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Diving seabirds share foraging space and time within and among species

JUAN F. MASELLO,[1,]† ROGER MUNDRY,[2] MAUD POISBLEAU,[1,4] LAURENT DEMONGIN,[1,4] CHRISTIAN C. VOIGT,[3] MARTIN WIKELSKI,[1] AND PETRA QUILLFELDT[1]

[1]*Max Planck Institute for Ornithology, Vogelwarte Radolfzell, Schlossallee 2, D-78315, Radolfzell, Germany*
[2]*Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, D-04103, Leipzig, Germany*
[3]*Evolutionary Ecology Research Group, Leibniz Institute for Zoo and Wildlife Research, Alfred-Kowalke-Strasse 17, D-10315, Berlin, Germany*

Abstract. Ecological theory predicts that animals with similar foraging strategies should not be able to co-exist without segregating either in space, time or diet. In communities, intra-specific competition is thought to be more intense than the competition among species, because of the lack of niche partitioning between conspecifics. Hence, while different seabird species can overlap in their foraging distribution, intra-specific competition can drive the neighboring populations of the same species to spatial segregation of foraging areas. To investigate ecological segregation within and among species of diving seabirds, we used a multi-species GPS-tracking approach of seabirds of four species on a small island in the Southwest Atlantic. The present study goes beyond previous work by analyzing simultaneous effects of species and colonies. We observed strikingly strong spatial foraging segregation among birds of the same species, breeding in colonies as close as 2 km from each other. Conspecifics from neighboring colonies used foraging places adjacent to their own colony, and there was little or no overlap with birds from the other colony. A zone with increased predator concentration was completely avoided during foraging trips, likely contributing to the spatial segregation. In addition to spatial segregation, we also observed intra-specific differences in other components of foraging behavior, such as time of day, dive depth and diet. These were most likely caused by optimal foraging of individuals in relation to habitat differences on a local scale, leading to a complex pattern of interactions with environmental covariates, in particular foraging daytime, foraging water layer temperature and depth, distance to coast and bathymetric depth of foraging areas. As mechanisms leading to the spatial segregation we propose a combination of optimal foraging and avoidance of predation.

Key words: colonial seabirds; diving seabirds; ecological segregation; foraging ecology; Gentoo Penguin, *Pygoscelis papua*; GPS-temperature-depth loggers; Imperial Shag, *Phalacrocorax (atriceps) albiventer*; Magellanic Penguin, *Spheniscus magellanicus*; optimal foraging; Rockhopper Penguin, *Eudyptes chrysocome*; space segregation; time segregation.

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[4] Present address: Department Biology–Ethology, University of Antwerp, Campus Drie Eiken, Universiteitsplein 1, 2610 Antwerp (Wilrijk), Belgium.

† **E-mail:** masello@orn.mpg.de

INTRODUCTION

The concept of ecological segregation seeks to explain how species or populations differ in their use of limited resources, particularly with regard to three main currencies: space, time, and energy

(see Pianka 1969). The principle of competitive exclusion predicts that similar species cannot co-exist in the long-term, in the absence of ecological differences (e.g., Gause 1934). Under the niche theory, segregation in the n-dimensional niche hyper-volume between sympatric and competing populations or species is essential for their co-existence (e.g., MacArthur 1958, Hutchinson 1959, Holt 2009). In this context, the way in which animals segregate in the use of the environment and its resources may vary in response to both inter- and intra-specific competition (see Wakefield et al. 2009). It has been proposed that intra-specific competition is often more intense because of the lack of niche partitioning between conspecifics (Begon et al. 2006).

Seabirds have evolved a multitude of foraging strategies in order to successfully prey on marine food, such as species-specific preferences of prey or the use of open-ocean versus coastal habitats (e.g., Shealer 2002). During the breeding season, seabirds are central-place foragers, exploiting resources within a given range around their colonies or nests. The foraging range is limited by the oceanographic conditions (e.g., bathymetry, sea-surface temperature, chlorophyll *a* concentration) influencing the distribution of prey, and by the movement capabilities of the species concerned (e.g., Ballance et al. 1997, Spear et al. 2001, Arnould and Kirkwood 2008, Nicol et al. 2008, Shaffer et al. 2009).

Owing to the limitation of suitable breeding places, as well as predation pressure and social constraints, many seabirds gather in large breeding colonies (e.g., Ainley et al. 1995, Gauthier-Clerc et al. 2002). Thus, intra-specific competition for food resources can be strong (Grémillet et al. 2004). If conspecifics use the same food sources, intra-specific competition can drive the neighboring populations to spatial segregation of foraging areas. In this scenario, a model proposed by Cairns (1989) predicts complete spatial segregation between the involved populations. Intra-specific competition can also lead to the evolution of sexual segregation of foraging areas, foraging periods during the day, dive depth, or prey choice (e.g., Croxall et al. 1991, Kato et al. 1996, Cook et al. 2007, Weimerskirch et al. 2009).

Due to space limitations or advantages in predator defense, mixed-species colonies with several simultaneously breeding species as well as adjacent colonies of two different species are widespread among seabirds (e.g., Croxall and Prince 1980, Frere et al. 2008). Yet, inter-specific competition has been found to reduce foraging efficiency in some pursuit-diving species (Henkel 2009). In those seabird communities, inter-specific competition is at least partially avoided by ecological segregation, such as species-specific differences in foraging areas (e.g., Croxall and Prince 1980, Trivelpiece et al. 1987, Weimerskirch et al. 1993, Frere et al. 2008, Wilson 2010), diving depths (e.g., Mori and Boyd 2004, Wilson 2010), diet choice (e.g., Baltz et al. 1979, Ridoux 1994, Kato et al. 1996, Weiss et al. 2009), or diurnal foraging patterns (Wilson 2010). Hutchinson (1959) suggested that species foraging on similar prey could reduce competition and co-exist if they were of different sizes, and thus forage on prey of different sizes, which is supported in some seabird assemblages (e.g., Spear and Ainley 2007).

However, as Wilson (2010) pointed out recently, although the premise of reduced competition by exploiting different niches is well established, practical demonstration in the wild is ambiguous. Due to the potentially large number of axes making up the niche hyper-volume, even small differences in a large number of axes will suggest overall separation of the niches (Wilson 2010). Moreover, exploiting different niches could fail to reduce competition for food if the prey is able to move along niche axes in space (e.g., vertical or horizontal migration), or if species are indirectly competing by exploiting different growth stages of the same prey (Wilson 2010).

In accordance with optimal foraging theory (MacArthur and Pianka 1966, Schoener 1971), nesting parents should optimize their prey delivery rate by minimizing traveling distances between colonies and food patches (cf. Weimerskirch et al. 1997, Shaffer et al. 2009) and by selecting patches where the gain per unit cost is high. In cases where neighboring colonies overlap in potential foraging range, Cairns (1989) predicted that the foraging areas used should reach an equilibrium defined by the need to minimize travel cost between the colony and the feeding area. Cairns (1989) also predicted that seabirds should forage in areas closer to their own colonies (the colony's hinterland) rather

than in other foraging areas closer to the neighboring colonies. If not, they should also nest at the closer colony, hence saving travel time to the feeding site (Cairns 1989). Moreover, unnecessarily extensive movements might increase the risk of predation (Andersson 1978 and references therein), and predator avoidance has been shown to influence the movements of many animals (e.g., Riou and Hamer 2008 and references therein).

We here use a multi-species tracking approach to investigate how sympatric diving seabirds (Rockhopper Penguins *Eudyptes chrysocome*, Magellanic Penguins *Spheniscus magellanicus*, Gentoo Penguins *Pygoscelis papua* and Imperial Shags *Phalacrocorax (atriceps) albiventer*) co-exist in the same marine area at the same time. Specifically, we investigated the following hypotheses: (1) There is intra- and inter-specific segregation in foraging daytime, use of marine areas and dive depths. (2) The birds behave in line with predictions of the optimal foraging theory, i.e., their foraging places are closer to their own colony than to conspecific colonies. (3) There are intra- and inter-specific differences in diet, which can be detected by stable isotope analysis.

Methods

Studied species and sites

The study was carried out at New Island Nature Reserve, Falkland Islands / Islas Malvinas, (51°43′ S, 61°18′ W), where Imperial Shags, Rockhopper, Magellanic and Gentoo penguins breed sympatrically (Fig. 1). These birds occur in large numbers at New I. (each species >5,000 to 13,000 breeding pairs; Strange et al. 2007). To reduce the impact of environmental variability over time, the study was carried out during a period of 24 days (19 December 2008–11 January 2009). All studied birds were attending chicks at the nest during this time. The Falkland/Malvinas Current generates an area of ocean water upwelling just west of New Island. This area of increased productivity (e.g., Agnew 2002, Barlow et al. 2002) attracts many seabird species, 13 of which breed in colonies distributed over New Island (2011 ha, 84 km of coastline; Strange et al. 2007).

Rockhopper Penguins breed in 5 colonies at New I., of which we studied the northernmost (Fig. 1, North End; 51°41.097′ S 61°15.123′ W) and the southernmost (Fig. 1, Settlement Colony; 51°42.903′ S 61°18.597′ W; e.g., Poisbleau et al. 2008) during the brooding period. At that time, only females feed the chicks while the males guard them. In general, Rockhopper Penguins are opportunistic feeders, preying on a mixture of crustaceans, cephalopods and fish (see Raya Rey et al. 2007). At New I., Thompson (1989, 1994) found that crustaceans *Euphausia* sp. (51%) and cephalopods (mainly *Gonatus antarcticus*; 46%) were the main items in the diet, with fish comprising only about 1% of the diet in 1986/87 (Appendix A, Fig. A1). Also at New I., Boersma et al. (2002) found that Rockhopper Penguins foraged both very close (<10 km) and at great (>100 km) distances from the colony.

Magellanic Penguins are widespread as nesting birds in New Island. For this study two groups of nests where selected: one close to a Thin-billed Prion *Pachyptila belcheri* area (Fig. 1, Prion patch; 51°43.739′ S 61°17.889′ W; e.g., Quillfeldt et al. 2008) on the East coast of the island, and one close to the airstrip in the South (Fig. 1, Airstrip; 51°44.844′ S 61°16.829′ W). A previous study at New I. found that Magellanic Penguins foraged at intermediate distances (10–90 km) from their burrows (Boersma et al. 2002). The diet of Magellanic Penguins is highly variable among sites and years, but relies mainly on fish and squid (Pütz et al. 2002). Thompson (1989, 1994), through the use of stomach flushing, found that the diet of Magellanic Penguins at New I. in 1986/87 contained both benthic and pelagic fish (main items: *Patagonotothen* sp., Nototheniidae, *Micromesistius* sp., and *Agonopsis* sp.; 40%), followed by cephalopods (mainly the squid *Gonatus antarcticus*; 31%) and crustaceans (lobster krill, 29%; Appendix A, Fig. A1).

