Foraging Behavior and Feeding Locations of Imperial Cormorants and Rock Shags Breeding Sympatrically in Patagonia, Argentina

ALEXANDRA SAPOZNIKOW[1] AND FLAVIO QUINTANA[1,2]

[1]Centro Nacional Patagónico—Conicet, Bvd. Brown s/n, (9120) Puerto Madryn, Chubut, Argentina
Internet: alexa@cenpat.edu.ar

[2]Wildlife Conservation Society, 2300 Southern Boulevard, Bronx, New York, NY 10460, USA

Abstract.—Although there have been several studies of the foraging behavior of the Imperial Cormorant (*Phalacrocorax atriceps*) and the Rock Shag (*Phalacrocorax magellanicus*), none document the feeding performance and the use of feeding areas by these birds breeding in mixed or adjacent colonies. We studied birds nesting sympatrically in two colonies at Malaspina Inlet, Patagonia, Argentina. Both colonies were located on islands separated by 2.2 km: Vernacci Oeste, inside Malaspina Inlet and Vernacci Este at the mouth of the inlet. Rock Shags from both islands and Imperial Cormorants from Vernacci Oeste fed inside the inlet, and showed similar dive duration, surface interval and foraging range. Imperial Cormorants from Vernacci Este foraged outside the inlet and showed longer dive duration, surface interval and foraging range. Imperial Cormorants made longer foraging trips than Rock Shags (4.9 ± 1.9 vs. 1.9 ± 0.7 h) regardless of its colony. There was no overlap between the foraging areas used by Imperial Cormorants from the two colonies. Despite Rock Shags from both islands feeding inside the inlet, there was a little overlap in their foraging locations (3-22%). Rock Shags and Imperial Cormorants breeding in the same colony showed an overlap in their foraging areas, being lower at Vernacci Este than at Vernacci Oeste. Although both species are usually described as having different diving capacities, we found that their diving behavior was similar when feeding in areas of similar environmental conditions. *Received 8 September 2002, accepted 20 December 2002.*

Key words.—Feeding behavior, Imperial Cormorant, Patagonia, *Phalacrocorax magellanicus*, *Phalacrocorax atriceps*, Rock Shag, segregation.

The Rock Shag (*Phalacrocorax magellanicus*) and the Imperial Cormorant (*P. atriceps*) are two species widely distributed in southern South America. Their breeding ranges overlap along the Patagonian coast (Harrison 1985; Narosky and Izurieta 1993) and the species often breed together in mixed colonies (Yorio *et al.* 1998). They are foot-propelled pursuit-divers that feed mainly inshore on benthic or demersal fish and invertebrates (Wanless *et al.* 1992; Punta *et al.* 1993; Malacalza *et al.* 1997). Like other avian divers, their feeding performance is likely to be influenced by a variety of environmental factors such as water depth, bottom substratum and prey density and size (Dewar 1924; Ydenberg and Forbes 1988; Croxall *et al.* 1991; Carbone and Houston 1994; Monaghan *et al.* 1994).

Diving behavior is controlled mainly by physiological constraints within a group: large species, with a potentially larger capacity for oxygen storage, should be able to stay submerged longer than smaller ones (Butler and Jones 1982; Butler and Stephenson 1987; Kooyman 1989). While the Rock Shag is a smaller bird (mean weight 1.5 kg; F. Quintana unpubl. data) with a range in mean dive duration of 28 s to 47 s (Wanless and Harris 1991; Quintana 1999), the Imperial Cormorant weighs on average 2.3 kg (F. Quintana unpubl. data) and its mean dive duration ranges from 40 s to 191 s (Cooper 1986; Wanless *et al.* 1992; Kato *et al.* 1996).

Sympatric seabird species with similar ecological requirements often show segregation in some niche dimension (Croxall and Prince 1980; Diamond 1983; Weimerskirch *et al.* 1986). Resource partitioning is one mechanism by which closely related species can coexist (Lack 1971). Although there have been several studies of the foraging behavior of the Imperial Cormorant (Croxall *et al.* 1991; Kato *et al.* 1992) and the Rock Shag (Wanless and Harris 1991; Quintana 1999, 2001), none document the feeding performance and the use of feeding areas by these species breeding in mixed or adjacent colonies. Examination of the segregation of the spatial component of trophic niches by

means of radio telemetry allowed us to analyze the habitat partitioning in the two sympatric cormorants. Here we present data on feeding areas, duration of foraging trips, and diving behavior of two cormorant species.

