

Foraging behaviour and habitat partitioning of two sympatric cormorants in Patagonia, Argentina

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Radiotelemetry was used to assess the distribution and diving behaviour of Rock Shags *Phalacrocorax magellanicus* and Red-legged Cormorants *Phalacrocorax gaimardi* breeding in sympatry, and Rock Shags breeding in isolation. When breeding in sympatry there was little overlap in the foraging locations of the two species, with the highest densities of each species separated by 10 km. Red-legged Cormorants fed significantly closer to the breeding colony than did Rock Shags and undertook shorter foraging trips, making almost twice as many foraging trips per day as Rock Shags. Rock Shags breeding in isolation had a shorter foraging range than the birds breeding in sympatry with Red-legged Cormorants and foraging trip duration was significantly shorter. However, the number of feeding trips per day was similar between areas of sympatry and allopatry. Differences in the foraging ecology of Rock Shags in areas of sympatry and allopatry may be due to interspecific competition, which forces niche differentiation. The distance between foraging sites, the speed of movement of the prey, a species tendency to move into prey-depleted areas and the length of the breeding season (during which the birds are constrained to be in the same area) may play critical roles in determining the extent to which differential area use by competitors is a strategy that benefits both parties.

Keywords: feeding ecology, interspecific competition, Pelecaniformes, resource use, Red-legged Cormorant *Phalacrocorax gaimardi*, Rock Shags *Phalacrocorax magellanicus*, seabirds, South America.

Interspecific competition for food is recognized as a major force in shaping the way animal communities develop and, ultimately, the way species co-exist (Hutchinson 1959, MacArthur & Levins 1967, Connell 1983, Schoener 1983, McDonald 2002, Ainley *et al.* 2004). Indeed, conventional theory negates the long-term co-existence of species competing for resources (Gause 1934) and so apparent competition observed in nature has often been explained by invoking niche shifts in one, or both, of the competing species (cf. Hutchinson 1958, 1959, 1978), although the resource may apparently stay the same. A major driver behind this thinking was the seminal paper by

MacArthur (1958), who explained the co-existence of sympatric warblers by pointing out that the species partitioned resources by foraging at different canopy heights. This study and more recent ones (e.g. Hodgson *et al.* 1997) explain niche differences by considering variance along single dimensions. In fact, the large number of possible axes in the n-dimensional niche hyper-volume (*sensu* Hutchinson 1958) means that there is huge potential for niche segregation between potentially competing species.

The Pelecaniformes are excellent study subjects for investigation of feeding-niche overlap and segregation between species in different areas of the ocean due to their colonial habits and the ease with which many colonies can be studied (Schreiber & Clapp 1987). In this regard, cormorants breeding in sympatry along the Patagonian coast of Argentina

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constitute an interesting model to explore foraging habitat partitioning in seabirds because there are four species and much is known about the distribution and size of the various colonies (Frere *et al.* 2005).

The Rock Shag *Phalacrocorax magellanicus* and the Red-legged Cormorant *Phalacrocorax gaimardi* are both widely distributed in southern South America. Although they breed sympatrically along the Patagonian coast of Argentina and Chile (Harrison 1985, Frere *et al.* 2005, Jaramillo 2005), they have distinct species-specific patterns in geographical distribution and abundance in Argentina. The breeding population of the Red-legged Cormorant numbers around 800 pairs distributed in only 13 colonies, restricted to the Santa Cruz Province (47°05'S–50°23'S) (Frere *et al.* 2005), whereas the Rock Shag is more widely distributed, with almost 7000 breeding pairs in 145 colonies, ranging from Peninsula Valdes (42°25'S, 64°31'W) to the Beagle Channel (55°01'S, 66°20'W) (Yorio *et al.* 1999, Frere *et al.* 2005). In Patagonia, the two species breed together at just eight sites (Yorio *et al.* 1998, Frere *et al.* 2005).

Both species appear to have similar ecological requirements. The Red-legged Cormorant is only 6% lighter than the Rock Shag (1.38 ± 0.05 kg, $n = 6$, vs. 1.46 ± 0.07 kg, $n = 50$ respectively), and both are pursuit-divers that feed mainly inshore on benthic or demersal fish and invertebrates (Quintana 1999, 2001, Frere *et al.* 2002, Gandini *et al.* 2005, Millones *et al.* 2005). They both select nest-sites with similar environmental features, tending to use vertical cliffs (Frere & Gandini 2001, Punta *et al.* 2003), and show a clear overlap in the timing of breeding (Frere *et al.* 2005).