Gentoo Penguins breed in two areas on New I.: one at the North End (Fig. 1; 51°41.402′ S 61°15.003′ W), and one at the South End (Fig. 1; 51°44.677′ S 61°17.683′ W). Gentoo Penguins have been found to be neritic foragers during the breeding season and among the main avian benthic consumers of the sub-Antarctic area, their diet varying greatly between locations (see Lescroël and Bost 2005 and references therein). Miller et al. (2009) found that the prey of Gentoo Penguins comprised mainly benthic prey but regularly included pelagic prey. Thompson's

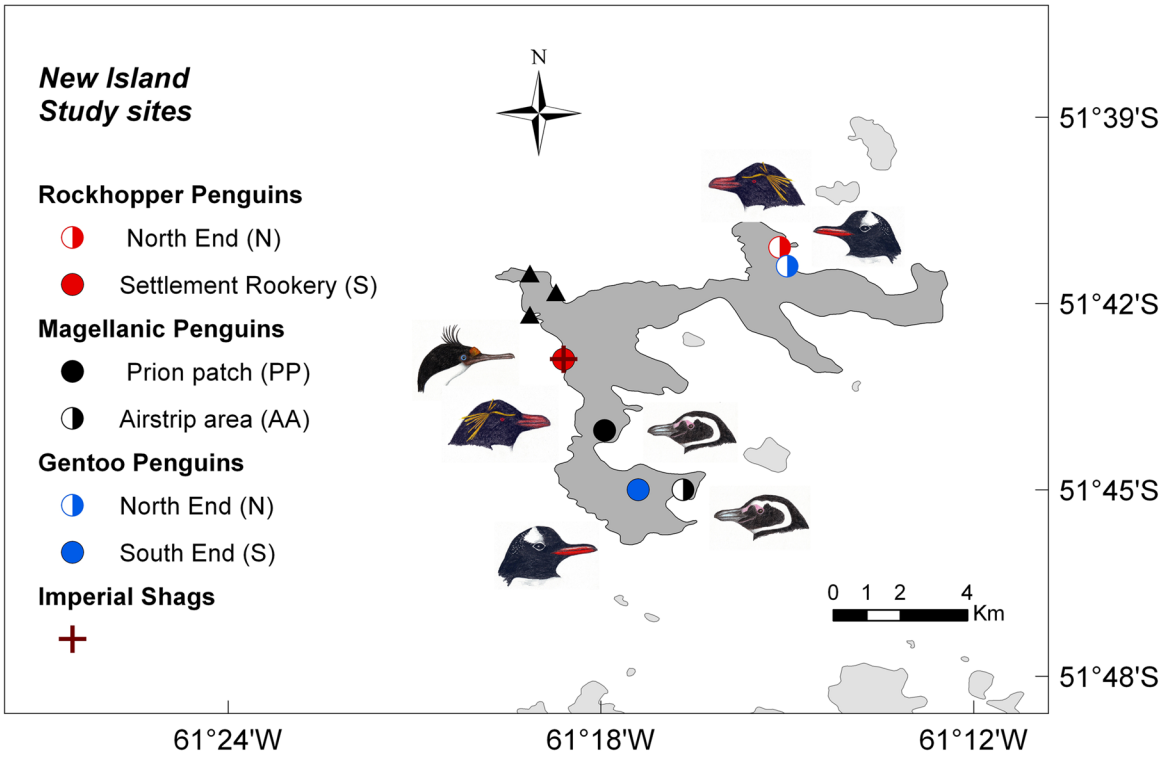

Fig. 1. Location of the seabird colonies studied at New Island Nature Reserve (in dark gray), Falkland Islands / Islas Malvinas, Southwestern Atlantic (51°43′ S, 61°18′ W). The fur seal colonies of New I. are indicated with black triangles. See bathymetric map in Appendix A, Fig. A2.

(1989, 1994) results on Gentoo Penguins at New I. were in line with these findings, as the diet comprised mainly lobster krill (*Munida gregaria*; 56%), followed by both benthic and pelagic fish (main items: *Micromesistius* sp., Nototheniidae and Perciformes; 34%) and squid (mainly *Gonatus antarcticus*; 9%) in 1986/87 (Appendix A, Fig. A1). For the North End colony at New I., Clausen et al. (2005) found that Gentoo Penguins foraged mainly on pelagic prey (*Sprattus fuegensis*). At New I., Boersma et al. (2002) found that Gentoo Penguins foraged very close (<10 km) to the breeding colony at the South End.

Imperial Shags breed on New I. at three sites, but the majority is found at the Settlement Colony (Fig. 1), the place we selected for accessibility reasons. In Patagonia, Imperial Shags have been found to feed close to the coast (<10 km, Sapoznikow and Quintana 2003), on a variety of benthic prey, fish being the most frequent item found, followed by crustaceans and cephalopods (e.g., Punta et al. 2003). Quintana et al. (2007) found that Patagonian Imperial Shags performed 1–2 foraging trips per day. Thompson (1989, 1994) found that the diet of Imperial Shags at New I. in 1986/87 contained mostly benthic fish (main items: *Patagonotothen* sp., *Notothenia* sp., *Harpagifer* sp., and *Agonopsis* sp.; 89%), with some crustaceans (lobster krill; 10%) and squid (1%; Appendix A, Fig. A1).

Instrumentation and fieldwork procedures

Gentoo and Rockhopper penguins as well as Imperial Shags were caught by hand, in the vicinity of their nests while guarding chicks. For Gentoo Penguins, the occasional help of a hook attached to a rod was needed. Magellanic Penguins were caught in their burrows by using a hook attached to a rod (Pütz et al. 2002) while attending their chicks. Extreme care was taken to minimize stress to the captured adults and to protect chicks from potential predators. Handling time was kept to a minimum, mostly below 15 minutes and always below 20 minutes. The

head was covered during handling in order to minimize adult stress. During this procedure the birds remained relatively calm and no strong signs of stress were detected. GPS-temperature-depth (GPS-TD, Earth & Ocean Technologies, Kiel, Germany) loggers were deployed on 26 Rockhopper, 18 Magellanic and 16 Gentoo penguins, and 19 Imperial Shags, using the methods described by Wilson et al. (1997). These loggers provide detailed position (longitude, latitude), dive depth, temperature and time of day. The GPS-TD loggers used for Gentoo Penguins weighed 145 g and measured 138 × 41 × 28.5 mm, representing 2.2% of the adult body mass (mean 6459 ± 172 g, range 5300 to 7890 g). The loggers used for Magellanic Penguins weighed 105 g and measured 117 × 39 × 26.5 mm and represented 2.6% of the adult body mass (mean 4057 ± 122 g, range 3230 to 4880 g). For Rockhopper Penguins and Imperial Shags, the loggers weighed 75 g and measured 96 × 39 × 26.5 mm, representing 2.9% and 3% of the respective adult body masses (Rockhoppers, mean 2565 ± 44 g, range 2220 to 2970 g; shags, mean 2522 ± 89 g, range 1990 to 3350 g). We took blood samples for molecular sexing and isotope analyses. Later on in the lab (Max Planck Institute for Ornithology, Seewiesen), all birds were molecularly sexed following standard methods (Griffiths et al. 1998). In Rockhopper Penguins, only females forage during the guard period, and the molecular sexing results confirmed that all Rockhopper Penguins deployed with loggers were females. Of the other species, only Imperial Shags are known to exhibit strong sexual dimorphism and differences in foraging ecology among the sexes (reviewed in Cook et al. 2007). Therefore, we analyzed the data for this species separately for the sexes. Gentoo and Magellanic Penguin data were checked for sexual differences graphically, but no differences were detected. Therefore, we here pooled the data of males and females. Blood sampling had no detectable adverse effects. The birds were released some 30 meters from their nests. All birds returned to their nests and attended their nestlings shortly after being released except in one case (Imperial Shag). Out of 79 GPS-TD deployments, only one case of nest desertion occurred among studied individuals (an Imperial Shag). GPS-TD-loggers have been successfully used, without negatively affecting the foraging behavior or the breeding success of the birds, in a series of recent studies (e.g., Grémillet et al. 2004, Garthe et al. 2007*a*, *b*, Mattern et al. 2007).

Rockhopper Penguins were recaptured in the vicinity of their nests after 3 days of logger deployment, while the other species were usually recaptured after 5 days. In a few cases, birds could be recaptured and loggers recovered up to 9 days after deployment. During the 79 deployments in this study five loggers were lost. In seven cases the loggers malfunctioned (logging of GPS data stopped after a few hours) and only partial data could be recovered (4 cases). In three cases the loggers were damaged by water reaching the electronic components.

GPS-TD-logger data

The sampling interval for the dive depth and temperature was 1 s, while for GPS data the interval was set to 1 (Gentoo Penguins) or 5 minutes (Magellanic and Rockhopper penguins, Imperial Shags). During dives, GPS fixes where attempted upon each surfacing. Depth data were recorded with a resolution of 3.5 cm, while temperature data had a resolution of 0.005°K.

GPS files, comprising location (WGS84) and time, and a separate file containing dive depth and water temperature data were successfully downloaded from recovered loggers belonging to 24 Rockhopper (57 foraging trips), 16 Magellanic (38 foraging trips), and 13 Gentoo penguins (46 foraging trips), and 15 Imperial Shags (66 foraging trips). We defined foraging trips from the time when the birds departed from the colony to the sea until returning to the colony.

Stable isotope analysis

Nitrogen stable isotope values ($\delta^{15}N$) mainly reflect the trophic level of assimilated prey, with an increase of 1.3–5.3‰ per trophic level across different animal groups (Minagawa and Wada 1984), and a mean 2.3‰ for bird blood (Caut et al. 2009). Carbon stable isotope values ($\delta^{13}C$) mainly reflect the carbon source in a food chain (DeNiro and Epstein 1978) and therefore differ among foraging locations. Large-scale changes in carbon isotope values with latitude (Kelly 2000, Quillfeldt et al. 2005, 2008, Cherel and Hobson 2007) are relevant in pelagic seabirds, while differences in $\delta^{13}C$ in diving seabird will reflect

smaller-scale changes like near-shore versus offshore habitats and benthic versus pelagic food webs.

