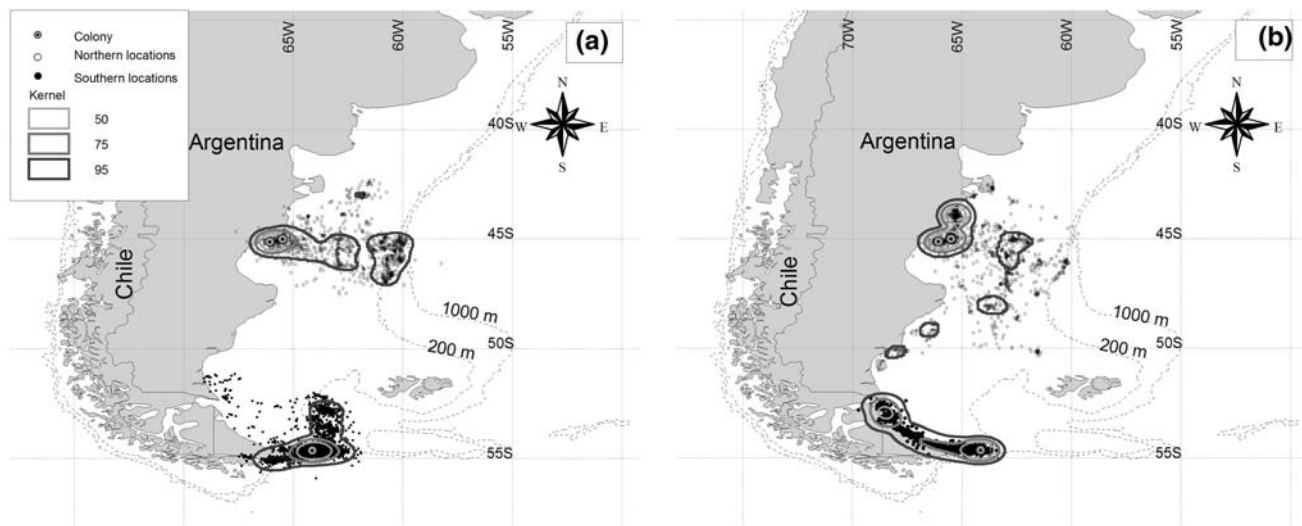


Fig. 2 At-sea distribution and marine areas (95, 75 and 50% kernel contours) used by tracked females (a) and males (b) Southern Giant Petrel from Patagonian colonies during the breeding period, 1998–2003

The total foraging area of northern males was 1.7 times greater than northern females (MCP, 448,280—males vs. 268,834 km²—females). Data from the only instrumented southern male reflected an opposite pattern (MCP, 175,062—male vs. 61,555 km²—females). At the northern colonies, maximum distances traveled from the colony were similar between sexes (521.9 ± 56.0 vs. 413.9 ± 255.9 km, *U* = 8, *P* > 0.1), whereas southern females covered smaller maximum distances than the only tracked male from Isla Observatorio (216.8 ± 161.8 vs. 422.5 km).

The spatial overlap between the activity areas of both sexes (kernel contours of 50, 75 and 95%), ranged between 35 and 94% (Table 2). The smallest spatial overlap corresponded to the activity range of 95%, except for males from the northern colonies (Table 2). For all activity ranges, except the area of 50% for males, the degree of overlap between sexes at the southern colony was lower than those recorded at the northern nesting sites (Table 2). In general, males used a higher percentage of the activity areas used by females (Table 2).

Foraging behavior

During the early chick rearing period (see “Methods”), we recorded a total of 204 foraging trips (85 from the northern colonies and 119 from the southern colony) performed by 16 instrumented birds (Table 3). Both sexes alternated foraging excursions with periods at the colony to feed chicks. Males and females from all sites covered distances that ranged from less than 100 km to more than 4,000 km (range: 12.6–4,497.3 km; Table 3). However, most of the foraging trips (48%) were of less than 200 km and in 36% exceeded 400 km. Even though the maximum foraging

Table 2 Overlap of the activity ranges (percentage) of female and male Southern Giant Petrels from northern and southern colonies in Patagonia, Argentina

Kernel area (%)	Northern colonies		Southern colony	
	Females	Males	Females	Males
50	86.5	49.6	78.7	64.0
75	94.3	51.2	79.8	40.1
95	42.8	53.1	42.2	35.8

