

Comparative foraging behaviour of sympatric Humboldt and Magellanic Penguins reveals species-specific and sex-specific strategies

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Abstract. How closely related marine organisms mitigate competition for resources while foraging at sea is not well understood, particularly the relative importance of interspecific and intraspecific mitigation strategies. Using location and time–depth data, we investigated species-specific and sex-specific foraging areas and diving behaviour of the closely related Humboldt (*Spheniscus humboldti*) and Magellanic (*S. magellanicus*) Penguins breeding in sympatry at Islotes Puñihuil in southern Chile during the chick-rearing period. The average duration of foraging trips was <20 h and did not differ significantly between species or between sexes of each species. Magellanic Penguins made significantly deeper and longer dives than Humboldt Penguins. Males of both species made significantly longer dives than females. Total distance travelled per foraging trip was significantly greater for males than for females, and females made more direct trips (less sinuous) than males. Foraging effort was concentrated in waters up to 15 km to the west and south-west of the colony. The overlap in density contours was lower between species than between sexes within a species. In general, dive characteristics and foraging areas differed more between Magellanic and Humboldt Penguins than between the sexes of each species. In contrast to the findings of studies of flying seabirds, the foraging behaviour of these penguins differs more between species than between sexes.

Additional keywords: Chile, diving, segregation, spatial ecology, Spheniscidae.

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Introduction

Interspecific and intraspecific competition play a major role in shaping animal communities. The competitive exclusion principle predicts that when two groups depend upon a common food resource it is likely that one excludes the other from using that resource (Gause 1934). Where ecologically similar species co-exist, there may be some degree of segregation in one or more niche dimensions that allows coexistence and helps avoid possible competition (Hutchinson 1959, 1978; MacArthur 1958; Lack 1971; Schoener 1983; McDonald 2002). Studies on seabirds have shown that resource partitioning occurs in various niche dimensions, including macrohabitat and microhabitat selection, type and size of prey, and the spatial and temporal distribution of foraging, particularly during the breeding season when seabirds

are central place foragers and are forced to return to land to perform parental duties and have to forage within a more restricted area than during the non-breeding season (Croxall and Prince 1980; Weimerskirch *et al.* 2009; Masello *et al.* 2010; Wilson 2010).

In diving seabirds such as penguins (Spheniscidae), sympatric species may co-exist through differences in the exploitation of the marine environment in both horizontal (surface distribution) and vertical (depth distribution) axes (Hull 1999, 2000; Masello *et al.* 2010; Kokubun *et al.* 2010; Thiebot *et al.* 2012). Differential depth-efficiency has also been identified as a potential factor allowing coexistence of sympatric penguin species foraging on the same prey (Mori and Boyd 2004; Wilson 2010).

In addition to interspecific competition, sexual segregation within species, at diverse temporal and spatial scales, is also characteristic of many animal communities (Catry *et al.* 2005). Sexual segregation is generally considered to result from both social dominance and competitive exclusion (usually of females by larger males) and niche specialization arising from differences in morphology or reproductive role (Gilardi 1992; Clarke *et al.* 1998; González-Solís *et al.* 2000; Cook *et al.* 2007; Quintana *et al.* 2011). Seabirds, including penguins, have shown certain degrees of sexual segregation in various niche dimensions, including differences in the species and size of prey taken (Volkman *et al.* 1980; Paredes *et al.* 2008; Dehnhard *et al.* 2011), foraging areas, depth utilisation and times of feeding (Phillips *et al.* 2004; Cook *et al.* 2007; Weimerskirch *et al.* 2009; Quillfeldt *et al.* 2011; Raya Rey *et al.* 2012).

Humboldt (*Spheniscus humboldti*) and Magellanic (*S. magellanicus*) Penguins have similar ecological requirements and breed in sympatry along 1100 km of the coast of the south-eastern Pacific Ocean of Chile, between Algarrobo (33°S) and Metalqui Island (42°S) (Simeone and Huckle-Gaete 1997; Simeone *et al.* 2009). However, mixed colonies of the two species are rare, with only three known. The colony at Islotes Puñihuil is the largest of these three mixed-species colonies (Duffy 1987; Wilson *et al.* 1995), with 458 breeding pairs of Magellanic Penguin and 76 pairs of Humboldt Penguin (Simeone 2004). At Islotes Puñihuil, both species feed on the same prey items, mainly anchovy (*Engraulis ringens*) and sardine (*Sardinops sagax*) and smaller amounts of crustaceans and cephalopods (Wilson *et al.* 1995; Hennenke and Culik 2005; Herling *et al.* 2005).