METHODS

Fieldwork was conducted at Caleta Malaspina (45°11'S, 66°30'W), Bustamante Bay, Chubut, Argentina (Fig. 1). This is an inlet of 34 km², with a maximum width of 4 km and a length of 10 km (Herrera 1997). At its mouth there is a group of islands of different size, soil and vegetation, where nine (56%) of the 16 breeding seabirds species of the Argentine Patagonian coast breed (Yorio *et al.* 1998). During the 1998 and 1999 breeding seasons, we studied the foraging patterns and feeding areas of the Imperial Cormorant and the Rock Shag breeding in two mixed colonies on two of these islands: Vernacci Este (VE) is at the mouth of the inlet and Vernacci Oeste (VO) inside the inlet, which are separated by 2.2 km. Yorio *et al.* (1998) reported 375 and 188 pairs of Imperial Cormorants and Rock Shags breeding at VE; while there were 298 and 234 nests of Imperial Cormorants and Rock Shags, respectively, at VO.

Deployment of Instruments

VHF radio transmitters (Standard model, Advanced Telemetry Systems, Betel, Minnesota) were deployed on 25 adult Rock Shags and nine adults Imperial Cormorants during the last week of incubation or the first ten days of the chick-rearing period. Average mass of the in-struments was 23.6 g (SD ± 1.5, N = 11), around 1.6% and 0.9% of adult body mass for Rock Shags and Imperial Cormorants, respectively. Devices were attached to a few tail feathers, using waterproof tape (Wanless *et al.* 1998). The procedure was completed in less than five minutes and birds quickly released. All birds carrying devices continued breeding normally during the study period.

Diving and Feeding Patterns

Radio signals were monitored from three tracking stations separated by 1.8-6.3 km. Each was between 10-100 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. The pulse rate of the signal was 65 pulses min^{-1}. Dives were identified as breaks in signal transmission and thus the durations of each dive and inter-dive recovery time within a trip could be determined (Wanless *et al.* 1991, 1992).

Colony attendance was recorded automatically every 10 min by a data logger (DCCII model, ATS, Inc.) connected to a scanning receiver (R2000 model, ATS, Inc.). This equipment was located 2-5 m from the nests of the studied birds. Trip duration was calculated as the time between the departure from and arrival back to the nest.

Feeding Locations

A feeding location was defined as the place where a bird dived repeatedly. Compass bearings were recorded for diving locations of each radio-tagged individual.
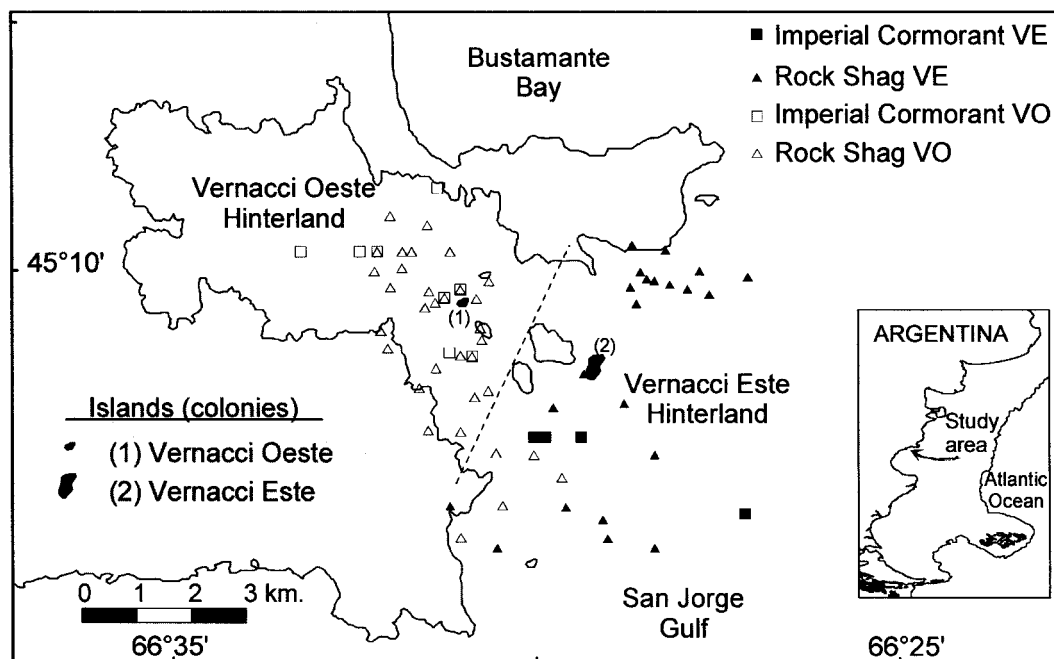

Figure 1. Foraging locations of Imperial Cormorants and Rock Shags breeding at Vernacci Este (VE) and Vernacci Oeste (VO) islands. The dotted line is equidistant between both colonies and represents the limit of the two hinterlands.