We analysed carbon and nitrogen stable isotopes of red blood cells and prey items obtained from food regurgitated during handling or spilled during chick-feeding. Of the two major constituents of whole blood, blood plasma and red blood cells, plasma has a much faster turnover with a half-life of ca. three days, while red blood cells have a half-life of ca. 30 days and are therefore integrating over a much longer time (Hobson and Clark 1993).

Dried diet samples were lipid extracted in a Soxhlet apparatus using petroleum ether for at least 6 hours until all lipids were extracted, the liquid no longer colored by any remaining lipids. The crustaceans were acid-washed to remove carbonate, 3.8 w/w % hydrochloric acid being slowly added until no further CO_2-gas was formed. The remaining tissue was cleaned with de-ionized water. Afterwards, all samples were dried at 60°C to constant mass, for at least one day. Blood samples were centrifuged and red blood cells were dried at 38°C in an oven for further analysis. Aliquots of around 0.7 mg of each dry sample were weighed into tin capsules.

Stable isotope analyses of blood cells were carried out at the Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany. Carbon and nitrogen isotope ratios were measured simultaneously by continuous-flow isotope ratio mass spectrometry using a Flash Elemental Analyser (Thermo Finnigan, Bremen, Germany) linked to a Delta V Advantage Isotope Ratio Mass Spectrometer (Thermo Finnigan, Bremen, Germany). Two laboratory standards were analysed for every 10 unknown samples, allowing any instrument drift over a typical 14 hour run to be corrected. Stable isotope ratios were expressed in δ notation as parts per thousand (‰) deviation from the international standards V-Pee dee belemnite (carbon) and AIR (nitrogen), according to the following equation $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$ where X is ^{15}N or ^{13}C and R is the corresponding ratio $^{15}N/^{14}N$ or $^{13}C/^{12}C$. Based on internal standards (N = 165, tyrosin; Roth, Germany), the analytical precision (±1 SD) equalled ±0.16‰ and ±0.29‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively.

Analyses of spatial and temporal data

Positional data obtained from GPS-TD-loggers were used to plot and analyze, with the use of ArcGIS 9.3, the trips performed by the birds. Trip length was calculated as the total cumulative linear distance between all positional fixes along the foraging trip, outside of the colony. For each trip, the maximum distance from the colony was calculated as the linear grand circle distance between the furthest point of the plotted trip and the geographical coordinates of the departure colony, determined by GPS. In a few cases, this technique could underestimate the true distance when e.g., birds swam around masses of land. The distance from the colony to the location of the first foraging dive was calculated in the same way. For all penguin species, birds of two different colonies were studied (as described above). In order to study optimality of the foraging performed, we also measured the linear distance between the location of the first foraging dive and the geographical coordinates of the second colony of the species on the island (e.g., if the bird was breeding in the southernmost colony, we measured the distance between the location of the first foraging dive and the geographical coordinates of the northernmost colony). Trip duration was determined as the time lapse between departure and return from the colony. First foraging dives after departure from the colony were identified using custom written software (Mattern et al. 2007). Dive events were only accepted when the dive depth exceeded 1 m and when at least one wiggle (vertical direction change during the bottom phase) was identified. The validity of the use of wiggles has not been tested for all species in this study. However, wiggles have been found to be associated with feeding behavior in several penguin species (number of beak openings: Takahashi et al. 2004, ingestion rate: Bost et al. 2007), and have been used as a measure of feeding activity in Rockhopper Peguins (Tremblay and Cherel 2000). We tested for differences in start time of foraging (a circular variable) using the Watson-Williams test as described in Zar (1999) with P-value based on a permutation approach (Adams and Anthony 1996, Manly 1997).

Kernel distribution

The nonparametric fixed kernel density estimator was used to determine the 20, 40, 60 and 80% density contour areas (the estimated foraging range; Wood et al. 2000). Kernel densities indicate where, during a foraging trip, birds spent most of their time (Wood et al. 2000). ArcGIS 9.3 was used for calculations together with Hawth's Analysis Tools (Beyer 2004). GPS data-points at the colonies were excluded from our analyses in order to avoid an overestimation the importance of areas very close to breeding colonies. The inter- and intra-specific overlap in the estimated foraging range was calculated with the use of the Intersect and Union tools of ArcGIS 9.3. These calculations were based on the 80% density contour areas.

Stable isotope data analyses and mixing model

Isotope signatures based on $\delta^{15}N$ and $\delta^{13}C$ values were compared among groups using discriminant analyses (Wilk's λ). To estimate diet compositions based on stable isotope values, we applied a Bayesian model in SIAR 4.0 (Stable Isotope Analysis in R, Parnell et al. 2008), which runs under the software R (R Development Core Team 2009). This model allows incorporating sources of uncertainty, in particular the variability in isotope signatures of prey species (Inger and Bearhop 2008, Moore and Semmens 2008). For further details, see Appendix A.

Multi-dimensional model

To determine segregation patterns, we binned the tracks that individuals took into three-space dimensions defined by a grid of 1 min latitude by 1 min longitude and 9 m depth layers. Time was also binned at 1-hour intervals. We only included data below 1 m depth, such that only diving time, i.e., foraging behavior, was analyzed. For each of the resulting four-dimensional cubes, we determined its depth, average sea floor depth, distance to coast, temperature, chlorophyll *a* concentration and time of day as environmental covariates, species identity as a categorical predictor and time spent per individual as response variable. We then used mixed models, controlled for autocorrelation, to examine what parameters determined how long an individual remained in each four-dimensional cube. Chlorophyll *a* concentration was obtained from the Giovanni Ocean Color Time-Series analysis system of the National Aeronautics and Space Administration (NASA, USA) ⟨http://reason.gsfc.nasa.gov/OPS/Giovanni/ocean.swf8D.shtml⟩. For further details, see Appendix A.

Results

Spatial and time segregation

The four species used almost all the marine area around New Island (foraging trips and density contour areas in Fig. 2 to 5; see also animations in Appendices B to G), with the exception of a narrow area to the west of New Island at 51°40′ S. Inter-specific overlap in the estimated foraging ranges was highest between Rockhopper and Gentoo penguins (18%), intermediate between Magellanic and Gentoo penguins (16%) and lowest between Magellanic and Rockhopper penguins (5%).

Foraging trip parameters strongly differed among species (Fig. 6; ANOVA, median trip duration of individuals, $F_{3,56} = 19.8$, $P < 0.001$; median trip length of individuals, $F_{3,56} = 11.2$, $P < 0.001$; median of maximum distance of individuals from the colony, $F_{3,56} = 4.2$, $P = 0.009$; median start time of foraging, circular permutation test, $F = 10.1$, $P = 0.001$). Overall, Magellanic Penguins performed the longest foraging trips, taking them furthest away from the colony, followed by Gentoo and Rockhopper penguins and Imperial Shags (Fig. 6, see homogeneous subsets, based on Tukey post-hoc tests; see also Appendix A, Table A1).

Complete, i.e., non-overlapping, spatial segregation was observed between the two Gentoo Penguin colonies (no intra-specific overlap in the estimated foraging range; Fig. 4; see animation in Appendix E), while a strong spatial segregation was also observed between the Rockhopper Penguin colonies (5% intra-specific overlap in the estimated foraging range; Fig. 2; see animation in Appendix C). Additionally, Rockhopper Penguins from the North End foraged closer to their colony than individuals at the Settlement Colony ($t = -3.8$, $P = 0.001$; North End $n = 12$, Settlement $n = 8$; Fig. 6; see Appendix A, Table A1).

All Magellanic Penguins from the Prion patch foraged in an area eastwards from the island, while most individuals from the Airstrip colony

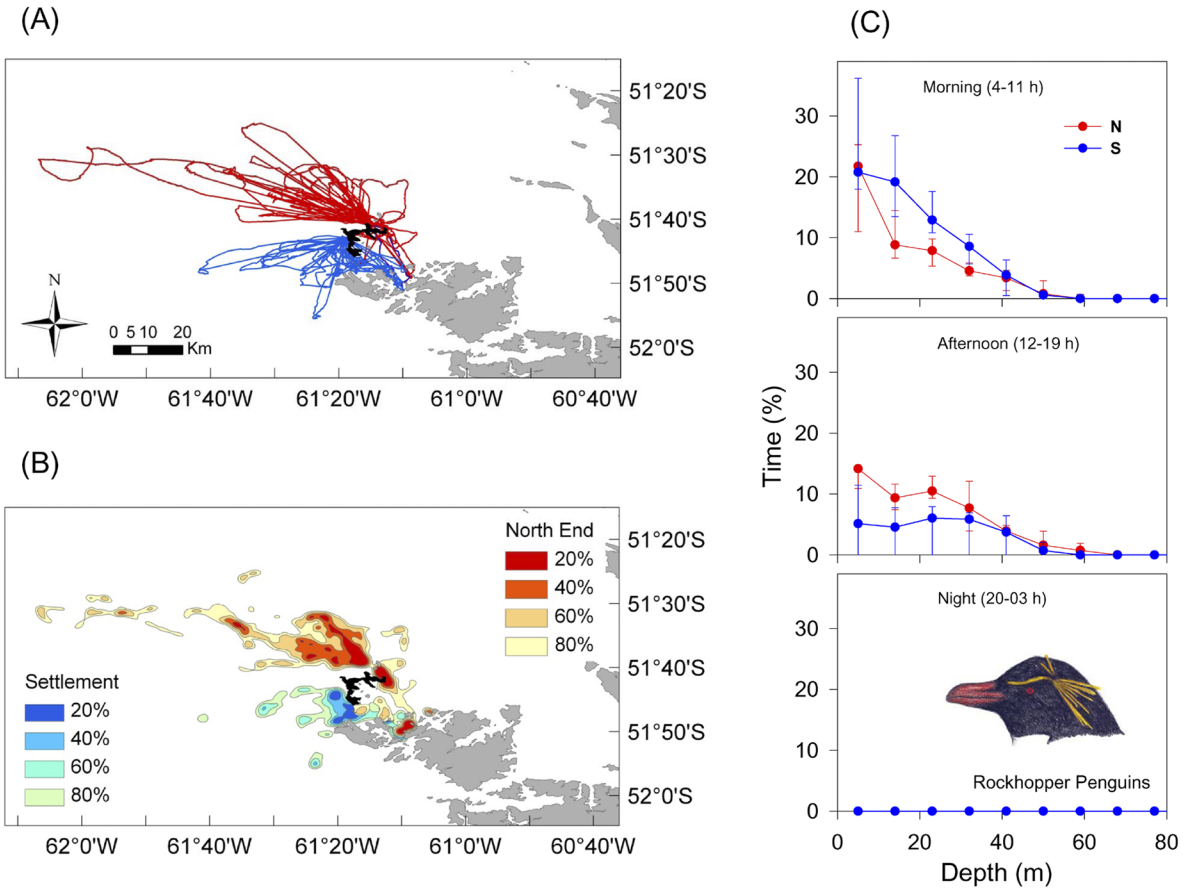

Fig. 2. Space and time segregation of Rockhopper Penguins breeding in two locations at New I. (in black). Performed trips (A) and 20, 40, 60 and 80% kernel density distribution, i.e., the places where the birds spent most of their forging time (B) for birds breeding in the North End (N; shades of red and red lines) and the Settlement (S; shades of blue, and blue lines) colonies. Panel (C) shows the time allocation of the individuals of the two colonies (median, 75 and 25% quartiles) among different depth strata and times of the day.