The aims of our study were to examine the foraging strategies of Humboldt and Magellanic Penguins in the seas off Islotes Puñihuil and determine the differences that mitigate competition between and within (males and females) species. In this context, the Islotes Puñihuil colony represents a unique opportunity to compare the relative importance of species and sex in the differentiation of the foraging strategies in the two sympatric species. As reported for other species (e.g. Mori and Boyd 2004; Wilson 2010), we predict that the two species will show differential depth-efficiency and vertical use of habitat. We predict that the larger species (Humboldt Penguin) will dive deeper and for longer. Along the horizontal axis, the two species may also differ in use of different foraging areas (e.g. Masello *et al.* 2010) and we predict that the more abundant species (Magellanic Penguin) will forage over a larger area (Cairns 1989). Within each species, we expect males, which are bigger than females, to dive deeper and for longer than females.

Materials and Methods

The study was conducted at the mixed-species breeding colony of Magellanic and Humboldt Penguins at Islotes Puñihuil (composed of two islets), on the exposed Pacific Ocean coast of Isla Grande de Chiloé (41°55'S, 74°02'W), in southern Chile. The coastal waters here are highly productive, mainly owing to input of nutrients from river outflows (Camus 2001; Escribano *et al.* 2003) and not influenced by the upwelling of the Humboldt Current (Lalli and Parsons 1997; Escribano *et al.* 2003).

We studied the spatial distribution of foraging, duration of foraging trips and diving behaviour of female and male Magellanic and Humboldt Penguins during the early chick-rearing period (chicks newly hatched to 15 days old), between 11 November and 15 December 2008. We captured breeding adult penguins by carefully taking them from their burrows by hand, and returning them to their nests after deploying the data-recording devices (see below). For both species, males are larger than females (Scolaro *et al.* 1983; Zavalaga and Paredes 1997; Wallace *et al.* 2008) and a sample of birds from Islotes Puñihuil taken earlier in the season of this present study also found significant differences in size between males and females (Table 1). We determined sex of individuals by visual comparison of size within pairs (measurements were not taken), when both adults were present at the nest, either during deployment or recovery of data-recording devices, assuming that, of the pair, the male was the bird with the longer bill.

We attached either time–depth recorders (TDR; model MK9, Wildlife Computers, Redmond, CA, USA) or global positioning system units with pressure-sensor devices (GPS; model GPS-TDlog, Earth & Ocean Technologies, Kiel, Germany). Devices were attached along the midline of the back as close as possible to the tail without covering the preen gland, using black tape (Tesa, Beiersdorf AG, Hamburg, Germany), following Wilson *et al.* (1997). The devices were finally covered with a layer of quick epoxy (Loctite 3430, Loctite Deutschland GmbH, Munich, Germany) to prevent the birds from removing the tape with their beaks. The process of fitting a device took less than 20 min per bird.

We successfully deployed TDR units on seven Humboldt Penguins (2 females, 5 males) and 10 Magellanic Penguins (5 females, 5 males) and GPS units on 12 Humboldt Penguins (8 females, 4 males) and 10 Magellanic Penguins (8 females, 2 males). We obtained dive data, from the TDR or GPS units, from 16 Humboldt Penguins (7 females, 9 males) and 15 Magellanic Penguins (9 females, 6 males); some devices did not function and at least one bird equipped with a TDR drowned in a gill-net (see Pütz *et al.* 2011). We obtained positional fixes from 30 trips, with more than one trip recorded for some individuals. For the horizontal spatial analysis we processed data from 16 trips by

Table 1. Morphometric data for male and female Humboldt and Magellanic Penguins from Islotes Puñihuil, southern Chile
Means are shown \pm s.d., with ranges in parentheses; $n = 10$ for all samples. P -values correspond to Mann–Whitney test

	Humboldt		P	Magellanic		P
	Males	Females		Males	Females	
Bill-length (mm)	63.5 \pm 3.4 (60.1–68.1)	57.5 \pm 2.1 (54.5–59.6)	0.01	59.2 \pm 1.5 (57.1–60.4)	54.6 \pm 2.8 (51.6–59.7)	0.04
Bill-depth (mm)	26.4 \pm 3.7 (21.9–32)	24.0 \pm 2.6 (21.4–27.1)	0.5	25.5 \pm 1.7 (23.2–27.2)	23.4 \pm 1.8 (21.2–25.4)	0.07
Mass (kg)	4.1 \pm 0.4 (3.7–4.3)	3.2 \pm 0.4 (2.7–3.9)	0.4	3.8 \pm 0.2 (3.6–4)	3.0 \pm 0.3 (2.6–3.3)	0.01

Humboldt Penguins (6 females, 4 males) and 14 trips by Magellanic Penguins (8 females, 2 males).