Foraging behaviour studies throughout the range of the Red-legged Cormorant (Frere *et al.* 2002, Gandini *et al.* 2005) and the Rock Shag (Wanless & Harris 1991, Quintana 1999, 2001, Sapoznikow & Quintana 2003) are based on studies of birds occurring in single-species colonies. There is no documentation of the foraging ecology of birds breeding in mixed colonies, even though the apparent similarity between these species would suggest the development of intense competition, which should ultimately lead to niche segregation (Croxall & Prince 1980, Diamond 1983, Weimerskirch *et al.* 1986).

We used radiotelemetry data to perform a comparative analysis of the feeding distribution and diving behaviour of Rock Shags and Red-legged Cormorants breeding in sympatry, and of Rock Shags breeding in isolation.

METHODS

Data used in this study derive from two nesting sites in coastal Patagonia, Argentina: Ría Deseado (47°45'S, 65°56'W), Santa Cruz, and Caleta Malaspina (45°11'S, 66°30'W), Chubut. The Ría Deseado is an old riverbed now flooded by the sea, to a length of 44 km, which has high local environmental heterogeneity associated with its variable topography. The Ría Deseado is subject to substantial tides (up to 6 m), water depths range between 0 and 28 m and there is a variety of substrates (mud, clay, pebbles and rocks) (Kühnemann 1969, Nautical Chart Nr. H361, Servicio de Hidrografía Naval de Argentina). Caleta Malaspina is an inlet with a maximum width of 4 km and a length of 10 km (Herrera 1997). The Rock Shag breeds on several islands inside Caleta Malaspina. The sea floor is highly heterogeneous, with substrates of rocks, pebbles, sand and mud and water depths ranging between 0 and 30 m (F. Quintana unpubl. data). In both areas, the soft substrates are characterized by a community of annelids dominated by polychaetes and the rock substrates by rockfishes and notothenids. All these animals are present in the diet of the two cormorants (Frere *et al.* 2005, Millones *et al.* 2005). Two other species of cormorants breed and forage inside both study areas, the Imperial Cormorant *Phalacrocorax atriceps* and the Neotropic Cormorant *Phalacrocorax olivaceus* (Sapoznikow & Quintana 2003, Frere *et al.* 2005). However, there are low numbers of these species (fewer than 200 individuals) at Ría Deseado (Frere *et al.* 2005, E. Frere unpubl. data).

At Ría Deseado, fieldwork was carried out at Isla Elena, Puerto Deseado, between 2 and 11 December 1999 on adult birds of the two species of cormorants during late incubation and early chick-rearing periods (Frere *et al.* 2002, Gandini *et al.* 2005). The foraging performance of Rock Shags at Caleta Malaspina was recorded during 1998 and 1999 breeding seasons, on adult breeders during the last week of the incubating period and the first week of the chick rearing (see Sapoznikow & Quintana 2003 for details). Some of our data on Red-legged Cormorants from Ría Deseado and Rock Shags from Caleta Malaspina have been published previously (Frere *et al.* 2002, Sapoznikow & Quintana 2003, Gandini *et al.* 2005), but these publications were not directly relevant to the current work.

Radiotelemetry and feeding patterns

VHF radio transmitters (Standard model, Advanced Telemetry Systems, Betel, MN) were deployed on a

total of six Red-legged Cormorants (Frere *et al.* 2002, Gandini *et al.* 2005) and eight Rock Shags from the Ría Deseado colony. All individuals were fitted with transmitters during their last week of incubation or the first week of the chick-rearing period. The average weight of the instruments was 18.4 g (sd = ± 0.2 , $n = 14$), which represented around 1.3% of adult body mass of the Red-legged Cormorant and 1.2% of the Rock Shag. Devices were attached to a few tail feathers using waterproof tape (Wanless *et al.* 1998). The procedure was completed in less than 5 min. Released birds flew directly to sea and returned to their nest shortly afterwards. All birds carrying devices continued breeding normally during the study period. Radio signals were monitored from three tracking stations separated by 3–5 km. Each was 20–50 m above sea-level.