Values under the columns labeled as “Females” correspond to the proportion of area used by females that was also used by males. “Males” columns indicate the proportion of area used by males that was also used by females

range of birds from both colonies was 500 km (Table 3), for most of the foraging trips (70%) the maximum foraging range did not exceed 100 km. The duration of the foraging trips was extremely variable ranging from hours to several days (range: 3.0–295.4 h) (see the following paragraphs and Table 3). However, half of the foraging trips lasted less than 24 h and exceeded the 72-h-long the 16% of the trips. For both sexes, the foraging trip duration was a good indicator of the total covered distance (Spearman correlation, *R*_{North Males} = 0.78, *R*_{North Females} = 0.91 y *R*_{South Male} = 0.96, *R*_{South Females} = 0.93, *P* < 0.0001) and the maximum foraging range (*R*_{North Males} = 0.71, *R*_{North Females} = 0.87, *R*_{South Male} = 0.94, *R*_{South Females} = 0.82, *P* < 0.0001).

Based on frequency distributions for both sexes, discontinuities were detected for the maximum foraging range at 100 km and for foraging trip duration at 24 h. Taking this into account, trips further away from the colony than 100 km and longer than 24 h were considered as “long

Table 3 Summary statistics of foraging trips performed during the chick-rearing period by the Southern Giant Petrel of the Patagonian colonies