These locations were defined by cartesian coordinates calculated by triangulation from at least two fixed antenna stations (see details in Quintana 2001). Foraging range was calculated as the distance from the colony to the location fix.

In accordance with the definitions used in Cairns' (1989) Hinterland Model, we divided the inlet in two areas by a line equidistant to both colonies (Fig. 1). We used Kernel analysis to characterize the spatial distribution of feeding locations following Naef-Daenzer (1993). For each colony, the overlap between species was calculated as the percentage of the foraging area of Rock Shags, which overlapped with that of Imperial Cormorants, and the percentage of the foraging area of Imperial Cormorants, which overlapped with that of Rock Shags (Naef-Daenzer 1993; Wood *et al.* 2000).

Data Analysis

Differences between individuals in foraging parameters (e.g., dive and recovery time, trip duration) were examined by using Kruskal-Wallis one-way ANOVA test. If the result was not significant, data from all individuals were pooled. Otherwise, a mean value was determined for each bird and means were then pooled to calculate overall mean values (±SD). Hurlbert (1984) showed that using non-independent observations is valid if the replicates are pooled to estimate a mean value.

RESULTS

During a foraging trip, a bird flew directly to the feeding area, where it made a single uninterrupted series of dives before returning directly to the colony. Imperial Cormorants from VE usually fed further out to sea and out of range of the receiving equipment, but we were sure that they were not feeding in the inlet.

Trip Duration

Trip durations of Imperial Cormorants from both islands were similar (mean: 5.7 h ± 2.5 h [SD], N = 4 birds and 4.4 h ± 1.1 h, N = 5 birds for VO and VE respectively, Mann Whitney U-test Z = 0.73; ns). Foraging trips of Rock Shags from VO and VE were also of similar duration (mean = 2.2 h ± 0.7 h, N = 12 birds, and 1.7 h ± 0.5 h, N = 8 birds, respectively; Mann Whitney U-test Z = -1.25; ns). On average, Imperial Cormorants conducted longer foraging trips than did Rock Shags (mean = 4.9 ± 1.9 vs. 1.9 ± 0.7 h, N = 9 Imperial Cormorants, N = 20 Rock Shags) (Mann-Whitney U-test Z = 4.24, P < 0.05).

In general, trip duration was not a good indicator of distance traveled to the foraging areas. Rock Shags at both colonies showed a significant, but weak, relationship between trip duration and foraging distance (Spearman correlation: VO: r_S = 0.4, N = 34; VE: r_S = 0.6, N = 21 trips, P < 0.05). Imperial Cormorants from VO showed no significant relationship (Spearman correlation r_S = -0.5, N = 8, n.s.). Insufficient data (N = 4) were collected on Imperial Cormorants at VE to allow a meaningful statistical analysis.

Diving Duration

Mean dive durations of individual Rock Shags were similar between colonies (Mann-Whitney U-test, Z = 1.2, n.s.) (means = 42 ± 12 s, N = 12 birds, 1,003 dives and 50 ± 10 s, N = 9 birds, 1,441 dives for VO and VE respectively). The mean dive duration of Imperial Cormorants from VO was 47 ± 4 s (N = 2 birds, 544 dives). Mean dive duration of Imperial Cormorants and Rock Shags from VO did not show a significant difference (Mann-Whitney U-test Z = 0.11, n.s.). The only Imperial Cormorant from VE that was tracked showed longer diving periods than individuals at VO (mean = 76 ± 3 s, N = 237 dives).

Mean recovery time showed the same pattern. Rock Shags from VO and VE spent 14 ± 7 s and 18 ± 6 s on surface between successive dives (N = 12 birds and 9 birds, respectively). Differences between colonies were not significant (Mann Whitney U-test Z = 1.2, ns). Mean recovery time of Imperial Cormorants from VO was 11 ± 3 s (N = 2 birds, 555 dives) and showed no significant difference from that of Rock Shags from the same island (Mann-Whitney U-test Z = 0.65, ns). The only Imperial Cormorant breeding at VE that was tracked had longer recovery periods than those observed at VO (mean = 38 ± 17 s, N = 232 dives).