The reception equipment consisted of a single-channel receiver (R161A model Advanced Telemetry Systems, Inc.) connected to a nine-element Yagi aerial (ATS Inc.). The detection range of the system was about 8–10 km for a transmitter at sea level (Sapoznikow & Quintana 2003, Gandini *et al.* 2005). The pulse rate of the signal was 65 pulses/min. Dives were identified by breaks in signal transmission and thus the duration of each dive and inter-dive recovery time within a trip could be determined (Wanless *et al.* 1991, Wanless & Harris 1993). Dive efficiency was defined as the ratio between mean diving time and mean recovery time (Dewar 1924).

Nest attendance was recorded by a data logger (DCCII model, ATS Inc.) connected to a scanning receiver (R2000 model, ATS Inc.). This equipment was located 2–15 m from the nests of the focal birds, which enabled us to monitor attendance of birds up to 15 m from nests. Nest attendance was automatically registered every 10 min. Trip duration was calculated as the time difference between the departure from and arrival to the colony (Sapoznikow & Quintana 2003, Gandini *et al.* 2005).

Feeding locations

A feeding location was defined as the place where a bird dived repeatedly (Quintana 2001, Gandini *et al.* 2005). Compass bearings were recorded for the diving locations of each radiotagged individual. These locations were defined by Cartesian co-ordinates calculated by triangulation (with a mean error of 19°) from at least two fixed antenna stations following the procedures documented by Quintana (2001) and Frere *et al.* (2002). Each foraging area visited during

a trip was characterized by a single position. Foraging range was calculated as the distance from the colony to the fixed location.

Kernel analysis was used to characterize the spatial distribution of feeding locations following Naef-Daenzer (1993). The overlap between species was calculated as the percentage of the foraging range of Rock Shags that overlapped with that of Red-legged Cormorants, and the percentage of the foraging range of Red-legged Cormorants that overlapped with that of Rock Shags (Naef-Daenzer 1993, Wood *et al.* 2000).

Statistical analysis

Generalized linear mixed models were used to test the effects of explanatory categorical variables on response variables, considering thus the non-independence of data between multiple measurements on the same individuals (Pinheiro & Bates 2000, Crawley 2007). Unless otherwise noted, we applied general linear mixed models (specifying Gaussian errors and an identity link function), where bird identity was included as a random effect. To test effects of explanatory variables on number of trips per day, we used generalized linear mixed models, specifying Poisson errors and a log link function. Reported results correspond to overall mean values (\pm sd) obtained by pooling the mean values for each bird. Statistical analyses were carried out using the LME4, LATTICE and NLME packages from R software, Version 2.6.1 (R Development Core Team 2007). All tests were two-tailed, and differences were considered significant at $P < 0.05$.

RESULTS

Feeding areas

Although both Rock Shags and Red-legged Cormorants from the same colony fed inside the Ría Deseado, there was little overlap in their foraging locations. The Rock Shags fed mainly at the mouth in the north-east of the ría, whereas all Red-legged Cormorants foraged in the ría 5–15 km upstream of the coast (Fig. 1). The high density feeding areas of each cormorant species (50% kernel contours) were separated from each other by 5–10 km (Fig. 1). The only zone of overlap at the 95% kernel contour represented a higher proportion of the feeding area of Red-legged Cormorants than of Rock Shags. The overlap of Red-legged Cormorant with Rock Shag at the 95% level contour was 8% whereas that for Rock Shag