foraged in an area southwest from New I. (Fig. 3; see animation in Appendix D). The 14% overlap observed in the foraging areas used by the two colonies of Magellanic Penguins was due to behavior of 5 of the 8 birds from the southernmost colony (Airstrip area) that foraged to the east or west of their colony on different foraging trips. Easterly trips contributed 5 of the 18 foraging trips of Magellanic Penguins from the Airstrip colony. From this colony, one individual also performed a foraging trip around the island.

Female and male Imperial Shags showed also little overlap in the foraging areas used around New I. (Fig. 5; see animation in Appendix F). Females were restricted to areas between New I. and neighboring islands, while males foraged predominantly in open waters (Fig. 5; Appendix F). Male ($n = 7$) and female ($n = 6$) Imperial Shags differed in most of the trip parameters (Fig. 6; see also Appendix A, Table A1), with males performing longer ($t = -2.5$, $P = 0.029$) and reaching further ($t = -2.3$, $P = 0.045$) foraging trips. Strong time segregation was observed between the genders: females started their foraging trips early in the morning, while males did not leave the colony until noon (Fig. 6; Appendix A, Table A1 and Appendix F).

Spatial distribution of foraging dives

The distance between the first foraging dives and the departure colony (DFFD-DC) differed between species (Fig. 6; ANOVA, $F_{3,58} = 10.6$, $P <$

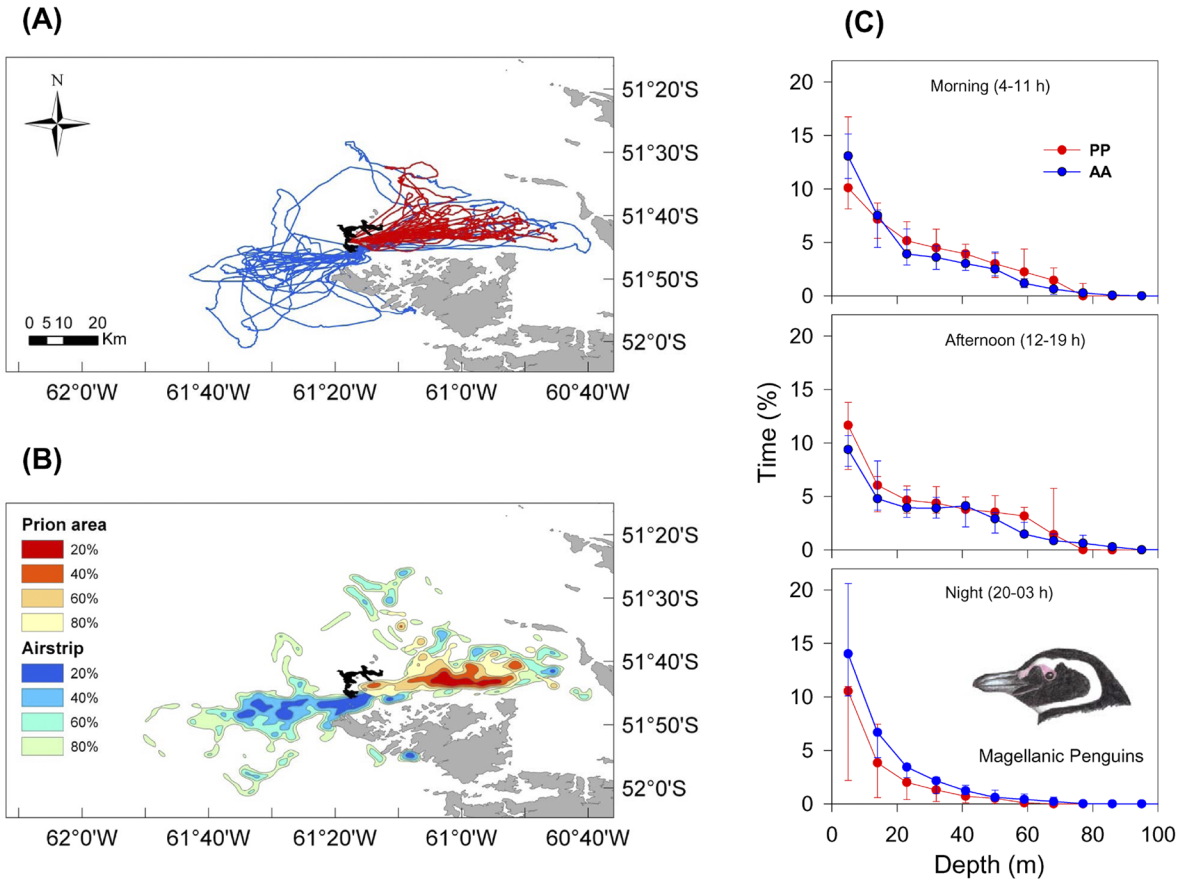

Fig. 3. Space and time segregation of Magellanic Penguins breeding in two locations at New I. (in black). Performed trips (A) and 20, 40, 60 and 80% kernel density distribution, i.e., the places where the birds spent most of their forging time (B) for birds breeding in a Thin-billed Prion patch (PP; shades of red and red lines) and close to the Airstrip area (AA; shades of blue, and blue lines). Panel (C) shows the time allocation of the individuals of the two colonies (median, 75 and 25% quartiles) among different depth strata and times of the day.

0.001, for positions of first foraging dives see Fig. 7). In general, penguins started to forage close to their colonies i.e., 300 m from the colony in Magellanic Penguins (Fig. 6; see also Appendix A, Table A1).

In order to test if penguins forage in areas closer to their own colonies rather than in other foraging areas closer to the neighboring colonies, we measured the linear distance between the location of the first foraging dive and the geographical coordinates of the second colony of the species on the island (DFFD-SC). All three penguins species in this study foraged closer to their own colonies rather than to the second colony of the species on the island (mean ± SD; Rockhopper Penguins: DFFD-DC = 2.3 ± 0.9 km, DFFD-SC = 10.4 ± 1.4 km, paired samples test, $t = -51.3$, $df = 20$, $P < 0.001$; Magellanic Penguins: DFFD-DC = 0.5 ± 0.3 km, DFFD-SC = 2.4 ± 0.4 km, $t = -17.2$, $df = 15$, $P < 0.001$; Gentoo Penguins: DFFD-DC = 1.1 ± 0.5 km, DFFD-SC = 7.9 ± 0.7 km, $t = -78.5$, $df = 13$, $P < 0.001$).

Dietary segregation

The distribution of stable isotope values (Fig. 8), as well as proportions resulting from the SIAR stable isotope mixing model (Fig. 9) suggested that Rockhopper Penguins took more krill than the other species, and Imperial Shags were the most piscivorous of the four species.

We observed intra-species segregation with regard to diet in Rockhopper Penguins (between

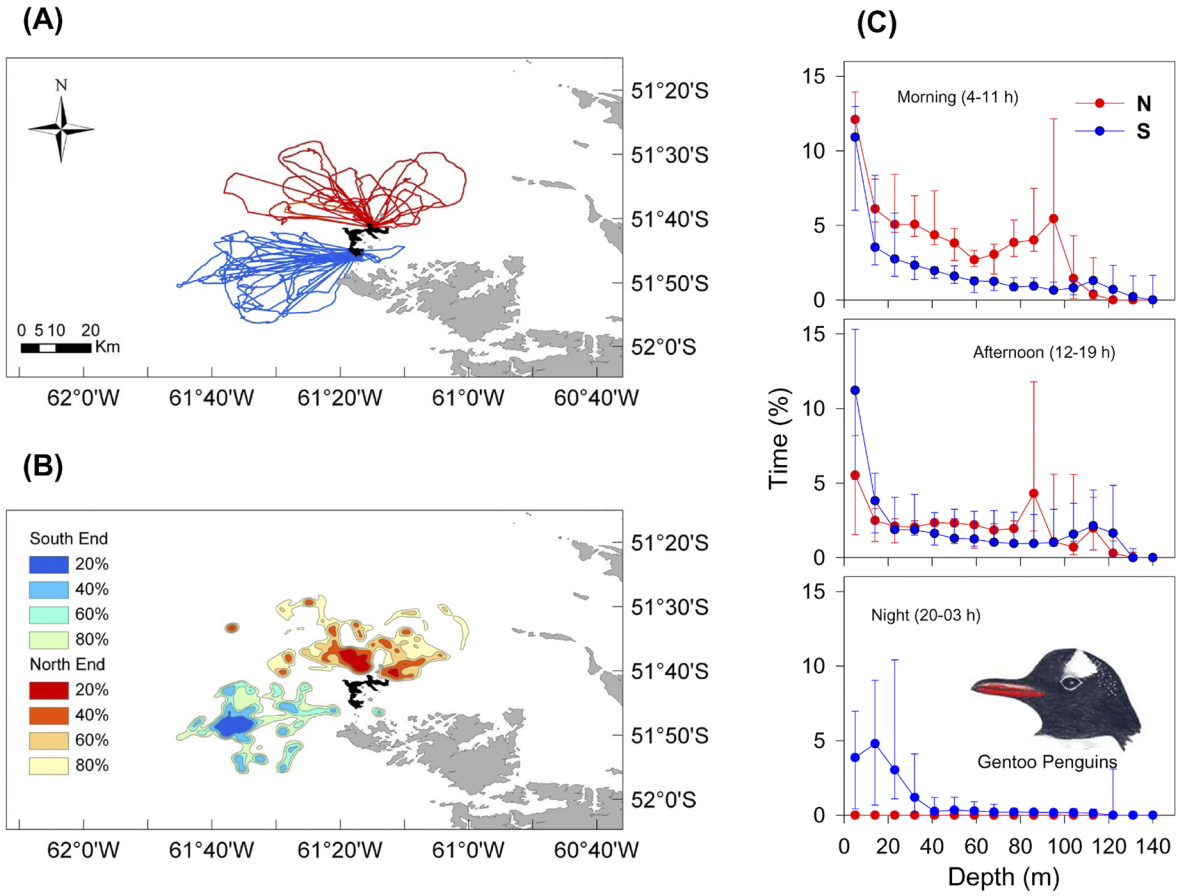

Fig. 4. Space and time segregation of Gentoo Penguins breeding in two locations at New I. (in black). Performed trips (A) and 20, 40, 60 and 80% kernel density distribution, i.e., the places where the birds spent most of their forging time (B) for birds breeding at the North End (N; shades of red and red lines) and South End (S; shades of blue, and blue lines) colonies. Panel (C) shows the time allocation of the individuals of the two colonies (median, 75 and 25% quartiles) among different depth strata and times of the day.