Feeding Areas

To quantify the consistence in the use of a particular area, we assigned foraging locations of each bird to 0.5 × 0.5 km grid squares. Birds where highly consistent in the use of one specific area: eight (67%) of the twelve birds with at least four feeding loca-

tions had more than 70% of their feeding locations in only two of the squares.

Foraging Range

Foraging range of Rock Shags from both islands and Imperial Cormorants from VO was extremely restricted. Rock Shags breeding in VO fed closer to the colony than their conspecifics from VE (mean ± SD: 2.0 ± 1.8 *vs.* 2.5 ± 1.2 km, N = 56 and 30 feeding locations for VO and VE, respectively) (Mann-Whitney U-test $Z = 2.8$, P < 0.05). Imperial Cormorants from VO had similar foraging ranges to those of Rock Shags nesting on the same island (1.5 ± 0.9 km, N = 9, Mann-Whitney U-test $Z = 0.93$, n.s.) and fed closer to their colony than Rock Shags from VE (Mann-Whitney U-test $Z = 2.53$, P < 0.05).

Comparable data for Imperial Cormorants breeding at VE were not available. Only four feeding locations were tracked (mean ± SD: 2.1 ± 1.2) and the remaining six were out of the range of the receiving equipment (>8 km), suggesting an average distance of 5.6 km.

Hinterland Overlap by Species

Although the colonies were only 2.2 km apart, there was no overlap in the foraging areas used by Imperial Cormorants from each island. All Imperial Cormorants from VO fed in their own hinterland, while all from VE foraged in the VE hinterland (only 40% of these locations could be determined, the rest was out of the range of the receiving equipment, but could not be in the hinterland of VO) (Fig. 1). Rock Shags from both colonies fed inside the inlet, but there was minimal overlap in their foraging locations. Only 3% of the foraging locations of Rock Shags breeding in VE were included in the VO hinterland, while 22% of the foraging locations of Rock Shags from VO were located in VE hinterland (Fig. 1).

Interspecific Overlap by Island

Rock Shags and Imperial Cormorants breeding on the same island showed an overlap in their foraging areas. In both islands, the zone of overlap represented a higher proportion of the feeding area of Imperial Cormorants than of Rock Shags. At VO, the overlap of Imperial Cormorants with Rock Shags was 64% while that for Rock Shags with Imperial Cormorants was 17% (Fig. 2). Birds breeding at VE showed a lower spatial overlap. In addition, the spatial overlap of feeding areas around this island was overestimated, since 60% of Imperial Cormorant feeding locations was not included in the Kernel analysis because they were out of the range of the receiving equipment. While Rock Shags fed mainly in the northeast of the inlet, Imperial Cormorants fed in the southern east area and out of the inlet. The overlap of Imperial Cormorants with Rock Shags breeding in VE was 31% while that for Rock Shags with Imperial Cormorants was 7% (Fig. 2).