Individual	Sex	Short trips						Long trips						
		<i>n</i>	Total distance (km)	Maximum distance (km)	Duration (hours)	Speed (km h ⁻¹)	Directness (%)	<i>n</i>	Total distance (km)	Maximum distance (km)	Duration (hours)	Speed (km h ⁻¹)	Directness (%)	Long trips (%)
Northern colonies														
5,819	F	4	207.9 ± 137.6	51.4 ± 25.7	36.8 ± 7.0	8.5 ± 3.1	26.3 ± 6.8	6	963.2 ± 316.6	313.5 ± 85.4	99.9 ± 38.1	12.0 ± 2.5	33.8 ± 7.0	60.0
			77.1–401.9	18.1–79.0	26.7–42.2	4.2–11.6	19.6–35.7		528.2–1,387	199.9–463.3	53.8–151.4	9.1–15.3	24.6–45.1	
10,101	F	20	136.8 ± 112.6	38.0 ± 32.7	12.2 ± 6.7	16.2 ± 7.0	30.4 ± 10.7	5	1,537.6 ± 697.3	357.8 ± 117.6	91.8 ± 37.0	22.7 ± 2.5	24.7 ± 5.1	25.0
			22.3–460.8	8.0–129.2	3.6–29.0	6.7–36.8	12.8–46.8		748.3–2,518.8	226.7–482.6	47.2–137.7	20.4–26.9	18.1–30.3	
25,135	F	1	262.2	100.7	14.6	20.4	38.4	2	2,448.7 ± 178.9	482.6 ± 21.1	232.8 ± 43.6	15.4 ± 2.3	19.7 ± 0.6	66.7
Mean ± SD			202.3 ± 62.9	63.4 ± 33.0	21.2 ± 13.5	15.1 ± 6.0	31.7 ± 6.2		2,322.2–2,575.2	467.6–497.5	201.9–263.6	13.7–17.0	19.3–20.1	50.6 ± 22.4
5,609	M	2	198.7 ± 183.3	36.9 ± 9.7	48.2 ± 34.5	5.2 ± 1.7	28.4 ± 21.3	0	1,649.8 ± 749.1	384.6 ± 87.7	141.5 ± 79.2	16.7 ± 5.5	26.1 ± 7.1	0
			69.0–328.3	30.0–43.8	23.8–72.5	4.1–6.4	13.3–43.5							
25,138	M	3	153.8 ± 122.5	42.3 ± 13.6	35.5 ± 30.7	12.0 ± 5.7	34.6 ± 14.9	1	2,533.1	416.5	239.6	16.4	16.4	25.5
			77.4–295.1	28.3–55.5	15.7–70.8	8.4–18.6	18.8–48.5							
10,100	M	25	110.8 ± 93.0	28.8 ± 25.9	9.8 ± 4.4	18.8 ± 14.1	28.6 ± 10.2	5	1,851.2 ± 891.7	419.3 ± 156.3	107.7 ± 21.9	23.7 ± 6.8	23.5 ± 3.4	16.7
			16.5–378.3	5.0–123.2	3.0–22	4.1–46.1	11.1–42.4		1,053.1–3,372.0	280.5–662.8	89.4–136.4	18.5–33.7	19.6–26.9	
10,102	M	1	391.1	60.5	55.4	10.0	15.5	1	1,644.6	149.3	295.4	11.2	9.1	50.0
10,103	M	1	510.8	91.4	36.1	22.3	17.9	0						0
10,104	M	8	68.2 ± 52.6	24.1 ± 21.9	8.9 ± 1.5	17.3 ± 10.2	35.1 ± 21.3	0						0
			19.1–182.7	7.2–76.1	7.1–11.5	5.0–35.6	13.3–41.7							
Mean ± SD			238.9 ± 174.0	47.3 ± 25.0	32.3 ± 19.3	14.3 ± 6.3	26.7 ± 8.3		2,009.6 ± 464.9	328.3 ± 155.1	214.2 ± 96.4	17.1 ± 6.3	16.3 ± 7.2	15.3 ± 20.0
Southern colony														
44,282	F	6	200.2 ± 152.5	57.4 ± 48.4	16.3 ± 7.4	20.9 ± 10.2	29.8 ± 8.3	0						0
			51.3–380.7	16.9–137.5	8.1–27.0	6.5–35.5	20.8–40.3							
44,283	F	11	322.3 ± 312.6	49.2 ± 33.5	17.5 ± 15.1	24.7 ± 10.9	22.6 ± 11.1	2	1,416.6 ± 51.8	138.5 ± 10.5	74.4 ± 15.0	31.1 ± 1.6	9.8 ± 1.1	15.4
			29.9–1,043.1	11.9–95.2	3.7–51.5	4.4–34.5	9.0–41.6		1,380.0–1,453.2	131.1–145.9	63.8–85.1	30.0–32.3	9.0–10.6	
39,791	F	3	166.3 ± 148.7	38.1 ± 18.7	9.3 ± 7.2	34.7 ± 14.9	29.0 ± 14.3	0						0
			78.9–338.1	19.9–57.2	3.2–17.3	19.9–49.6	16.9–44.9							
39,792	F	4	209.8 ± 298.4	33.8 ± 40.2	12.1 ± 7.6	16.6 ± 14.5	24.4 ± 13.0	0						0
			31.2–654.9	12.3–94.1	7.9–23.4	4.2–37.4	14.3–42.3							
39,793	F	24	315.8 ± 247.5	49.5 ± 32.7	19.3 ± 13.7	25.7 ± 13.2	21.3 ± 10.6	9	1,675.7 ± 1,240.6	205.4 ± 120.6	97.9 ± 73.2	28.5 ± 8.0	14.1 ± 4.9	27.3
			23.1–791.0	7.2–143.0	2.7–48.1	8.2–66.5	6.7–43.3		583.1–4,497.3	100.9–495.8	28.6–241.5	19.8–44.3	8.5–21.5	
39,794	F	19	226.5 ± 226.9	54.2 ± 37.5	11.9 ± 9.9	26.4 ± 12.6	30.6 ± 10.2	10	1,335.6 ± 643.7	193.8 ± 59.4	63.5 ± 28.4	31.9 ± 5.2	16.6 ± 6.7	34.5
			18.7–750.7	5.4–121.5	2.9–33.2	7.1–53.0	11.2–44.6		592.9–2,479.9	136.6–292.4	28.1–102.4	21.9–36.8	8.9–32.1	
Mean ± SD			240.1 ± 64.2	47.0 ± 9.2	14.4 ± 3.9	24.8 ± 6.1	26.3 ± 4.1	3	1,475.9 ± 177.7	179.2 ± 35.8	78.6 ± 17.5	30.5 ± 1.8	13.5 ± 3.4	12.9 ± 15.4
44,281	M	20	196.8 ± 134.5	57.8 ± 39.6	12.1 ± 6.2	24.1 ± 9.8	29.8 ± 7.4	11	1,468.0 ± 522.7	337.7 ± 60.4	92.9 ± 49.1	24.8 ± 5.2	24.5 ± 5.4	
			12.6–510.8	3.3–167.8	3.3–23.8	3.1–46.4	18.4–40.9		778.1–2,584.6	227.6–421.1	30.7–190.6	17.4–35.9	16.3–34.0	
Mean			196.8	57.8	12.1	24.1	29.8		1,468.1	337.7	92.9	24.8	24.5	35.5