birds breeding at New Island North and at the Settlement Colony: discriminant function analysis, Wilk's $\lambda = 0.7$, $df = 2$, $P = 0.034$) and Imperial Shags (between the genders: Wilk's $\lambda = 26.9$ $df = 2$, $P < 0.001$). We found no differences in stable isotope values between colonies in Gentoo Penguins (Wilk's $\lambda = 0.98$, $df = 2$, $P = 0.905$) or Magellanic Penguins (Wilk's $\lambda = 0.9$, $df = 2$, $P = 0.503$).

We further tested for differences in the importance of each prey type, using the mean proportions of the 12 models obtained for each colony. We estimated a range of different proportions of fish (Fig. 9, $F_{7,88} = 6.6$, $P < 0.001$) and krill ($F_{7,88} = 5.2$, $P < 0.001$), with differences observed mainly at the species level. We found no differences in the estimated proportion of *Munida* ($F_{7,88} = 0.4$, $P = 0.902$) and squid ($F_{7,88} = 1.6$, $P = 0.138$).

Diving model

We observed complex inter-species effects (Appendix A, Table A2). Overall, the entire collective of predictor variables and interactions had a highly significant impact on time spent in a certain cube in the water body (likelihood ratio test comparing fit of full with fit of null model: $\chi^2 = 1036.6$, $df = 79$, $P < 0.001$). The time an individual spent in a cube depended on all parameters except chlorophyll *a*. In addition, it was influenced by a complex pattern of interactions between species and the environmental

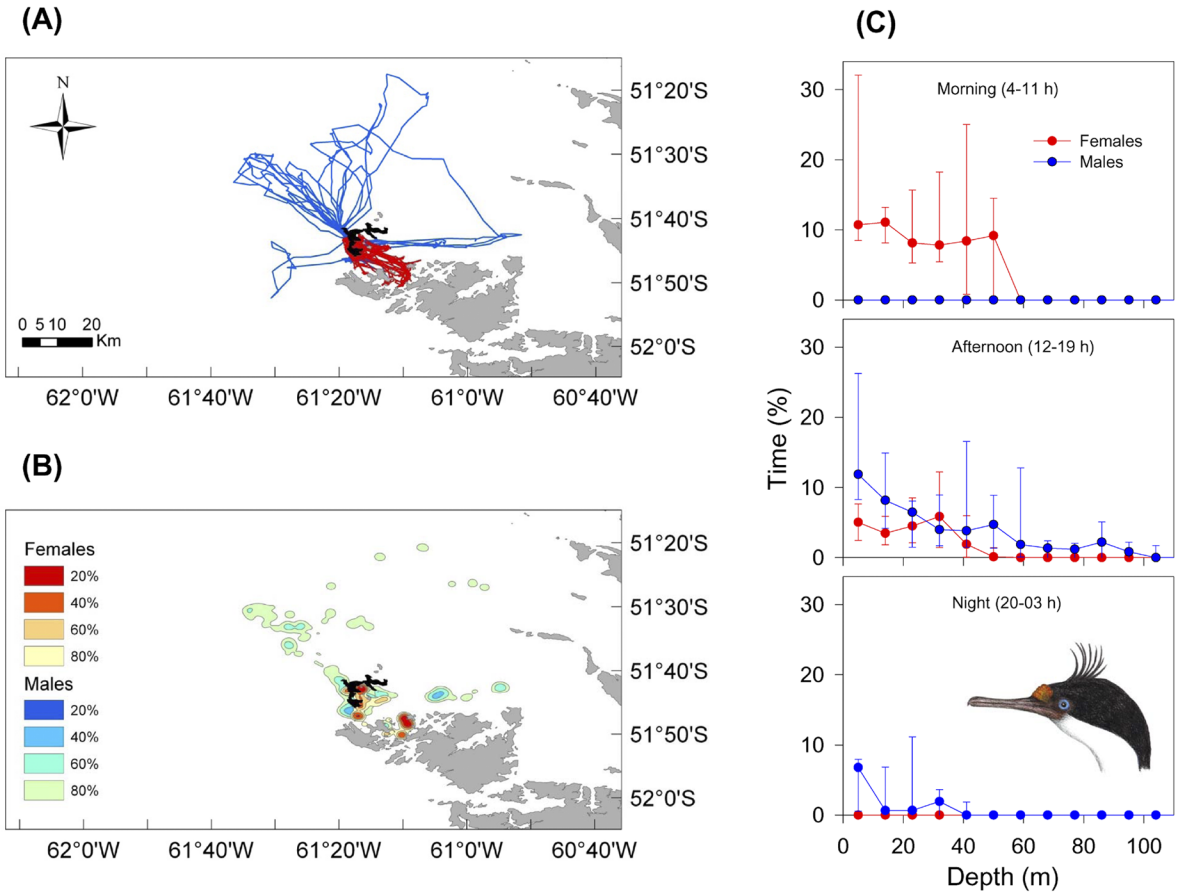

Fig. 5. Space and time segregation of Imperial Shags breeding at the Settlement Colony, New I. (in black). Performed trips (A) and 20, 40, 60 and 80% kernel density distribution, i.e., the places where the birds spent most of their forging time (B) for male (shades of blue, and blue lines) and female (shades of red and red lines) shags. Panel (C) shows the time allocation of the individuals of the two sexes (median, 75 and 25% quartiles) among different depth strata and times of the day.

covariates (Appendix A, Table A2). For example, preferred depths varied diurnally, with the pattern of variation differing between species (Figs. 2c, 3c, 4c, 5c; Appendix A, Table A2, three-way interaction between species, squared cube depth and daytime; Appendix G). Similarly complex interactions were observed between species, daytime and squared distance to coast, species and squared temperature, and species and bathymetric depth (Appendix A, Table A2, Fig. A2).

To study intra-specific segregation patterns, we included individuals from two different colonies of each penguin species (Fig. 1). All colonies were at New Island and within 2 to 7 km distance from each other. In all three species, penguins from the two colonies used different foraging areas (Figs. 2a–b, 3a–b, 4a–b; Appendices B to G). Moreover, penguins of the same species but from different colonies did not only forage at different locations, but also exhibited different preferences with regard to ecological covariates at foraging localities. In fact, models fitted to each species separately showed a pattern of variation between colonies being almost as complex as that between species in the previous analysis (comparison of model with factor colony and its interactions, with model without colony and its interactions, likelihood ratio tests, separately for each species: Gentoo Penguins, $\chi^2 = 144.7$, $df = 18$, $P < 0.001$; Rockhopper Penguins, $\chi^2 = 78.9$, $df = 18$, $P < 0.001$; Magellanic Penguins, $\chi^2 = 38.1$, $df = 18$, $P =$

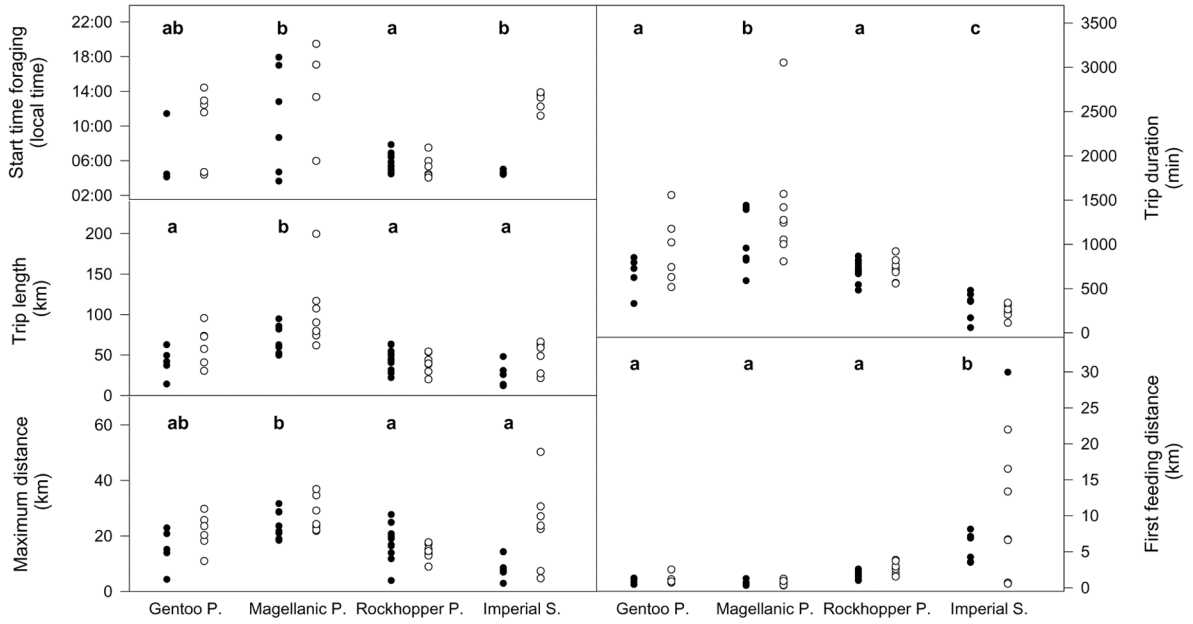

Fig. 6. Distribution of median values of foraging trip parameters during chick-feeding at New I., Falkland Is., determined using GPS-TD loggers. Homogeneous subsets are indicated, as obtained from multiple comparisons of estimated marginal means. Data from the different penguin colonies are plotted separately and each dot represents one individual. In the case of shags, sexes are plotted separately. Gentoo Penguins: full circles for North End colony, open circles for South End colony. Magellanic Penguins: full circles for Prion patch colony, open circles for Airstrip area colony. Rockhopper Penguins: full circles for North End colony, open circles for Settlement Colony. Imperial Shags: full circles for females, open circles for male. 'P.' denotes penguin.