DISCUSSION

The spatial distribution of the colonies at Caleta Malaspina constituted an adequate model that enabled us to analyze the spatial segregation when feeding at sea of two sympatric cormorants. A few studies have shown that birds from neighboring colonies feed in zones bounded by lines equidistant between the colonies (Berruti 1987; Weimerskirch *et al.* 1988; Wanless and Harris 1993). Our results showed breeding cormorants from adjacent colonies fed mostly in mutually exclusive foraging areas. However, some overlap did occur between feeding areas of Rock Shags from VO and VE. This small overlap could be partially explained in areas where an extra food supply existed (i.e., discard from fisheries; Weimerskirch *et al.* 1988), and/or where the food source is abundant or patchily distributed (Cairns 1989). No extra food supplies exist for cormorants at Caleta Malaspina. However, the heterogeneity of the substratum (Herrera 1997) suggests the existence of areas with high concentration of prey supporting some spatial overlap during the breeding season. In addition, the north of San Jorge Gulf is one of the most productive areas along the coast (Fundación Patagonia Natural 1996), and originates from tidal fronts north of San Jorge gulf (Glorioso
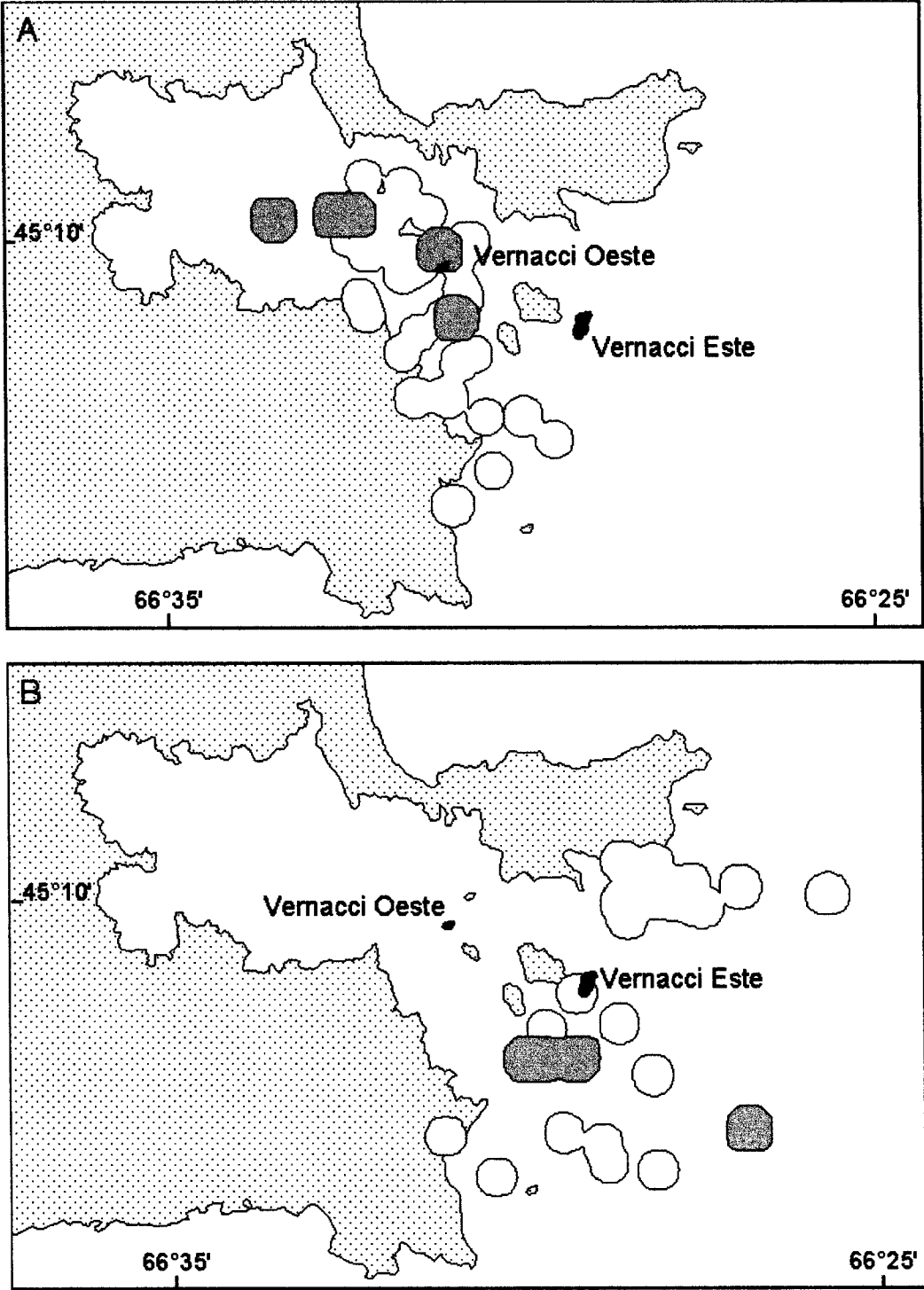
Figure 2. Activity ranges derived from kernel analyses on the validated locations given in Figure 1 for Imperial Cormorants (filled circles) and Rock Shags (open circles). A—breeding at Vernacci Oeste (VO) and B—Vernacci Este (VE) islands.

1987; Carreto *et al.* 1986). Satellite images show that near-surface phytoplankton biomass remains high throughout the summer (when this study was carried out) along tidal front areas (Podestá 1990). These particular conditions could be responsible for abundant and well distributed food resources at Caleta Malaspina and be one of the reasons explaining not only the spatial overlap of this two species, but also the coexistence of nine breeding seabirds species in the area.