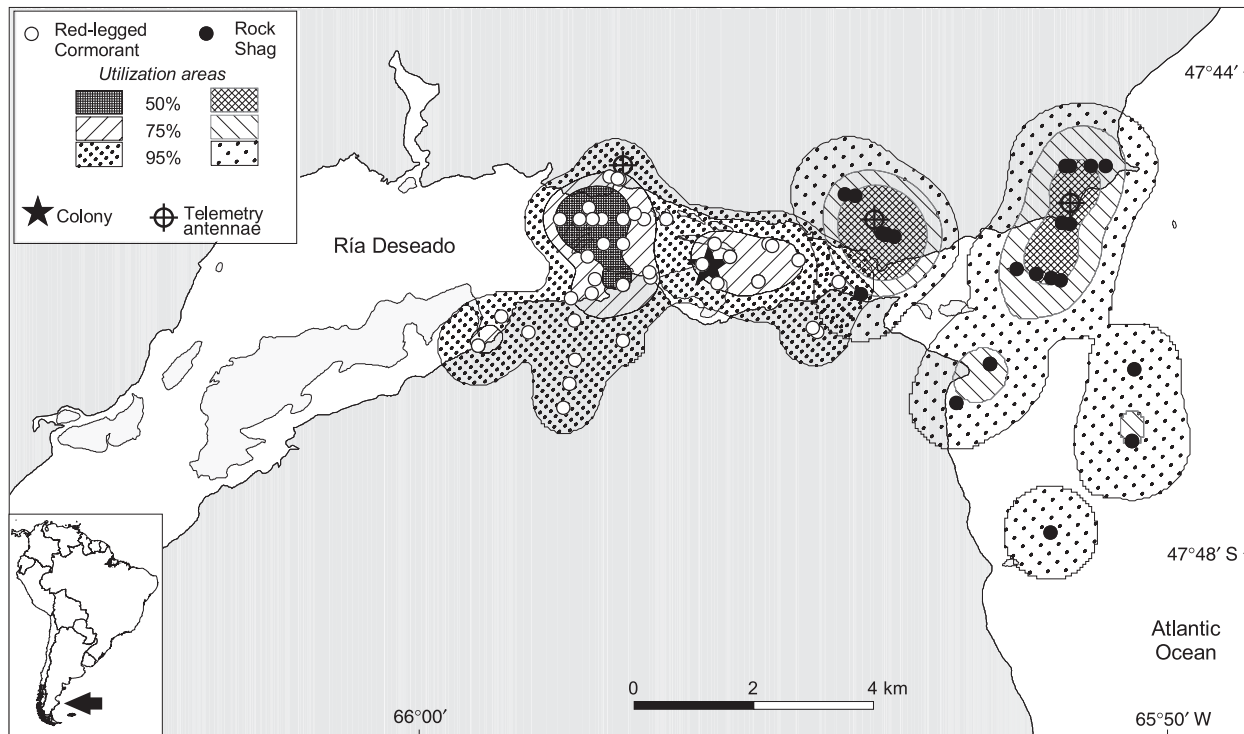


Figure 1. Foraging locations of the Red-legged Cormorant and Rock Shag at Ría Deseado, Argentina.

with Red-legged Cormorant was 5%. The foraging ranges of both Rock Shags and Red-legged Cormorants were extremely restricted, although Red-legged Cormorants fed closer to the colony than did the Rock Shags. Whereas the Red-legged Cormorants fed at a mean maximum distance of 1.91 ± 0.90 km (Gandini *et al.* 2005), the Rock Shags did so at 5.01 ± 1.80 km ($n = 28$ feeding locations; $F_{1,11} = 114.5$, $P < 0.0001$). All feeding locations of Red-legged Cormorant were located less than 1 km from the shore (Gandini *et al.* 2005), and Rock Shag locations were less than 4 km from the shore.

Trip duration and diving performance

Trip duration was not a good indicator of distances travelled to the foraging areas, as both Rock Shags and Red-legged Cormorants showed a nonsignificant relationship between trip duration and foraging distances (Pearson correlation, $P > 0.05$). Rock Shags spent 4.4% ($n = 12$ trips) of the time of their feeding trips flying to and from the foraging areas. A similar proportion of time (4%) was determined by Gandini *et al.* (2005) for the Red-legged Cormorants at the same colony.

On average, Rock Shags undertook longer foraging trips than did Red-legged Cormorants ($F_{1,11} = 48.2$, $P < 0.0001$) (Table 1). Red-legged Cormorants made almost twice as many foraging trips per day (birds only foraged during hours of daylight) as the Rock Shags ($z = 3.9$, $P < 0.0005$) (Table 1). Rock Shags invested more time in foraging (hours at sea per day; mean: 5.65 ± 0.54 h/day, $n = 7$ birds) than the Red-legged Cormorants (mean: 4.63 ± 0.55 h/day, $n = 5$ birds; $F_{1,10} = 6.8$, $P = 0.03$) (Table 1).

Mean dive duration and recovery time of individual Rock Shags were higher than that of Red-legged Cormorants ($F_{1,12} = 15.8$, $P < 0.005$ and $F_{1,12} = 6.6$, $P = 0.02$, respectively) (Table 1). There were no species-specific differences in either dive efficiency or the total time spent underwater ($F_{1,12} < 3.1$, $P > 0.10$) (Table 1). The range of depths of the foraging areas used by both species at Ría Deseado was similar (less than 24–28 m) (see below and Gandini *et al.* 2005).