0.004). For example, in Rockhopper Penguins diurnal patterning of preferred diving depths clearly differed between the two colonies (three-way interaction between species, daytime cube depth squared and in Appendix A, Table A3; Fig. 2c).

Discussion

We here studied simultaneous effects of species and colonies in the spatial and temporal foraging segregation of a diving seabird assemblage, sharing a small sector of the Southwestern Atlantic Ocean during the breeding season. Because the studied seabird colonies are much closer to each other (7 km in Rockhopper and Gentoo Penguin colonies, 2 km in Magellanic Penguin colonies) than the average foraging range of the species (see Appendix A, Table A1), we expected large overlaps among the foraging areas. However, we found little, if any, overlap due to strong spatial and temporal segregation. Particularly striking, we observed strong differences in foraging areas, diving depth, time of foraging and prey choice among birds of the same species, breeding in different colonies at the same island.

More specifically, the data on trips and the kernel density distribution suggested complete spatial segregation between the two colonies of Gentoo Penguin. The data indicated very strong spatial segregation between the two Rockhopper Penguin colonies and between male and females Imperial Shags, while the observed segregation was moderately strong between the two Magellanic Penguin breeding sites. Our diving model and the data on time allocation among different depth strata and times of the day also showed a strong segregation in the preferred depths that varied diurnally, with the pattern of variation differing among species. Strikingly, intra-specific differences were also observed between Gentoo Penguins from the North End and South End colonies, and Rockhopper Penguins breeding at

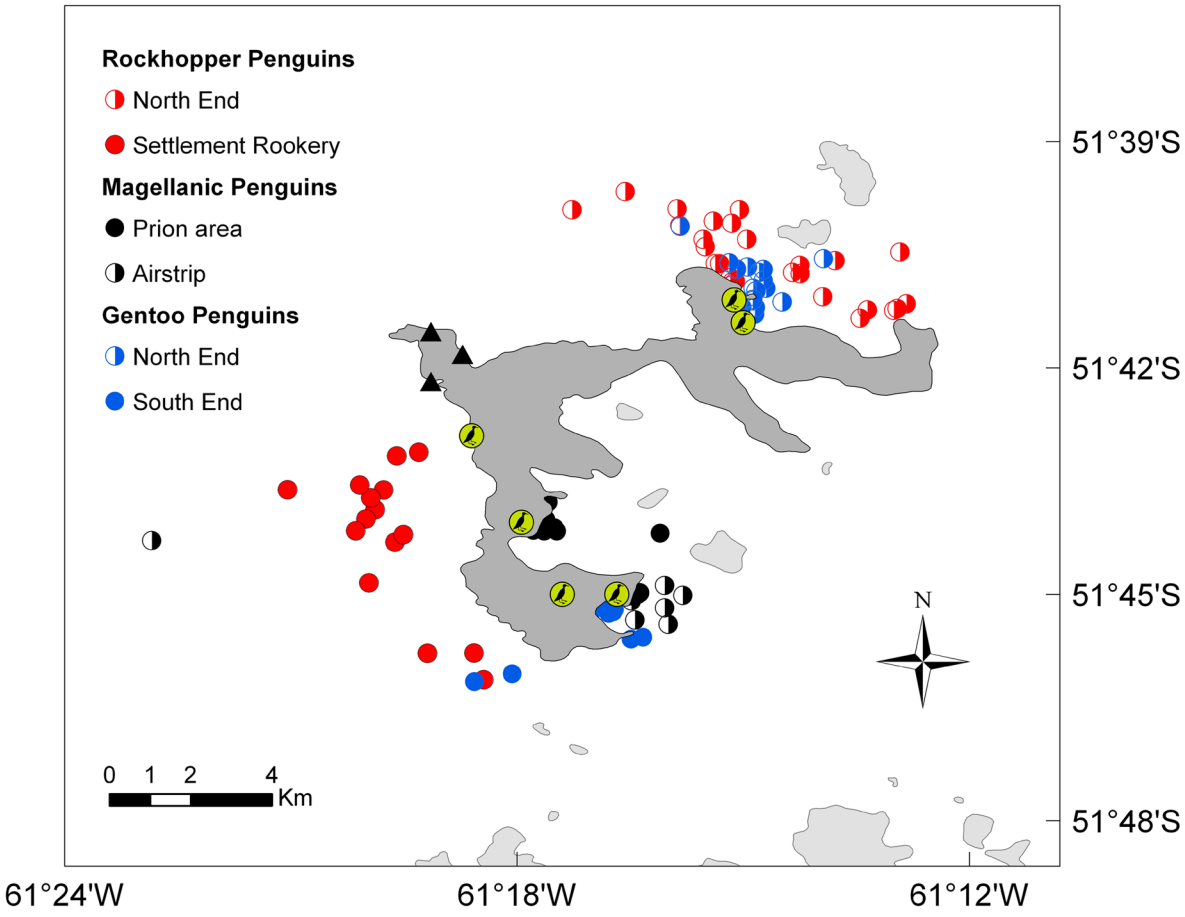

Fig. 7. Location of individual first foraging dives of penguins and shags breeding at New I. (in dark gray). For more details on the location of the penguin, shag and fur seal colonies see also Fig. 1.

New I. North and at the Settlement Colony. The time an individual spent in a cube of the diving model depended on all studied parameters except chlorophyll *a*, and was influenced by a complex pattern of interactions between species and the environmental covariates. Again, in addition to some inter-specific segregation pattern, we observed strong intra-species dietary segregation between the two Rockhopper penguin colonies, and between male and female Imperial Shags.

Patterns of spatial and temporal segregation

According to niche theory, animals segregate in the use of the environment to avoid both inter- and intra-specific competition (e.g., Wakefield et al. 2009 and references therein). Conspecific seabirds breeding in nearby colonies at the same island could avoid intra-specific competition for food by segregating in space and/or time in their foraging areas. However, if this were the mechanism used in a given community, previous models predict complete spatial segregation between the populations (see Cairns 1989). Yet, most studies have found incomplete segregation of the foraging areas used (e.g., Brothers et al. 1998, Huin 2002, Lynnes et al. 2002, Ainley et al. 2003, Grémillet et al. 2004, Kokubun et al. 2010 and references therein; but see for complete segregation: Wanless and Harris 1993, and Imperial Shags in Sapoznikow and Quintana 2003). In our study a mixed situation was observed, i.e., complete segregation in Gentoo Penguins, and partial segregation in Magellanic and Rockhopper penguins.

Optimal foraging theory (MacArthur and

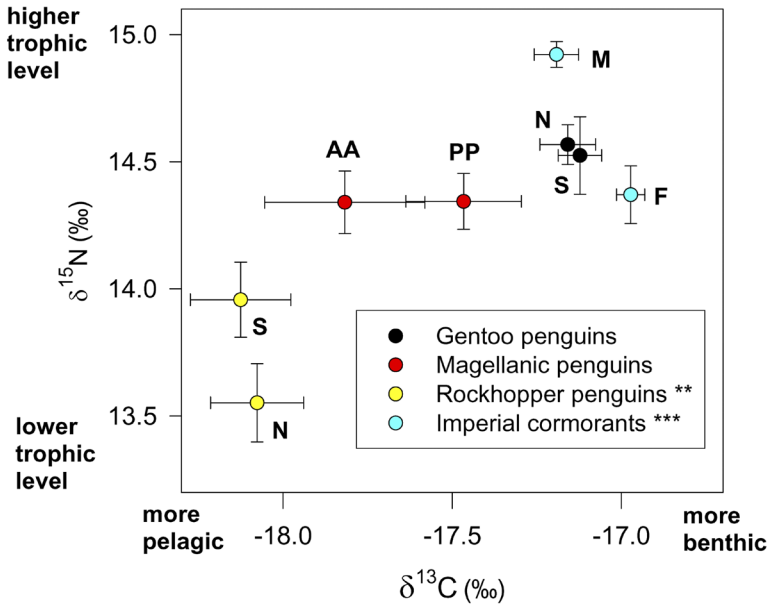

Fig. 8. Stable isotope values of red blood cells (mean, s.e.) of the four species, sampled at New I. during the chick-rearing period. For the penguins, two colony locations were compared, namely North End (N) and South End (S) for Gentoo Penguins, North end (N) and Settlement Colony (S) for Rockhopper Penguins, and Airstrip area (AA) and Prion patch (PP) for Magellanic Penguins. In Imperial Shags, we compared isotope values of males (M) and females (F).

Pianka 1966, Schoener 1971) predicts that, in addition to selecting patches abundant in resources, the individuals will also minimize the traveling distances to those patches and thus the energy expenditure and predation risk. In this scenario, where neighboring colonies overlap in potential foraging range, the individuals should forage in areas closer to their own colonies rather than in other foraging areas closer to the neighboring colonies (Cairns 1989). In all foraging trips here studied, all individuals started foraging closer to their own colonies rather than to the other colony of the species on the island. This result suggests that the individuals behaved in an optimal way, as predicted, thus minimizing the costs associated with foraging. During the guard stage, one adult always remains with the chick, and is thus unable to feed. After the partner relieves it, the adult leaves to forage. During the first part of the foraging trip, penguins will seek to quickly replenish their own reserves, leading to relatively near-shore first foraging sites in a trip. Penguins then usually carry out a foraging trip in a loop shape. In colonies that face opposite shores, such as in the case of the Gentoo Penguins at New I., this combination of a close-by foraging site and loop-shaped trip may lead to the spatial segregation observed.