Some observational studies (Johnstone 1974; Weimerskirch *et al.* 1988; Balance *et al.* 1997) on seabird distribution at sea suggest that spatial partitioning while foraging may be a common mechanism to avoid ecological overlap in seabirds. In this study, the spatial segregation between species breeding in the same island was not evident. At the two studied colonies we found a partial overlap between the foraging areas of the two species. However, our results showed that the overlap in the spatial component was greater at VO than at VE (17-64% vs. 7-31%). In this area, the potential foraging range of birds breeding at VO seems to be restricted both by geographical (coasts of the inlet) and ecological (VE hinterland) constraints. Birds nesting at VE, in the mouth of the inlet, could avoid the spatial overlap due to the existence of a much broader potential foraging ground in open waters outside the inlet. In contrast, cormorants nesting at VO are confined by land and by individuals from VE feeding in the area.

Several authors (Colwell and Futuyma 1971; Abrams 1980; Glasser and Price 1988) have cautioned that interspecific competition is not proportional to overlap in resource use; niche overlap is neither a necessary nor a sufficient condition for interference competition, and it is only a necessary but not a sufficient condition for exploitation competition (Pianka 1976). Studies of closely related sympatric seabirds indicate the existence of adaptations that can act in the segregation of other niche dimensions. These adaptations usually involve some combination of timing of breeding, diet and differential use of foraging areas (Ashmole and Ashmole 1967; Croxall and Prince 1980). During the study period, the Imperial

Cormorant and Rock Shag differed by 7-15 days in their timing of breeding and their feeding performance showed similar foraging periods during daylight hours (F. Quintana, unpublished data). Previous studies in the area reveal a high number of prey items in common (Punta *et al.* 1993), but the proportion of pelagic prey seems to be greater in the diet of the Imperial Cormorant than in the Rock Shag (G. Punta, pers. comm.).

Rock Shags and Imperial Cormorants have been previously reported as foragers with different diving capacity (Croxall *et al.* 1991; Wanless and Harris 1991, 1993; Quintana 1999). According to Cooper (1986), dive duration is positively related with body mass, so we would expect the heavier Imperial Cormorants to dive longer than Rock Shags. This did not occur when birds of both species fed in the same hinterland or in areas of similar environmental conditions (i.e., birds from VO island). Although feeding behavior is restricted by physiological limits, environmental factors may influence feeding performance, changing the pattern described for the species and relaxing interspecific differences. The difference between dive duration and recovery time between Imperial Cormorants breeding at VO and the predicted by Cooper's regression (body size) could be a consequence of the feeding conditions within the hinterland (i.e., depth, diet, etc.). Water depth, bottom substratum, prey density and size, and therefore energy payoff, are important components determining or limiting diving pattern (Dewar 1924; Ydenberg and Forbes 1988; Carbone and Houston 1994; Monaghan *et al.* 1994a). The similar diving pattern (dive duration and recovery time) found for Rock Shags and Imperial Cormorants from VO could be explained by assuming that, at the same hinterland, both species are bottom-feeders exploiting similar depths. Preliminary studies of maximum dive depths indicate that this assumption is true for both species feeding at the VO hinterland. Imperial Cormorants from VE feeding at open waters dived to greater depths (F. Quintana, unpubl. data). A positive relationship between dive time and water depth has been

documented in other cormorants (Dewar 1924; Wilson and Wilson 1988; Wanless and Harris 1991; Hustler 1992).

Although both species from VO island foraged at the same distance from their breeding colonies and used a low proportion of the total time at sea to reach and return from the foraging sites, the foraging trips of the Imperial Cormorant were longer than trips of the Rock Shag (and similar to their conspecifics at VE). As the Imperial Cormorant is larger than the Rock Shag, and both species feed on similar prey, mainly small fishes such as rock cod (*Notothenia* sp.), crustaceans and polychaetes (Punta *et al.* 1993), they would need more food to meet their daily energetic requirements. Longer foraging trips associated with poor food conditions (in terms of abundance or energy) have been reported in other seabirds and marine mammals (Costa *et al.* 1989; Feldkamp *et al.* 1989).

Our results suggest that foraging performance might be modified by the environmental condition of the feeding area. Although diving is restricted by physiological limits (Butler and Jones 1982), foraging parameters are not fixed for each species. Further studies of diet and diving depth of these birds will clarify to what extent they use different strategies in the presence of conspecifics and sympatric species breeding at the same and/or adjacent colonies.