Foraging patterns of Rock Shag in allopatry vs. sympatry

The Rock Shags breeding in isolation at Caleta Malaspina had a significantly shorter foraging range

Table 1. Summary of foraging performance and diving behaviour (mean \pm sd) of Red-legged Cormorants and Rock Shags fitted with radio-transmitters in Ría Deseado, Argentina. *A full 24-h day was not recorded. Data on Red-legged Cormorant from Gandini *et al.* (2005).

Bird	No. of trips	No. of days recorded	Trip duration (h)		Foraging effort (h/day)	Mean dive duration (s)	Mean recovery time (s)	Diving efficiency	Time under water (%)
Red-legged Cormorant									
12	30	7	1.07 \pm 0.58	3.86 \pm 0.90	4.2 \pm 0.79	25.2 \pm 10.8	9.3 \pm 4.3	2.93 \pm 1.32	73 \pm 4
54	29	7	0.88 \pm 0.44	3.86 \pm 1.07	4.13 \pm 1.68	24.5 \pm 8.3	8.8 \pm 3.3	3.00 \pm 1.51	70 \pm 7
85	21	6	1.44 \pm 1.30	4.33 \pm 0.52	5.03 \pm 1.79	26.2 \pm 9.8	9.3 \pm 5.0	3.12 \pm 1.27	73 \pm 4
114B	8	2	1.02 \pm 0.47	4.5 \pm 0.71	4.42	30.8 \pm 12.6	10.8 \pm 5.0	3.08 \pm 1.52	74 \pm 3
123	29	7	1.38 \pm 0.74	3.86 \pm 0.69	5.39 \pm 1.50	27.0 \pm 11.3	8.9 \pm 4.72	3.41 \pm 1.62	74 \pm 4
153	2	–*	1.21 \pm 0.06	–	–	28.0 \pm 4.3	8.2 \pm 1.72	3.62 \pm 0.71	78
Mean \pm sd	–	–	1.20 \pm 0.20	4.10 \pm 0.30	4.63 \pm 0.55	26.8 \pm 2.0	9.2 \pm 0.9	3.2 \pm 0.3	74 \pm 3
(n)			(6)	(5)	(5)	(6)	(6)	(6)	(6)
Rock Shag									
133A	5	4	4.73 \pm 1.16	1.20 \pm 0.45	5.19 \pm 0.06	37.5 \pm 6.0	14.1 \pm 3.7	2.81 \pm 0.85	73 \pm 2
133B	5	3	2.70 \pm 1.86	2.50 \pm 0.71	6.33 \pm 2.06	34.7 \pm 6.8	11.5 \pm 3.7	3.25 \pm 1.42	75 \pm 1
104	–	–	–	–	–	42.1 \pm 6.1	11.2 \pm 2.4	3.84 \pm 0.79	78 \pm 2
164	13	7	2.99 \pm 1.57	2.43 \pm 1.72	5.52 \pm 0.70	29.9 \pm 6.1	9.4 \pm 4.6	3.40 \pm 0.99	76 \pm 5
45	20	8	2.75 \pm 1.90	2.71 \pm 0.95	6.44 \pm 1.26	29.5 \pm 10.1	9.8 \pm 5.5	3.35 \pm 1.14	76 \pm 5
23B	3	2	2.81 \pm 1.38	2.00	5.75	42.4 \pm 6.7	12.9 \pm 2.8	3.38 \pm 0.68	76 \pm 1
23A	11	6	1.95 \pm 1.35	2.25 \pm 0.96	5.06 \pm 1.34	46.7 \pm 8.0	17.4 \pm 6.9	2.91 \pm 0.83	74 \pm 2
114A	10	5	2.67 \pm 0.44	2.00	5.33 \pm 0.51	51.7 \pm 9.0	20.7 \pm 7.2	2.66 \pm 0.69	71 \pm 4
Mean \pm sd	–	–	2.90 \pm 0.80	2.20 \pm 0.50	5.65 \pm 0.54	39.3 \pm 7.9	13.4 \pm 3.9	3.2 \pm 0.38	75 \pm 2
(n)			(7)	(7)	(7)	(8)	(8)	(8)	(8)

Table 2. Foraging variables (mean \pm sd) of Rock Shags breeding in Ría Deseado (sympatry) and Caleta Malaspina (allopatry), Argentina.