Foragers are faced with the need of weighing up the risks, gains and missed opportunity costs linked to foraging (see e.g., Lima 1998, Shrader et al. 2008). A vital risk influencing foraging behavior is predation. In an effort to reduce predation risk, prey may avoid certain areas or habitats (e.g., Kotler et al. 1991). Consequently, individuals may not use habitats uniformly due to spatial differences in perceived predation risk and thus, will forage across 'landscapes of fear' (see e.g., Laundré et al. 2001, Shrader et al. 2008). This non-lethal effects of predation on local prey populations can determine, at least in part, the density and dispersion of prey over relatively large areas (Lima 1998). Three Fur Seal (*Arctocephalus australis*) colonies, holding an estimated 2,000 individuals, are located on the northwestern tip of New I. (Fig. 1; Strange et al. 2007). Notoriously, in our study, a zone to the west and around the three Fur seal colonies was completely avoided during all penguin foraging trips (see

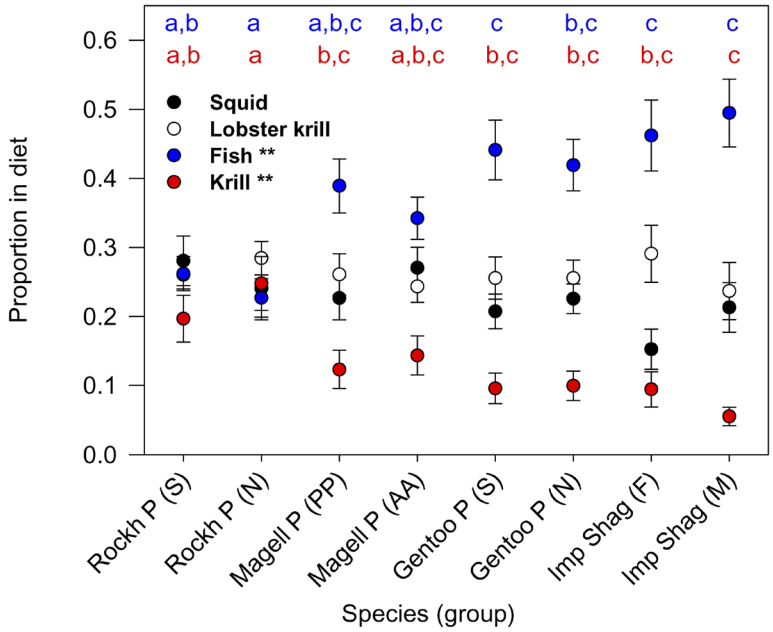

Fig. 9. Results of a SIAR stable isotope mixing model, carried out on stable isotope values of red blood cells of four species of diving seabirds at New I., sampled during the chick-rearing period. Estimated proportions of main prey types in the diet are given (mean, s.e.). Colonies belonging to homogenous subsets obtained by ANOVA with Tukey post-hoc tests are marked with the same letter (blue for fish and red for krill). For abbreviations see Fig. 8.

Figs. 2 to 4, 7; see also animations in Appendices C to E). Indeed, this was the only area around New I. not used by any of the three penguin species, suggesting that the penguins actively avoided this area of increased predation risk. Non-lethal effects of predation on seabird foraging behavior have been described (e.g., Riou and Hamer 2008 and references therein), and in the present study, most likely contribute to the spatial segregation observed.

The observed foraging areas and temporal distribution of the individuals during their foraging trips was therefore strongly influenced by the location of their colonies and those of their predators, which depend on coastal features (see Cairns 1989) like the availability of suitable cliffs (Rockhopper Penguins), sandy beaches in the vicinity of relatively plain terrain (Gentoo Penguins), soft terrain where to excavate burrows (Magellanic Penguins) or low rocky coasts (Fur Seals).

The complex pattern of interactions observed in the diving model in the present study between species or colonies and environmental covariates (average sea floor depth, distance to coast, temperature, time of day; see Appendix A) might therefore reflect differences in the habitat and prey availability encountered in the "hinterland" of each colony. Adaptations to avoid intra- and interspecific competition might further trigger differences in spatial and temporal distribution patterns. The random slopes of the dive model show that there are also individual preferences that might contribute to the spatial and temporal distribution patterns recorded.

Dietary segregation

Ecologically similar coexisting species often show a minimum size difference between trophic apparati (Hutchinson 1959). The four species in this study show differences in body size, maximum dive (see Figs. 2 to 4) depth and bill size and shape, which might influence the optimal prey size and type for each species (e.g., Gurd 2007 and references therein). Thus, ecological segregation might also be found in the diet.

Previous studies (Thompson 1989), using stomach content analysis, had suggested dietary

segregation among the four diving species, though Gentoo and Magellanic penguins showed large dietary overlap (Appendix A, Fig. A1): We here found the same pattern in stable isotope analysis and a mixing model, suggesting a stable pattern of dietary segregation among years.

Differences were especially observed in the degree of piscivory, and in the preferred crustacean type (Appendix A, Fig. A1, Fig. 9). All species took some amount of crustaceans. But while Rockhopper Penguins took more than half of their food by mass as euphausiids (krill) *Euphausia vallentini*, *E. lucens* and *Thysanoessa gregaria*, which are part of the subantarctic pelagic foodweb, the other three seabird species took decapods *Munida gregaria* (lobster krill), which form part of the Patagonian shelf food web. In line with previous findings (Weiss et al. 2009), Rockhopper Penguins had the lowest trophic level, Magellanic Penguins were intermediate and Gentoo Penguins and Imperial Shags had the highest trophic level of the diving seabirds at New Island.

We further found within-species segregation in Rockhopper Penguins between birds breeding at New Island North End and at the Settlement Colony (Fig. 8). Birds from New Island North had the lowest trophic level, and the lowest carbon stable isotope values, indicating more pelagic foraging, in line with a higher krill content (Fig. 9). Such a difference most likely reflects small-scale differences in the marine prey base at the foraging sites, and not inherent changes in preference.

Thus, we found that partial intra- and interspecific differences in diet can contribute in the ecological segregation of species as well as colonies.

Concluding remarks

The present study goes far beyond previous work by analyzing simultaneous effects of species and colonies. Previous analyses of simultaneous habitat segregation have been restricted to comparisons between two or three sympatric species (e.g., Weimerskirch et al. 1988, Lynnes et al. 2002, Sapoznikow and Quintana 2003, Mori and Boyd 2004, Frere et al. 2008, Kokubun et al. 2010, Wilson 2010) or between two more distant populations of one species (e.g., Cape Gannets at 100 km distance: Grémillet et al. 2004, Gentoo Penguins at 55 km distance: Lescroël and Bost 2005).

We here show that birds from different colonies of each species did not only forage at different locations, but also exhibited different preferences with regard to foraging daytime and ecological covariates at foraging localities. Diving seabirds are flexible in their use of more pelagic or more benthic diving according to differences in the conditions among years (e.g., Miller et al. 2009). We here show that such flexibility is also encountered in response to small-scale habitat differences such as observed here in conspecifics from nearby colonies. The birds in the present study behaved in line with predictions of the optimal foraging theory, using foraging places adjacent to their own colony and adapting their spatial and temporal behavior accordingly. Nonlethal effects of predation played a notorious role in the avoidance of specific areas.

Further studies on this topic should also contemplate inter-individual variation in foraging behavior and diet (see Bolnick et al. 2003 and references therein). The degree of individual specialization varies among species and among populations, reflecting a diverse array of physiological, behavioral, and ecological mechanisms that could generate intra-population variation (Bolnick et al. 2003) in foraging patterns.

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Appendix A

Stable Isotope Mixing Model

To estimate diet compositions based on stable isotope values, we applied a Bayesian model in SIAR 4.0 (Stable Isotope Analysis in R, Parnell et al. 2008), that runs under the free software R (R Development Core Team 2009). This model allows incorporating sources of uncertainty, in particular the variability in isotope signatures of prey species (Inger and Bearhop 2008, Moore and Semmens 2008). SIAR uses Markov Chain Monte Carlo modeling, takes data on animal isotopes and fits a Bayesian model to their dietary habits based upon a Gaussian likelihood with a dirichlet prior mixture on the mean. The model assumes that each target value (i.e., the stable isotope data of each individual) comes from a Gaussian distribution with an unknown mean and standard deviation. The structure of the mean is a weighted combination of the food sources' isotopic values. The standard deviation depends on the uncertainty around the fractionation corrections and the natural variability between target individuals within a defined group (in this case, a colony of a species). We used the standard setting (20,000 iterations), and carried out 12 runs, to evaluate different combinations of isotopic discrimination rates for diet-blood in birds (reviewed in Caut et al. 2009), using $\Delta^{15}N$ values of 0, 1‰, 2‰ and 3‰, and $\Delta^{13}C$ values of −0.2‰, 0.2‰ and 0.6‰. SD was set to 0.5 for $\Delta^{15}N$ and $\Delta^{13}C$, which is at the upper end of the range of values suggested by (Caut et al. 2009). We included the four major

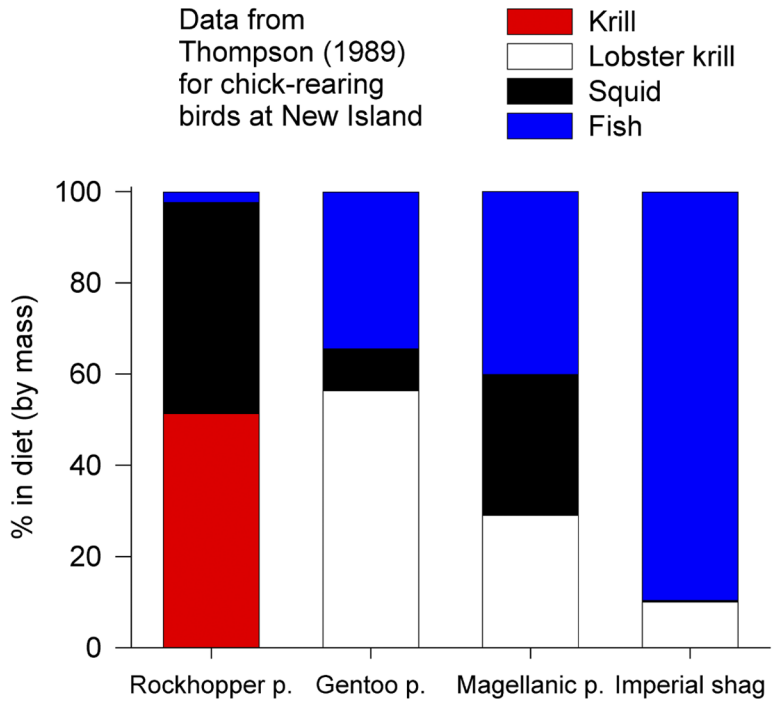

Fig. A1. Diet during the chick-rearing period at New Island according to Thompson (1989). "p." denotes "penguin".

prey types (fish, squid, krill and lobster krill) as sources in the mixing model, given the very minor importance of all other prey. By using the same four prey types in all the models (Fig. 9), we likely underestimated some preferred prey species. For example, krill in Rockhopper Penguins might be underestimated in favor of lobster krill, which is scarcely found in diet samples. Nevertheless, our mixing models reflected the dietary segregation well, as Rockhopper Penguins still appeared as consuming the highest amount of krill among the species.