LITERATURE CITED

Abrams, P. 1980. Some comments on measuring niche overlap. Ecology 61: 44-49.

Ashmole, N. P. and M. J. Ashmole. 1967. Comparative feeding ecology of seabirds of a tropical oceanic island. Peabody Museum of Natural History. Yale University Bulletin 24.

Balance, L. T., R. L. Pitman and S. B. Reilly. 1997. Seabird community structure along a productivity gradient: importance of competition and energetic constraint. Ecology 78: 1502-1518.

Berrutti, A. 1987. The use of Cape Gannets, *Morus capensis* in management of the purseseine fishery of the Western Cape. Unpublished. Ph.D. dissertation, University of Natal, South Africa.

Butler, P. J. and D. R. Jones. 1982. The comparative physiology of diving in vertebrates. Advances in Comparative Physiology and Biochemistry 8: 179-364.

Butler, P. J. and R. Stephenson. 1987. Physiology of breath-hold diving: a bird's eye view. Scientific Progress, Oxford 71: 439-458.

Cairns, D. K. 1989. The regulation of seabird colony size: a hinterland model. American Naturalist 134: 141-146.

Carbone, C. and A. I. Houston. 1994. Patterns in the diving behavior of the pochard *Aythya ferina*: a test of an optimality model. Animal Behavior 48: 457-465.

Carreto, J. I., H. H. R. Benavides, R. M. Negri, and P. D. Glorioso. 1986. Toxic red tide in the Argentine sea. Phytoplankton distribution and survival of the toxic dinoflagellate *Gonyaulax excava* in a frontal area. Journal of Plankton Research 8: 15-28.

Cooper, J. 1986. Diving patterns of cormorants *Phalacrocoracidae*. Ibis 114: 360:366.

Costa, D., J. P. Croxall, and C. D. Duck. 1989. Foraging energetics of Antarctic fur seals in relation to changes in prey availability. Ecology 70: 596-606.

Colwell, R. K. and D. J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology 52: 567-577.

Croxall, J. P. and P. A. Prince. 1980. Food, feeding ecology and ecological segregation of seabirds at South Georgia. Biological Journal of Linnean Society 15: 103-131.

Croxall, J. P., Y. Naito, A. Kato, P. Rotery and D. R. Briggs. 1991. Diving patterns and performance in the Antarctic Blue-eyed Shag, *Phalacrocorax atriceps*. Journal of Zoology, London 225: 177-199.

Dewar, J. M. 1924. The bird as a diver. Whiterby. London.

Diamond, A. D. 1983. Feeding overlap in some tropical and temperate seabird communities. Studies in Avian Biology 8: 24-46.

Feldkamp, S. D., R. L. Delong and G. A. Antonelis. 1989. Diving patterns of California sea lions, *Zalophus californianus*. Canadian Journal of Zoology 67: 872-883.

Fundación Patagonia Natural. 1996. Plan de manejo integrado de la zona costera patagónica: diagnosis y recomendaciones para su elaboración. Fundación Patagonia Natural and Wildlife Conservation Society. Puerto Madryn, Argentina.

Glaser, J. W. and H. J. Price. 1988. Evaluating expectations deduced from explicit hypothesis about mechanisms of competition. Ecology 51: 57-70.

Glorioso, P. D. 1987. Temperature distribution related to shelf-sea fronts on the shelf. Continental Shelf Research 7: 27-34.

Harrison, P. 1985. Seabirds: an identification guide. Houghton Mifflin. Boston.

Herrera, G. O. 1997. Dieta reproductiva de la gaviota de Olrog *Larus atlanticus* en la provincia del Chubut. Unpublished. Undergraduate thesis, Universidad Nacional de la Patagonia San Juan Bosco. Puerto Madryn, Argentina.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54: 187-211.

Hustler, K. 1992. Buoyancy and its constraints on the underwater foraging behavior of Reed Cormorants, *Phalacrocorax africanus* and Darters, *Anhinga melanogaster.* Ibis 134: 229-236.

Johnstone, G. W. 1974. Field characters and behavior at sea of giant petrels in relation to their oceanic distribution. Emu 74: 209-218.

Kato, A., J. P. Croxall, Y. Watanuki and Y. Naito. 1992. Diving patterns and performance in male and female Imperial Cormorants *Phalacrocorax atriceps* at South Georgia. Marine Ornithology 19: 117-129.