Locality	Foraging range (km)	Trip duration (h)	Trips per day	Source
Ría Deseado	5.0 \pm 1.8 (n = 28*)	2.90 \pm 0.84 (n = 7**)	2.2 \pm 0.5 (n = 7**)	This study
Caleta Malaspina	2.1 \pm 1.5 (n = 86*)	1.90 \pm 0.70 (n = 20**)	2.4 \pm 0.7 (n = 12**)	Sapoznikow & Quintana (2003)

*Trips where locations were determined.

**Number of birds.

($F_{1,28} = 27.3$, $P < 0.0001$) and trip duration ($F_{1,26} = 11.3$, $P < 0.005$) than the birds breeding in sympatry with Red-legged Cormorants at Puerto Deseado (Table 2). However, the number of feeding trips per day was similar between localities ($z = 0.6$, $P > 0.5$) (Table 2). Water depths of the foraging areas used by Rock Shags in the two study sites were relatively similar. In Caleta Malaspina, Rock Shags foraged in water shallower than 20 m, with most foraging occurring in water less than 10 m deep (Sapoznikow & Quintana 2003, Nautical Chart No. H264, Servicio de Hidrografía Naval de Argentina). In Ría Deseado, these birds exploited areas with depths shallower than 28 m; 50% of the feeding locations had depths between 5–15 m (Nautical Chart No. H361, Servicio de Hidrografía Naval de Argentina).

DISCUSSION

At Ría Deseado there was a clear spatial segregation in foraging areas between the two species, with almost no overlap. Similar patterns have been observed in a number of seabird species (e.g. Weimerskirch *et al.* 1988, González-Solis *et al.* 2000). Rock Shags used sites for foraging that were further from the colonies than those used by Red-legged Cormorants by a factor of about 2.4. Accordingly, the Rock Shags also spent longer on their foraging trips, also by a factor of 2.4. As both species spent about 4% of their total foraging trips flying (which therefore equates with the differences in distance to the foraging sites), the proportion of time spent in the foraging area was the same, and this correlates with the time actually spent

underwater. Therefore, longer foraging trips equate with a proportionately longer time spent foraging, so that both species had virtually identical tactics in terms of investment of time, energy and acquisition of resources. Although the Red-legged Cormorants undertook shorter foraging trips, they conducted more trips per day than did the Rock Shags to compensate. Based on these foraging parameters, therefore, it would seem that the case of the two cormorant species in Ría Deseado mirrors the case of the warblers studied by MacArthur (1958). MacArthur's study, however, implied that the different warbler species taking prey from different heights in the vegetation were somehow adapted to their own particular height niche. This appears to be less the case with the two cormorant species considered unless somehow Rock Shags were better adapted for flying farther than Red-legged Cormorants. This appears unlikely because the Rock Shags breeding in isolation had foraging ranges and durations very similar to those of the Red-legged Cormorant breeding in sympatry. Similarly, the dive to pause ratio (Cooper 1986) for the two species was identical (0.33), suggesting similar diving capacities.

Niche separation between competing species, however, is postulated to only come about via competitive advantages accrued by one species over the other in particular areas of the n-dimensional hyper-volume. Our inability to define what this might be for the sympatric cormorants may be due simply to our assessment of foraging parameters being too crude to allow us to address this. Otherwise, competitive advantages might not be simply reflected in physical performance. Rather, the two species may have differential sensory abilities with, for example, one species being more able to find prey in turbid water than another. Although the use of vision has been considered important in prey location (Katzir & Howland 2003), recent experimental work shows that the Great Cormorant *Phalacrocorax carbo*, at least, has poor visual capacities while underwater (White *et al.* 2007), so other sensory systems may be used (Dehnhardt *et al.* 1998).