Data-recording devices

The TDR devices weighed ~30 g, which is <1% of the mean body mass of either species of penguin, with maximum dimensions of $67 \times 17 \times 17$ mm, equivalent to ~2% of the cross-sectional area of a penguin's body. Data were stored on a 64-Mb non-volatile flash memory (Wildlife Computers). The TDR were each equipped with pressure, light and temperature sensors. They were programmed with MK9HOST (Wildlife Computers) with a time measurement-interval of 3 s. Temperature and light measurements were not included in our analyses. The pressure sensor recorded the depth of dives between 0 and 350 m, accurate to within 0.5 m (depths of 0–20 m), 1 m (20–200 m) or 5 m (200–350 m).

The GPS loggers had a hydrodynamic, waterproof housing measuring $96 \times 39 \times 27$ mm, corresponding to ~6.5% of the cross-sectional area of a penguin's body, and weighed 75 g, equivalent to ~1.7% of the mean mass of Magellanic Penguins (Humboldt Penguins are heavier so the weight of the logger is <1.7%). Data were stored on a 2-MB flash memory card. The GPS loggers use an active patch-antenna to record geographical position to $0.001'$ of latitude and longitude, with an absolute accuracy of ~5 m in continuous GPS mode and 20 m in intermittent mode (when the device is programmed to switch on at preselected intervals; see Ryan *et al.* 2004 for details). Devices were programmed to record at 1-min intermittent mode (1 fix min^{-1}). The GPS loggers also recorded depth of dives at 3-s intervals, with an accuracy of 0.3 m.

Data analysis

Diving data, duration of foraging trips and foraging activity

We analysed dive data from both TDR and GPS devices using MULTITRACE 7.7.09 (Jensen Software Systems, Kiel, Germany). We considered a penguin to have dived when the maximum depth reached was ≥ 3 m (Schiavini and Raya Rey 2004). For each dive the following parameters were calculated: total duration, start time of dive, maximum depth, bottom time (time spent at 75% of maximum dive depth attained during the dive; after Tremblay and Cherel 2000), rate of descent (determined from beginning of the dive to the onset of the bottom phase), rate of ascent (from end of bottom phase to end of dive) and post-dive interval (i.e. time between completion of one dive and onset of next). Before analysis, data were corrected for a drifting surface level (i.e. to correct the surface level for differences in wave action).

Duration of foraging trips was calculated as the sum of the duration of all dives and post-dive intervals. When the interval without dives was >3 h, we considered the foraging trip to have ended at the completion of the last dive recorded (Raya Rey *et al.* 2012).

As a measure of foraging effort, we calculated the percentage of time spent underwater (sum of the duration of all dives per trip as a proportion of the duration of the foraging trip), dive-rate (number of dives per trip as a proportion of the duration of the foraging trip) and vertical travel distance (VTD), which is defined

as twice the sum of the maximum dive-depth for all dives performed during each trip (Horning and Trillmich 1997). As a measurement of foraging activity we calculated bottom time (min) per hour underwater (as the sum of all bottom time during a foraging trip divided by the total duration of a foraging trip). Diving efficiency was estimated following Ydenberg and Clark (1989) as:

$$\text{Diving efficiency} = \text{bottom time} \div (\text{dive duration} + \text{post-dive interval})$$

However, this calculation has some limitations as it does not account for some factors, such as oxygen-loading curves and their relationship with swimming speed and rates of prey encounter (Wilson 2010). Because birds tended to dive serially to a specific depth zone, consecutive dives to the same depth zone were called intra-depth zone (IDZ) dives (cf. Tremblay and Cherel 2000). The IDZ was defined as the maximum depth reached by the preceding dive $\pm 10\%$.