Data corresponds to those tracks considered as foraging trips (see "Methods"). In cells with 2 lines of values, upper line corresponds to Mean ± SD values, lower line to the range. *n* is the number of trips performed by the same individual

trips” and as “short trips” otherwise (Table 3). During short trips, the mean covered distance was less than 240 km, and the maximum foraging range was less than 63 km. Mean duration of short trips varied between 12 and 32 h (all data pooled, Table 3). For longer trips, mean total distance covered was less than 2,010 km, and the maximum foraging range did not exceed 328 km. Foraging trip durations for these longer trips ranged between 78 and 214 h (all data pooled, Table 3). The horizontal speed and the track directness (see “Methods”) were similar for long and short foraging trips for both females and males breeding in the northern colonies ($U > 4$, $P > 0.1$) (Table 3). In contrast, the tracks directness of short trips was greater than the longer ones in females from the south (26.3 vs. 13.5%, $U = 0$, $P < 0.05$) (Table 3).

As mentioned, males and females from both nesting sites alternated short with long foraging trips during the chick rearing period. Nonetheless, a sexual difference was observed in the proportion of each type of trip. While all females breeding in the northern colonies made both short and long foraging trips, only three of the six instrumented males performed both kinds of trips, and the other three performed short trips only. On the other hand, while more than half of the foraging trips performed by females (50.6%) were long, only 15.3% of the foraging trips performed by males was classified within this category ($U = 1.5$, $P = 0.05$, Table 3). At the northern colonies, foraging trip characteristics did not differ between sexes ($U > 1.0$, $P > 0.1$), with the exception of traveling speed ($U = 1$, $P < 0.05$), which was higher for females from Isla Observatorio. The rest of the characteristics of short trips were similar for females from both study sites ($U > 4$, $P > 0.1$) (Table 3). During long foraging excursions, the maximum foraging range and track directness was greater for the northern females, while horizontal speed was again higher for the southern females ($U = 0$, $P < 0.05$, in all cases) (Table 3). The duration of foraging trips for northern males was more than twice that of the only instrumented male from the south (Table 3). All birds from the southern colony performed few foraging trips where the maximum foraging range exceeded 400 km (1.1 and 3.2% for females and males, respectively), while birds from the northern colonies made several foraging trips where the maximum range exceeded that distance (13 and 8% of the females and males foraging trips, respectively).

Discussion

Satellite tracking studies of giant petrels are uncommon. The first study was carried out in Antarctica in the 80s, where Strikwerda et al. (1986) reported the potential use of

the PTT technology, the total distances covered by the tracked birds and a brief description of their trajectories. More recently, studies in Georgias del Sur (South Georgia), Antarctica and Macquarie Island used satellite telemetry on the two species of giant petrels (*Macronectes* spp.) to study the spatial segregation between species and sexes (Patterson and Fraser 2003; González-Solís and Croxall 2005; González-Solís et al. 2008; Trebilco et al. 2008). We presented the findings from the first detailed study on the at-sea distribution and foraging behavior of the Southern Giant Petrel breeding in Argentina (but see Quintana and Dell’Arciprete 2002).

Habitat use and foraging pattern

During the breeding season, Southern Giant Petrel was widely distributed over the Patagonian Shelf. Even though adult birds spent a large amount of time near to their colonies, they also reached distant waters as far as 700 km offshore. The extensive use of the Patagonian Shelf is not restricted to the breeding season. Recent satellite tracking studies during the non-breeding season (May to August) (F. Quintana and S. Copello, unpublished data) and results from banded birds (Copello et al. 2009) showed that the area is also used by adults and juveniles from northern Patagonian colonies. The use of the same areas during both the breeding and the non-breeding periods has also been observed in other albatross species from the Southern Ocean, but it is not a common pattern for this group of seabirds (Warham 1996; Brothers et al. 1997, 1998; Hedd and Gales 2005; Stahl and Sagar 2006).