Kato, A., Y. Naito, Y. Watanuki and P. Shaughnessy. 1996. Diving pattern and stomach temperatures of foraging King cormorants at Subantarctic Macquarie Island. Condor 98: 844-848.

Kooyman, G. L. 1989. Diverse Divers: Physiology and Behavior. Springer. Berlin.

Lack, D. 1971. Ecological isolation in birds. Oxford University Press. Oxford.

Malacalza, V., N. M. Bertellotti and T. Poretti. 1997. Variación estacional de la dieta de *Phalacrocorax magellanicus* (Aves: Phalacrocoracidae) en Punta Loma (Chubut, Argentina). Neotrópica 43 (109-110): 35-37.

Monaghan, P., P. Walton, S. Wanless, J. D. Uttley and M. D. Burns. 1994. Effects of prey abundance on the foraging behavior, diving efficiency and time allocation of breeding guillemots *Uria aalgae.* Ibis. 136: 214-222.

Naef-Daenzer, B. 1993. GRID. Calculations for home range and spatial analysis—Swiss Ornithological Institute.

Narosky, T. and D. Yzurieta. 1993. Guía para la identificación de las aves de Argentina y Uruguay. Asociación Ornitológica del Plata. Vazquez Mazzini, Buenos Aires.

Podestá, G. P. 1990. Migratory pattern of Argentine hake (*Merluccius hubbsi*) and oceanic processes in the southwestern Atlantic Ocean. Fishery Bulletin. 88: 167-177.

Pianka, E. R. 1976. Competition and niche theory. Pages 114-141 *in* Theoretical ecology (R. M. May, Ed.). Blackwell, Oxford.

Punta, G., J. Saravia and P. Yorio. 1993. The diet and foraging behavior of two Patagonian cormorants. Marine Ornithology. 21: 27-36.

Quintana, F. 1999. Diving behavior of Rock Shags at a Patagonian Colony of Argentina. Waterbirds 22: 466-471.

Quintana, F. 2001. Foraging behavior and feeding locations of Rock Shags, *Phalacrocorax magellanicus*, from a colony in Patagonia, Argentina. Ibis 143: 547-553.

Wanless, S. and M. P. Harris. 1991. Diving patterns of full-grown and juvenile Rock Shags. Condor 93: 44-48.

Wanless, S. and M. P. Harris. 1993. Use of mutually exclusive foraging areas by adjacent colonies of Blue-eyed Shags (*Phalacrocorax atriceps*) at South Georgia. Colonial Waterbirds 16: 176-182.

Wanless, S., M. P. Harris and J. A. Morris. 1991. Foraging range and feeding locations of shags *Phalacrocorax aristotelis* during chick rearing. Ibis 133: 30-36.

Wanless, S., M. P. Harris and J. A. Morris. 1992. Diving behavior and diet of the blue-eyed shag at South Georgia. Polar Biology 12: 713-719.

Wanless, S., D. Grémillet and M. P. Harris. 1998. Foraging activity and performance of Shags *Phalacrocorax aristotelis* in relation to environmental characteristics. Journal of Avian Biology 29: 49-54.

Weimerskirch, H., J. A. Bartle, P. Jouventin and J. C. Stahl. 1986. Comparative ecology of six albatross species breeding on the Crozet Islands. Ibis 128: 195-213.

Weimerskirch, H., J. A. Bartle, P. Jouventin and J. C. Stahl. 1988. Foraging ranges and partitioning of feeding zones in three species of southern albatrosses. Condor 90: 214-219.

Wilson, R. P. and M. P. T. Wilson. 1988. Foraging behavior in four sympatric cormorants. Journal of Animal Ecology 57: 943-955.

Wood, A. G., B. Naef-Daenzer, P. A. Prince and J. P. Croxall. 2000. Quantifying habitat use in satellite-tracked pelagic seabirds: application of kernel estimation to albatross locations. Journal of Avian Biology. 31: 278-286.

Ydenberg, R. C. and L. S. Forbes. 1988. Diving and foraging in the western grebe. Ornis Scandinavica 19: 129-133.

Yorio, P., E. Frere, P. Gandini and G. Harris. 1998. Atlas de la distribución reproductiva y abundancia de aves marinas del litoral patagónico Argentino. Plan de Manejo Integrado de la Zona Costera Patagónica. Fundación Patagonia Natural and Wildlife Conservation Society, Patagonia, Argentina.