Tracking data and foraging areas

Tracks of foraging trips were displayed using a geographical information system (GIS) program using a Gauss Krüger projection (ArcGIS 9.3, ESRI, Redlands, CA, USA). For each trip we calculated the maximum distance reached (D; the maximum distance reached in a straight line from the colony), total distance travelled (L), global straightness index (D/L) (Benhamou 2004), and area (calculated as the area enclosed by the path). For each study group (each species, each sex) and for each species (sexes pooled) we calculated a utilisation grid with the kernel density from the density function in the spatial analysis extension in ArcGIS 9.3 with a search radius of 1000 m and an output cell-size of 10 m and given the extension covered by the species during their foraging trips and the maximum distance reached (Hemson *et al.* 2005; Falabella *et al.* 2009). We categorized kernel density grids into three separate percentile regions corresponding to the 50, 75 and 95% density of position estimates, where the 95% was the least used (where the probability of occurrence is the lowest) and the 50% was the kernel with the highest density (Wood *et al.* 2000). The overlap in the kernel contours between studied groups was also analysed using tools in ArcGIS 9.3. To quantify the overlap of the foraging areas between species and sexes, we quantified the percentage of the kernel area (50, 75 and 95%) that overlapped with the other species or sex within each species. The degree of overlap was calculated, for example, as the percentage of the area used by Humboldt Penguins that overlapped with the area used by Magellanic Penguins and vice versa and the same between sexes within a species. Since the total area from which the percentage was calculated was different for each species and sex, we calculated a percentage overlap for Humboldt Penguins with respect to Magellanic Penguins and a percentage overlap for Magellanic Penguins with respect to Humboldt Penguins (González-Solís *et al.* 2000) and the same for sex. To characterise the habitat utilised during foraging, we overlaid the foraging kernel polygons with sea surface temperature (SST), ocean colour, as shown by levels of chlorophyll-*a* (chl-*a*), which represent the water productivity and bathymetry images. Chl-*a* and SST data were obtained from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) Ocean (4.5-km resolution, see

<http://oceancolor.gsfc.nasa.gov/>, accessed 7 April 2013) monthly composite images from November 2008. Bathymetry data (ETopo Digital Maps, see <http://www.ngdc.noaa.gov/mgg/bathymetry/relief.html>, accessed 7 April 2013) were obtained at a spatial resolution of 2' latitude and longitude. We used the Marine Geospatial Ecology Tools (Roberts *et al.* 2010) in ArcGIS 9.3 to handle the oceanographical data.

Statistical analysis

The effects of sex and species (as well as their interactions) on the different trip, dive and track parameters were analysed using generalized linear mixed effects models (GLMM) fitted by restricted maximum likelihood with a Gaussian distribution of errors and identity link function. Sex and species were included as fixed factors and bird identity as a random factor to avoid pseudoreplication (Hurlbert 1984). When appropriate, data were log-transformed or arcsin square root transformed to fulfil the criterion of normality. We used a likelihood ratio test to evaluate the significance of the inclusion of individuals as a random factor. Analyses were performed using the statistical package R (version 2.12; R Development Core Team 2010). All means are presented \pm s.d. and values of $P < 0.05$ are considered statistically significant.

Results

We recorded a combined total of 47 foraging trips by male and female Magellanic and Humboldt Penguins during chick-rearing at Islotes Puñihuil (Table 2). Most trips were completed within 1 day, except for one overnight trip by a female Humboldt Penguin (8% of female Humboldt foraging trips) and three overnight trips by male Magellanic Penguins (33% of male Magellanic foraging trips).

Diving behaviour and foraging trips

Diving and foraging trips differed between species and sexes (Table 2). The inclusion of individuals as a random effect was significant ($P < 0.001$) for the analysis for all the dependent variables. In both species, the mean duration of foraging trips

was < 20 h and did not differ significantly between species ($F_{1,27} = 0.7$, $P = 0.4$) or between males and females ($F_{1,27} = 3.93$, $P = 0.06$), nor was the interaction of factors significant ($F_{1,27} = 0.4$, $P = 0.5$). For Humboldt Penguins, maximum diving depth was 67 m for females and 75 m for males, and maximum duration of dives was 141 s for both sexes. For female and male Magellanic Penguins, respectively, maximum diving depth was 100 and 67 m and duration of dives 192 and 177 s. Mean depth of dives by Magellanic Penguins was significantly deeper than those by Humboldt Penguins ($F_{1,27} = 5.36$, $P = 0.03$), but there were no significant differences between sexes ($F_{1,27} = 2.0$, $P = 0.2$) nor in the interaction of the two factors ($F_{27,1} = 0.005$, $P = 0.9$). Accordingly, dive duration was significantly longer in Magellanic Penguins than in Humboldt Penguins ($F_{1,27} = 6.1$, $P = 0.02$), and also significantly longer for males than for females ($F_{1,27} = 8.9$, $P = 0.005$), but the interaction was not significantly different ($F_{1,27} = 0.001$, $P = 0.9$). Other foraging parameters and dive characteristics (Table 2) did not differ significantly between the studied groups (species, sexes).