The Patagonian Shelf is an important area in terms of the intensity of use (migration and foraging) by seabird species breeding in coastal Patagonia, as well as those breeding at more remote places such as Australia, New Zealand, Chile and Islas Georgias del Sur (South Georgia Islands) (e.g. King, Magellanic and Rockhooper penguins, White-chinned Petrel, Northern Royal Albatross, Southern and Northern Giant Petrels (Pütz 2002; Pütz et al. 2002, 2003, 2006; González-Solís and Croxall 2005; Nicholls et al. 2005; Wilson et al. 2005; Phillips et al. 2006). The area is also important for foraging elephant seals and sea lions breeding in Patagonia (Campagna et al. 2001, 2006), the Malvinas (Falklands) and Georgias del Sur (South Georgia) (Croxall and Wood 2002). Like the Southern Giant Petrel, Black-browed Albatrosses (*Thalassarche melanophrys*) breeding at the Malvinas (Falklands) Islands also use the Patagonian Shelf during the whole year (Grémillet et al. 2000; Huin 2002). Since it has been generally suggested that during the breeding season seabirds migrate or disperse to other areas because of the reduction in prey abundance and availability (Schreiber 2002), the same habitat use pattern observed for Southern

Giant Petrels over the year and the presence of other species coming from distant areas could be indicative of the existence of abundant food resources during the whole year in the Patagonian Shelf. High inter-specific trophic overlap has been observed for 14 of the 17 seabird species nesting along the Patagonian coast of Argentina (Forero et al. 2004). This also suggests the presence and availability of abundant food resources in the area, allowing the coexistence of several species (Forero et al. 2004). On the other hand, the oceanographic characteristics of the marine areas used by the SGP, at least during the breeding season, showed favorable conditions such as high productivity (eutrophic and enhanced waters), temperate sea surface temperatures (between 8 and 19°C), high squid abundance (at least near the northern colonies) and carrion supply near the colonies (F. Quintana and S. Copello, unpublished data).

The extent of the foraging trips of the SGP was extremely variable; birds covered distances from tens to thousands of kilometers and trip durations ranged from hours to several days. Most of the instrumented individuals alternated “short” and “long” foraging trips as it has been observed in other procellariiform species (Weimerskirch et al. 1994). Weimerskirch et al. (1997a) suggested that short foraging trips ensure a high rate of food delivery to the chicks, while long trips allow adults to replenish their own energetic requirements. The high proportion of short foraging trips to areas close to the colonies reported here is similar to that observed in other albatross and petrel species (Stahl and Sagar 2000; Fernández et al. 2001; Freeman et al. 2001; Nel et al. 2002; Hedd and Gales 2005) as, for example, the SGP of Antarctica (Obst and Nagy 1992; Patterson and Fraser 2003, www.wbur.org) and of Georgias del Sur (South Georgia) (see review Phillips et al. 2005).

The SGP made a selective use of the space. We identified major foraging areas, coastal and pelagic ones, some of them 500 km away from the colonies, as it has been reported for the SGP of Georgias del Sur (South Georgia) during the incubation period (González-Solís et al. 2000, 2002a). The intensive use of coastal areas near colonies has been also observed in other albatross species (Weimerskirch 1998a; Hedd et al. 2001; Huin 2002). As mentioned, the use of areas adjacent to colonies and the “short” foraging trips used by both sexes may be beneficial during the chick rearing stage when breeding birds face a critical period of high energy requirements (Weimerskirch et al. 1997b; Weimerskirch 1998b). Energetic constraints during this period could be less costly for Patagonian giant petrels due to the existence of abundant food supply from fishing discards (see Copello and Quintana 2009b) and other prey items (mainly penguin carrion and squid) very close to the colonies (Copello et al. 2008). The inter-annual similarity found in the diet of the giant petrels from

northern Patagonia (Copello et al. 2008) could also support the idea of food availability relatively stable and predictable across years. Moreover, the absence of nearby colonies of its sibling species, the Northern Giant Petrels (*Macronectes halli*), a species whose diet consists principally of carrion (Hunter 1983; Hunter and Brooke 1992), would greatly reduce any potential interspecific competition, making the access to resources easier for Patagonia SGPs.