If we assume that some (albeit ill-defined) differential foraging abilities have led to the space-dependent niche separation, then we must also assume that there is virtually no interaction between prey types between the two geographically distinct areas in which these birds forage, because inter-area flux by the prey would theoretically tend to negate any advantages accrued by either bird species. Despite the critical nature of prey flux between

feeding sites in modulating competition, this issue was not considered in MacArthur's (1958) study and, to our knowledge, has not been examined since. The matter is perhaps less relevant for our study though because most prey on which these two cormorants feed are slow-moving, bottom-dwelling species (Frere *et al.* 2005, Millones *et al.* 2005), tending to have a restricted range. Theoretically though, and in a general sense, the distance between foraging sites, the speed of movement of prey and its likely tendency to move into prey-depleted areas presumably determine the extent to which differential area use by competitors is a strategy that benefits both parties. Although we are unable to ascribe prey densities to the areas used by the cormorants for foraging, and do not have any data on prey movements, we suggest for future studies that more careful consideration of these elements might shed light on mechanisms that lead to interspecific segregation.

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REFERENCES

- Ainley, D.G., Ribic, C.A., Ballard, G., Heath, S., Gaffney, I., Karl, B.J., Barton, K.J., Wilson, R. & Webb, S. 2004. Geographic structure of Adélie Penguin populations: overlap in colony-specific foraging areas. *Ecol. Monogr.* **74**: 159–178.
- Connell, J.H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat.* **122**: 661–696.
- Cooper, J. 1986. Diving patterns of cormorants Phalacrocoracidae. *Ibis* **114**: 360–366.
- Crawley, M.J. 2007. *The R Book*. West Sussex, England: John Wiley and Sons Ltd.
- Croxall, J.P. & Prince, P.A. 1980. Food, feeding ecology and ecological segregation of seabirds at South Georgia. *Biol. J. Linn. Soc.* **15**: 103–131.
- Dehnhardt, G., Mauck, B. & Bleckmann, H. 1998. Seal whiskers detect water movements. *Nature* **394**: 235–236.
- Dewar, J.M. 1924. *The Bird as a Diver*. London: H.F. Witherby.
- Diamond, A.W. 1983. Feeding overlap in some tropical and temperate seabird communities. *Stud. Avian Biol.* **8**: 24–46.
- Frere, E. & Gandini, P. 2001. Aspects of the breeding biology of the Red-legged Cormorant *Phalacrocorax gaimardi* on the Atlantic coast of South America. *Mar. Ornithol.* **29**: 67–70.