Maximum diving efficiency was high (> 0.28) but at different ranges of depths for each the four study groups (species, sexes; Fig. 1). Maximum diving efficiency of Magellanic Penguins was at greater depths than Humboldt Penguins (Magellanic Penguin: males, 15–45 m, females, 20–40; Humboldt Penguins: males, 10–25 m, females, 10–35 m; Fig. 1).

Foraging areas

We successfully recorded a combined 30 tracks of females and males of the two species of penguin (Table 3). In general, penguins headed either north-east or south-west when leaving the colony to forage, and overall foraging effort was concentrated to the west and south-west of the colony (Fig. 2). Penguins foraged up to 15 km away from the colony. Although foraging routes and areas showed differences, there were also similarities between species and sexes. The total distance travelled by both species was similar ($F_{1,10} = 2.7$, $P = 0.1$), but was significantly greater for males than for females ($F_{1,10} = 14.1$, $P = 0.004$), with no significant difference in the interaction of factors $F_{1,10} = 4.04$,

Table 2. Characteristics of foraging trips and dives of Humboldt and Magellanic Penguins breeding at Islotes Puñihuil, Chile
All means presented \pm s.d.

	Humboldt Penguin		Magellanic Penguin	
	Female ($n = 7$)	Male ($n = 9$)	Female ($n = 9$)	Male ($n = 6$)
Number of trips	12	12	14	9
Duration of trips (h)	9.3 \pm 4.4	11.8 \pm 3.7	10.0 \pm 4.7	18.9 \pm 13.3
Proportion of trip time spent underwater (%)	52.8 \pm 19.5	61.1 \pm 20.5	54.6 \pm 14.7	52.6 \pm 13.8
Dives per hour ($n h^{-1}$)	34.0 \pm 9.9	33.7 \pm 11.1	32.0 \pm 9.9	26.4 \pm 8.6
Mean depth of dives (m)	18.6 \pm 5.7	22.2 \pm 8.6	23.6 \pm 8.0	27.5 \pm 7.3
Maximum depth of dives (m)	40.3 \pm 15.0	48.8 \pm 14.7	55.6 \pm 20.3	59.3 \pm 11.8
Post-dive interval (s)	69.2 \pm 80.0	53.8 \pm 45.4	61.7 \pm 39.5	75.6 \pm 42.0
Mean duration of dives (s)	54.9 \pm 8.6	65.7 \pm 11.5	63.1 \pm 11.1	74.0 \pm 13.0
Maximum duration of dives (s)	104.8 \pm 21.8	117.8 \pm 14.6	120.3 \pm 28.5	143 \pm 21.8
Mean bottom time (s)	21.0 \pm 6.9	24.4 \pm 7.5	20.4 \pm 5.3	23.4 \pm 4.3
Bottom time per hour underwater (min)	12.6 \pm 6.7	14.1 \pm 6.8	10.8 \pm 4.4	10.1 \pm 3.1
Descent rate ($m s^{-1}$)	1.0 \pm 0.2	1.0 \pm 0.2	1.0 \pm 0.2	0.9 \pm 0.2
Ascent rate ($m s^{-1}$)	1.0 \pm 0.2	1.0 \pm 0.2	1.0 \pm 0.2	1.0 \pm 0.2
Distance covered per hour ($m h^{-1}$)	1282.4 \pm 497.0	1488.8 \pm 712.7	1436.9 \pm 489.0	1403.1 \pm 533.3
Intra-depth zone value (%; see Methods)	84.2 \pm 11.5	88.0 \pm 8.2	80.3 \pm 10.8	77.7 \pm 9.1

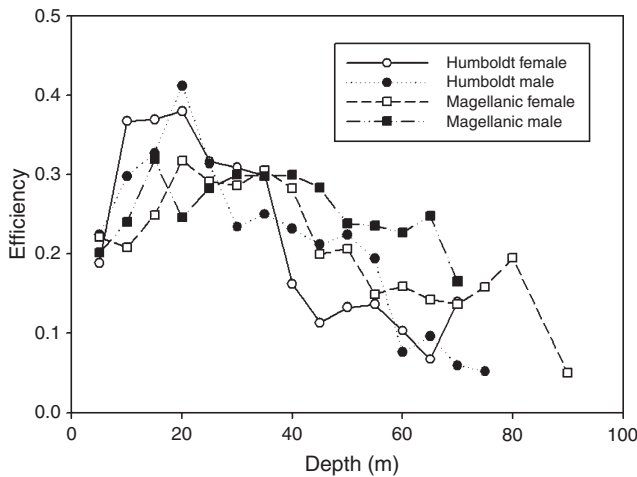


Fig. 1. Diving efficiency as a function of maximum depth for male and female Magellanic and Humboldt Penguins breeding at Islotos Puñihuil, Chile.