Sexual habitat segregation

Previous studies on this species at Georgias del Sur (South Georgia) and in Antarctica showed some degree of sexual partitioning in diet (Hunter 1983; Hunter and Brooke 1992; Coria 2006), foraging behavior (González-Solís et al. 2002a), foraging areas (González-Solís et al. 2000, 2008), trophic level (Forero et al. 2005), and also sexual differences in the concentration of metals in the blood (González-Solís et al. 2002b). These studies showed that even though both sexes fed on carrion, females also exploited pelagic prey. Males frequently made trips to coastal areas, while females engaged in longer pelagic trips. Our results showed a weak sexual segregation in the foraging areas of Patagonia Southern Giant Petrel. Even though females foraged at the shelf break undertaking a higher number of “long trips” and males exploit primarily coastal areas, both sexes have the ability to use either foraging strategy, with males undertaking long pelagic trips to the middle shelf and females foraging in coastal areas. These findings were similar to those reported for northern giant petrels at Georgias del Sur (South Georgia) during incubation (González-Solís et al. 2000). Data from both northern and southern sites showed a partial overlap in the marine areas used by both sexes, with the highest overlap being that of males on female foraging areas, rather than vice versa, similar to those reported for giant petrels at Georgias del Sur (South Georgia) during incubation (González-Solís et al. 2000). This overlap could be partially explained by the existence of a low level of competition between sexes due to the abundance and availability of food resources in the area. In fact, penguins were the food item occurring most frequently in the diet of the SGP from the northern colonies (Copello et al. 2008) and form an abundant and predictable food source along the Patagonian coast. The highest densities of these carrion/prey items are concentrated at coastal northern San Jorge Gulf adjacent to the northern SGP colonies (Copello et al. 2008). Punta Tombo, the biggest Magellanic Penguin colony of the world (~175,000 breeding pairs) (Schiavini et al. 2005) is located less than 100 km from Isla Arce and Isla Gran Robredo. On the South, there are two major penguin colonies closed by the southern SGP colony at Isla Observatorio. One is on

Franklin Bay, Isla de los Estados at 43 km, which is the second biggest Rockhopper Penguin colony of the Southern Atlantic Ocean (174,000 breeding pairs, (Schiavini et al. 2005)). The second one is at only hundreds of meters from the SGP colony and constitute the second biggest colony of Magellanic Penguins of the Patagonian coast (~100,000 breeding pairs) (Schiavini et al. 2005). On the other hand, the partial sexual segregation observed in the foraging areas could reduce any potential inter-sexual competition in shared areas or allow different access to prey that cover sex-specific energetic demands (Lewis et al. 2002). In this way, studies using stable isotopes revealed a trophic sexual segregation in the birds breeding at Arce and Gran Robredo Islands (Forero et al. 2005).

Comparison between Northern and Southern colonies

Although no spatial overlap was observed between the foraging areas of giant petrels from the northern and southern colonies, birds from both sites have in common the use of coastal, middle shelf and shelf break waters of the Patagonian Shelf. The maximum foraging range and the total area covered by giant petrels from the south were smaller than those exhibited by individuals from the north. The different topography surrounding the colonies probably condition foraging patterns. The shelf break is at approximately 400 km from the northern sites and at only 100 km from the southern one.

Conservation issues and future research

We believe our results will provide valuable input to international efforts to protect a network of critical marine sites for the long-term viability of naturally occurring seabird populations. The identification of important marine areas and the determination of intersexual and intercolony differences in the use of habitat are essential steps, either for a future SGP Conservation Plan, and/or any regional or national initiative to create and manage marine protected areas on the Patagonia Shelf. To reach that goal, more information about the at-sea distribution of this species is needed. With tracking data on juveniles and adults during the non-breeding season and from other important locations, a more complete spatial pattern distribution of SGP on the Patagonian shelf would be obtained. One of these important locations is the Malvinas (Falkland) Islands where approximately 200,000 breeding pairs of giant petrels breed annually (Reid and Huin 2008). Finally, we recommend that future research evaluate the role of environmental factors in the at-sea distribution and foraging patterns of the SGP of the Patagonian Shelf to understand its spatial and temporal variability and the susceptibility of the species to environmental changes.

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