- Frere, E., Gandini, P. & Quintana, F. 2002. Diving behavior of the Red-legged Cormorant in Southeastern Patagonia, Argentina. *Condor* **104**: 440–444.
- Frere, E., Quintana, F. & Gandini, P. 2005. Cormoranes de la costa patagónica: estado poblacional, ecología y conservación. *Hornero* **20**: 35–52.
- Gandini, P., Frere, E. & Quintana, F. 2005. Feeding performance and foraging area of the Red-legged Cormorant. *Waterbirds* **28**: 41–45.
- Gause, G.F. 1934. *The Struggle for Existence*. Baltimore: Williams and Wilkins.
- González-Solís, J., Croxall, J.P. & Wood, A.G. 2000. Foraging partitioning between giant petrels *Macronectes* spp. and its relationship with breeding population changes at Bird Island, South Georgia. *Mar. Ecol. Prog.* **204**: 279–288.
- Harrison, P. 1985. *Seabirds: an Identification Guide*. Boston: Houghton Mifflin.
- Herrera, G. 1997. *Dieta reproductiva de la gaviota de Olrog Larus atlanticus en la provincia del Chubut*. Sede Trelew, Facultad de Ciencias Naturales: Universidad Nacional de la Patagonia 'San Juan Bosco'.
- Hodgson, J.R., He, X., Schindler, D.E. & Kitchell, J.F. 1997. Diet overlap in a piscivore community. *Ecol. Freshw. Fish.* **6**: 144–149.
- Hutchinson, G.E. 1958. Concluding remarks. *Cold Spring Harbor Symp. Quant. Biol.* **22**: 415–427.
- Hutchinson, G.E. 1959. Homage to Santa Rosalia, or why are there so many different kinds of animals? *Am. Nat.* **93**: 145–159.
- Hutchinson, G.E. 1978. *An Introduction to Population Ecology*. New Haven: Yale University Press.
- Jaramillo, A. 2005. *The Birds of Chile*. Princeton: Princeton University Press.
- Katzir, G. & Howland, H.C. 2003. Corneal power and underwater accommodation in great cormorants *Phalacrocorax carbo*. *J. Exp. Biol.* **206**: 833–841.
- Kühnemann, O. 1969. Vegetación marina de la Ría de Puerto Deseado. *Opera Lill.* **17**: 1–23.
- MacArthur, J.W. & Levins, R. 1967. The limiting similarity, convergence and divergence of co-existing species. *Am. Nat.* **101**: 377–385.
- MacArthur, R.H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* **39**: 599–619.
- McDonald, R.A. 2002. Resource partitioning among British and Irish mustelids. *J. Anim. Ecol.* **71**: 185–200.
- Millones, A., Frere, E. & Gandini, P. 2005. Dieta del cormorán gris (*Phalacrocorax gaimardi*) en la Ría Deseado, Santa Cruz, Argentina. *Ornitol. Neotrop.* **16**: 519–527.
- Naef-Daenzer, B. 1993. *GRID. Calculations for Home Range and Spatial Analysis*. Sempach: Swiss Ornithological Institute.
- Pinheiro, J.C. & Bates, D.M. 2000. *Mixed-Effects Models in S and S-Plus*. Berlin: Springer.
- Punta, G., Yorio, P., Saravia, J.R. & Garcia Borboroglu, P. 2003. Breeding habitat requirements of the Imperial Cormorant and Rock Shag in Central Patagonia, Argentina. *Waterbirds* **26**: 176–183.
- Quintana, F. 1999. Diving behavior of Rock Shags at a patagonian colony of Argentina. *Waterbirds* **22**: 466–471.
- Quintana, F. 2001. Foraging behaviour and feeding locations of Rock Shags *Phalacrocorax magellanicus* from a colony in Patagonia, Argentina. *Ibis* **143**: 547–553.
- R Development Core Team. 2007. *R: a Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Sapoznikow, A. & Quintana, F. 2003. Foraging behavior and feeding locations of Imperial Cormorants and Rock Shags breeding sympatrically in Patagonia, Argentina. *Waterbirds* **26**: 184–191.
- Schoener, T.W. 1983. Field experiments on interspecific competition. *Am. Nat.* **122**: 240–285.
- Schreiber, R.W. & Clapp, R.B. 1987. Pelecaniform feeding ecology. In Croxall, J.P. (ed.) *Seabird Feeding Ecology and Role in Marine Ecosystems*: 173–188. Cambridge, UK: Cambridge University Press.
- Wanless, S. & Harris, M.P. 1991. Diving patterns of full-grown and juvenile Rock Shags. *Condor* **93**: 44–48.
- Wanless, S. & Harris, M.P. 1993. Use of mutually exclusive foraging areas by adjacent colonies of Imperial Shags (*Phalacrocorax atriceps*) at South Georgia. *Col. Waterbirds* **16**: 176–182.
- Wanless, S., Harris, M.P. & Morris, J.A. 1991. Foraging range and feeding locations of Shags *Phalacrocorax aristotelis* during chick rearing. *Ibis* **133**: 30–36.
- Wanless, S., Grémillet, D. & Harris, M.P. 1998. Foraging activity and performance of Shags *Phalacrocorax aristotelis* in relation to environmental characteristics. *J. Avian Biol.* **29**: 49–54.
- Weimerskirch, H., Bartle, J.A., Jouventin, P. & Stahl, J.C. 1986. Comparative ecology of six albatross species breeding on the Crozet Islands. *Ibis* **128**: 195–213.
- Weimerskirch, H., Bartle, J.A., Jouventin, P. & Stahl, J.C. 1988. Foraging ranges and partitioning of feeding zones in three species of southern albatrosses. *Condor* **90**: 214–219.
- White, C.R., Day, N., Butler, P.J. & Martin, G.R. 2007. Vision and foraging in Cormorants: more like Herons than Hawks? *PLoS ONE* **2**: e639. doi:10.1371/journal.pone.0000639.
- Wood, A.G., Naef-Daenzer, B., Prince, P.A. & Croxall, J.P. 2000. Quantifying habitat use in satellite-tracked pelagic seabirds: application of kernel estimation to albatross locations. *J. Avian Biol.* **31**: 278–286.
- Yorio, P., Frere, E., Gandini, P. & Harris, G. 1998. *Atlas de la Distribución Reproductiva y Abundancia de Aves Marinas del Litoral Patagónico Argentino*. Buenos Aires: Instituto Salesiano.
- Yorio, P., Frere, E., Gandini, P. & Conway, W. 1999. Status and conservation of seabirds breeding in Argentina. *Bird Conserv. Int.* **9**: 299–314.

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