Table 3. Characteristics of foraging trips by Humboldt and Magellanic Penguins breeding at Islotos Puñihuil Islands, Chile

D, maximum distance reached in a straight line from the colony; L, total distance travelled; D/L, global straightness index; area is total area covered

	Humboldt Penguin		Magellanic Penguin	
	Female (n=6)	Male (n=4)	Female (n=8)	Male (n=2)
Number of trips	11	5	9	5
D (km)	6.5±2.1	8.3±1.1	8.6±2.5	10.9±2.8
L (km)	31.5±14.3	48±6.7	42.8±18.0	79.2±37.4
D/L	0.4±0.1	0.3±0.06	0.5±0.2	0.3±0.2
Area (km ²)	8.8±9.7	13.8±6.9	11.3±7.9	15.5±11

$P=0.07$). Females made more direct trips than males, shown by their significantly higher global straightness index ($F_{1,10}=5.7$, $P=0.03$); there were no differences in the global straightness index between species ($F_{1,10}=1.3$, $P>0.05$) or in the interaction of factors ($F_{1,10}=1.1$, $P>0.05$). In both species, males and females covered similar areas ($F_{1,10}=4.3$, $P=0.06$).

Kernel area locations and sizes for female and male Magellanic and Humboldt Penguins are shown in Fig. 2. Irrespective of sex, Magellanic Penguins covered larger areas than Humboldt Penguins. Foraging areas were characterised by very high values of chl-*a* ($12.8 \pm 5.5 \text{ mg m}^{-3}$) and SST ($15.1 \pm 4.3^\circ\text{C}$), and values were similar within the different kernel contours in both species and sexes. However, the whole area used by penguins (for the 95% kernel contour for both species) had high chl-*a* values during the study period. Magellanic Penguins foraged in deeper water than Humboldt Penguins (both sexes combined) when considered at the 95% kernel (Magellanic, $76.5 \pm 5.7 \text{ m}$; Humboldt, $46 \pm 1.4 \text{ m}$) and 75% kernel (combined with the 50% kernel) ($55.5 \pm 6.3 \text{ m}$; $32.5 \pm 3.5 \text{ m}$).

The overlap in the different density contours was lower between species than between sexes within a species and the overlap was greater for all the combinations including the transit areas (95%) than for core areas (75, 50%) (Tables 4, 5). Within the 95% kernel areas, for both species, the overlap of areas used by

females with areas used by conspecific males was $>60\%$ (Table 5).

Discussion

Interspecific and intraspecific sexual segregation in foraging seabirds has been extensively studied, although there have been few studies of penguins that have examined both factors simultaneously (Hull 1999, 2000). We obtained several clear results in this study despite our small sample size. Unlike studies of volant seabirds (e.g. González-Solís *et al.* 2007; Weimerskirch *et al.* 2009) we found greater differences in foraging behaviour between the two species – the Humboldt and Magellanic Penguins – than between sexes within each species. Interspecific differences in foraging areas and some diving characteristics were greater than differences between sexes, but the only differences in foraging routes observed were between sexes and not between species.

We did not directly assess the effect of the data-recording devices on the foraging behaviour of the penguins, but equivalent studies in the congeneric African Penguin (*Spheniscus demersus*) showed no strong evidence of effects of data-recording devices on their foraging behaviour (Petersen *et al.* 2006). In our study, all animals fitted with devices were able to continue their chick-rearing during the time when they were equipped with devices.

Interspecific strategies

It has been hypothesised that interference competition may lead to spatial segregation between species with similar ecological requirements, as has been shown for several species of penguin (Hull 1999, 2000; Lynnes *et al.* 2002; Kokubun *et al.* 2010; Masello *et al.* 2010; Wilson 2010). Even though ocean productivity in our study area is generally high and the populations of penguins fairly small, we have shown spatial differences in foraging behaviour between the two species, in particular in both vertical (depth) and horizontal (area) foraging range. In our study, dives by Magellanic Penguins were deeper than those of Humboldt Penguins. Magellanic Penguins also had higher diving efficiencies at a greater range of depths, including deep depths. Differential depth-efficiency has been described in some subantarctic and Antarctic penguins of similar size (Mori and Boyd 2004; Wilson 2010). The depth of dives might be determined by any combination of extrinsic factors (such as location of prey), intrinsic factors (such as physiology), or interspecific or intraspecific competition. Because Magellanic Penguins, the smaller species, dive deeper it is possible that the differences between the two species are not a result of physiological differences and we suggest they may be the result of interspecific competition. We also found spatial differences in the foraging areas of both species, with Magellanic Penguins covering a larger area to the south of the colony. The observation that the more abundant species, the Magellanic Penguin, foraged over a larger area than the less abundant species, confirms one consequence of the hinterland model of Cairns (1989), which proposes that seabirds from neighbouring colonies typically occupy non-overlapping foraging zones and that population of a colony is a function of the sizes of these zones.

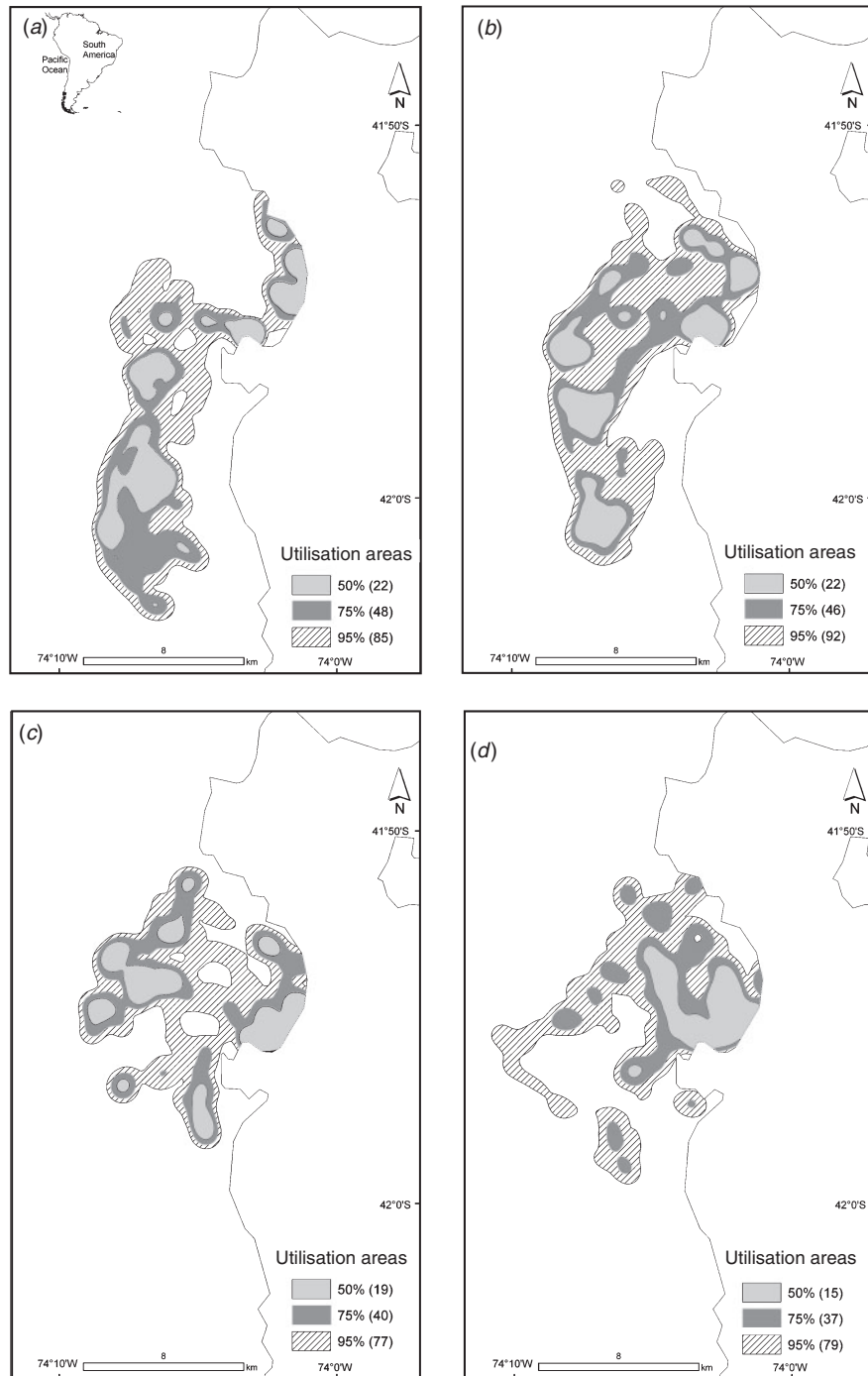


Fig. 2. Maps of 50, 75 and 95% kernel contours of at-sea distribution for (a–b) Magellanic Penguins: (a) males, (b) females; and (c–d) Humboldt Penguins: (c) males, (d) females. In the key, figures in parentheses for each kernel contour are effective areas (km²). The star indicates the location of the breeding colony.

Intraspecific strategies

Sexual differences in foraging behaviour and at-sea distribution have been shown in several groups of seabirds, including penguins (e.g. Phillips *et al.* 2004; Pütz *et al.* 2006; Weimerskirch *et al.* 2009; Raya Rey *et al.* 2012). Larger marine animals tend to

dive deeper (e.g. Schreer *et al.* 2001; Halsey *et al.* 2006) and this has been reported for sexually dimorphic seabirds, with the larger sex diving to greater depths (Weimerskirch *et al.* 2009; Quintana *et al.* 2011). All penguins show some sexual size dimorphism, with males generally being heavier and having larger flippers and

Table 4. Overlap of the three kernel contours areas for Humboldt and Magellanic Penguins (sexes combined)

Numbers are the percentage of the kernel contour area of a species that overlaps with the same kernel contour area for the other species

Kernel area	Humboldt Penguins	Magellanic Penguins
95%	56	49
75%	31	27
50%	26	20

Table 5. Overlap of the three kernel contours areas for males and females within each species

For each species, numbers are the percentage of the kernel contour area of one sex that overlaps with the same kernel contour area for the other sex

Kernel area	Humboldt Penguins		Magellanic Penguins	
	Males	Females	Males	Females
95%	67	63	67	62
75%	36	38	43	45
50%	29	36	25	25

bills than females (Fairbairn and Shine 1993; Williams 1995). Magellanic and Humboldt Penguins are also sexually dimorphic, with males on average ~10% heavier than females (Zavalaga and Paredes 1997; Bertellotti *et al.* 2002; also see Table 1). In our study, during the early chick-rearing period, we found only minor differences between sexes in diving parameters, with males undertaking longer dives than females in both species. However, the depth of dives did not differ between sexes. There have been few studies of penguins that have examined sexual differences in foraging behaviour but, where it has been studied, most variability between sexes was recorded during the incubation period and it has been suggested to occur when availability of prey is low (Pütz *et al.* 2006; Raya Rey *et al.* 2010, 2012).

Both species of penguin studied here showed differences between sexes in the parameters of foraging trips: males travelled further than females, but females undertook more direct trips than males. It has been suggested that the sinuosity of a predator's foraging track correlates with abundance and distribution of prey, or both, as well as predator satiation (Zollner and Lima 1999; Bailleul *et al.* 2008), with individuals moving in straighter paths when travelling when prey is scarce or when their energetic levels are low. Larger animals (males) have larger mass-specific energy reserves and might swim more quickly at the same rate of energy expenditure. By following those strategies, females may acquire less food in a shorter time in predictable places whereas males are able to travel further and potentially catch more food. Whether the differences in foraging strategies we observed were related to the prey taken, differences in parental role or energetic needs is not known.

Conclusions

Our study of two similar sympatric species has shown differences in a number of foraging parameters, both between species and between sexes within each of the two species. Niche separation may be related to the competitive advantages of one species over another (Wilson 2010). One possible explanation for the differences between species may be that Humboldt Penguins at Islotes

Puñihuil are at the extreme southern edge of their distributional range (Duffy 1987; Wilson *et al.* 1995; Simeone and Hucke-Gaete 1997; Hiriart-Bertrand *et al.* 2010), which may mean the species is at a competitive disadvantage compared with Magellanic Penguins. The differences between sexes we observed in diving behaviour were consistent with the results of previous studies conducted during the chick-rearing period (Raya Rey *et al.* 2012) but our analysis of the foraging areas of sexes was the first such study and showed that sexes adopted different strategies, although further study is needed given the small sample size of our study.

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