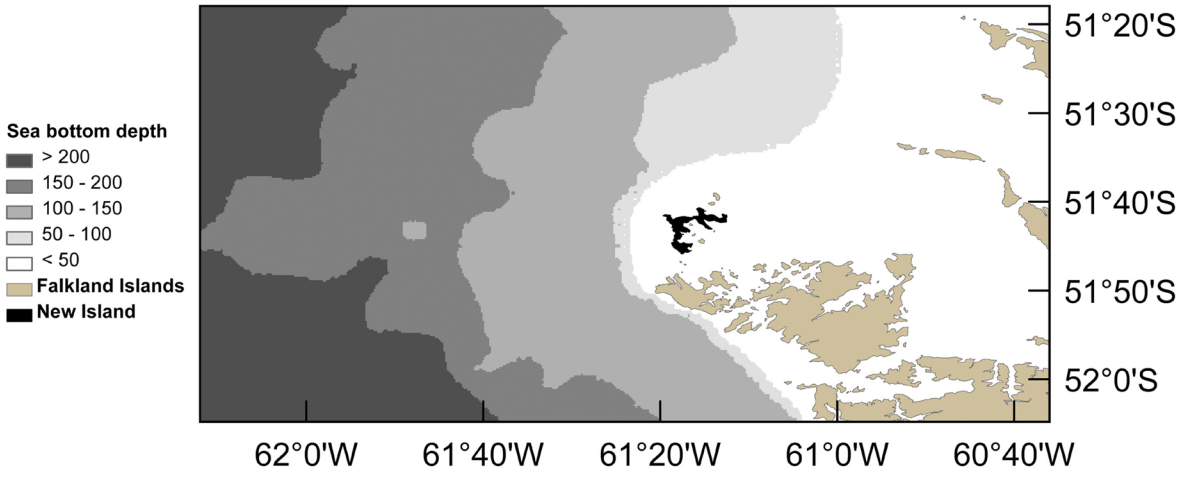

Fig. A2. Sea bottom depth zones around New Island, Southwest Atlantic Ocean.

Table A1. Parameters of foraging trips of Rockhopper Penguins *Eudyptes chrysocome*, Magellanic Penguins *Spheniscus magellanicus*, Gentoo Penguins *Pygoscelis papua* and Imperial Shags *Phalacrocorax (atriceps) albiventer* during chick-feeding at New Island, Falkland Islands, determined using GPS-TD loggers.

	n	Trip length	Maximum distance from colony	Trip duration (min)	DFFD-DC	Start time of foraging (local time)
Rockhopper Penguins						
North End	1	45.4 ± 13.2	17.9 ± 6.2	689.9 ± 116.9	1.8 ± 0.6	5:41:26 ± 0:18:16
	2	(21.9–63.9)	(3.9–27.7)	(482.5–866.8)	(1.0–2.6)	(4:27:34–7:50:49)
Settlement colony	8	39.9 ± 11.5	14.2 ± 2.7	718.6 ± 121.9	2.9 ± 0.8	4:57:57 ± 0:22:36
		(19.8–54.3)	(8.9–17.7)	(558.1–920.1)	(1.5–3.9)	(4:02:11–7:30:06)
t-test for equality of means		$t = 0.955$	$t = 1.581$	$t = -0.528$	$t = -3.803$	$F = 1.500$
		$P = 0.352$	$P = 0.131$	$P = 0.604$	$\mathbf{P = 0.001}$	$P = 0.493$
Magellanic Penguins						
Prion area	8	67.0 ± 17.8	24.0 ± 5.0	1037.1 ± 330.2	0.6 ± 0.3	11:15:35 ± 2:01:06
		(49.7–94.7)	(18.4–31.6)	(590.8–1441.2)	(0.3–1.3)	(3:38:12–17:55:14)
Airstrip	8	101.1 ± 43.7	26.8 ± 6.0	1428.0 ± 699.1	0.5 ± 0.3	14:36:50 ± 1:40:56
		(61.8–199.7)	(21.8–36.8)	(808.9–3052.4)	(0.3–0.9)	(5:58:06–19:56:56)
t-test for equality of means		$t = -2.044$	$t = -0.986$	$t = -1.430$	$t = 0.120$	$F = 0.836$
		$P = 0.060$	$P = 0.341$	$P = 0.175$	$P = 0.906$	$P = 0.406$
Gentoo Penguins						
North End	5	41.0 ± 17.9	15.4 ± 7.2	666.4 ± 205.2	1.0 ± 0.4	5:30:13 ± 1:11:05
		(14.0–62.7)	(4.3–22.9)	(331.9–851.6)	(0.4–1.5)	(4:07:36–11:25:14)
South End	6	61.7 ± 23.8	21.4 ± 6.5	941.1 ± 389.0	1.1 ± 0.6	10:51:09 ± 1:42:18
		(30.4–95.5)	(11.0–29.7)	(517.2–1557.7)	(0.7–2.5)	(4:22:50–15:33:36)
t-test for equality of means		$t = -1.601$	$t = -1.446$	$t = -1.415$	$t = -0.263$	$F = 3.207$
		$P = 0.144$	$P = 0.182$	$P = 0.191$	$P = 0.797$	$P = 0.158$
Imperial Shags						
Females	6	26.8 ± 13.2	9.1 ± 4.5	310.9 ± 163.2	5.6 ± 2.0	4:40:32 ± 0:06:37
		(12.0–48.0)	(2.9–14.3)	(58–481)	(3.5–8.2)	(4:24:12–5:01:13)
Males	7	49.2 ± 18.0	23.7 ± 15.2	240.9 ± 75.7	9.8 ± 11.0	13:15:02 ± 0:36:07
		(21.3–66.3)	(4.7–50.2)	(113.5–340.5)	(0.6–29.9)	(11:10:44–16:11:07)
t-test for equality of means		$t = -2.517$	$t = -2.258$	$t = 1.020$	$t = -0.907$	$F = 23.585$
		$\mathbf{P = 0.029}$	$\mathbf{P = 0.045}$	$P = 0.330$	$P = 0.384$	$\mathbf{P = 0.008}$

Notes: median data for each individual were compared, i.e., one data point per individual was used to determine means, standard deviations and ranges, and to test for differences among colonies (penguins) and genders (shags). DFFD-DC: distance between the first foraging dives and the departure colony. Start times were tested with a circular permutation test. Significant *P*-values are marked bold. Distances are given in kilometers.

Multi-dimensional Model

For the analyses we first laid a grid of one min latitude by one min longitude on the studied area, considering only those grid cells, which were actually used by the study birds. For each of these grid cells we determined bathymetric average depth, distance to coast, and chlorophyll *a* concentrations (separately for different time periods). Bathymetric data were provided by the Falkland Islands Fisheries Department. The data included grid cells close to the coast with altimetry values. In such cases, no bathymetric data were available and thus a depth of 10 meters was assigned to the grid cells (304 out of 1160 cells). For most cells, distance to the coastline was determined as the smallest grand circle distance between the cell's mid point and any point of the coastline of the Falkland Islands. Coastline coordinates where obtained from the Falkland Islands Department of Mineral Resources ⟨http://www.falklands-oil.com⟩. For some cells comprising parts of the islands we set distance to the coast to zero (55 out of 1160 cells). Chlorophyll *a* concentration was obtained from the Giovanni Ocean Color Time-Series on-line visualization and analysis system of the National Aeronautics and Space Administration (NASA, USA) ⟨http://reason.gsfc.nasa.gov/OPS/Giovanni/ocean.swf8D.shtml⟩. This site provides SeaWiFS average 8-day chlorophyll *a* data per approx. six min (0.083°) × six min grid cell. Eight-day intervals, for which chlorophyll *a* data were available, were 19 to 26 December 2008, 1 to 8 January and 9 to 16 January 2009. Presumably due to cloud cover and also to the lack of coverage between 27 and 31 December 2008, for some combinations of grid cells and time periods, chlorophyll *a* data were not available. In such cases, we took the average chlorophyll *a* content of the same cell for other

Table A2. Estimated coefficients from the model comparing diving behavior of all four species studied at New Island. Indicated are estimates for main effects and significant interactions derived from a GLMM.

Effect	Imperial Shag	Gentoo Penguin	Magellanic Penguin	Rockhopper Penguin	χ^2	*df*	*P*
Intercept	3.279	3.290	3.646	4.083			†
sin(day time)	0.327	0.117	−0.155	−0.677			†
cos(day time)	0.172	0.241	0.126	−0.725			†
Chlorophyll *a*	0.003				0.1	1	0.781‡,§
Bathymetric depth	0.052	0.316	0.285	0.201	19.1	3	<0.001‡
Bathymetric depth‡	0.164				10.8	1	0.001§
Distance to coast	0.190	0.241	0.071	−0.158			†
Distance to coast‡	0.241	0.114	−0.154	−0.503			†
Temperature	0.009	0.251	0.341	0.422			†
Temperature‡	0.009	0.040	0.018	−0.036	21.8	3	<0.001¶
Diving depth	0.654	0.024	−0.924	−2.464			†
Diving depth‡	0.361	0.194	−0.122	−0.755			†
sin(day time): distance to coast	0.511	−0.062	−0.597	−1.177	108.4	12	<0.001#
sin(day time): distance to coast‡	0.195	−0.039	−0.186	−0.418			
cos(day time): distance to coast	0.253	0.275	−0.001	−0.137			
cos(day time): distance to coast‡	0.062	0.152	0.127	0.048			
sin(day time): Diving depth	0.147	−0.050	−0.232	−0.354	323.2	12	<0.001||
sin(day time): Diving depth‡	0.052	−0.040	−0.095	−0.043			
cos(day time): Diving depth	0.032	0.082	−0.143	−0.459			
cos(day time): Diving depth‡	0.009	−0.230	−0.245	−0.223			
Autocorrelation term	0.633						

† Significance test not indicated because it is not meaningful for a term involved in a significant interaction or also occurring squared.

‡ Tests based on model with non-significant two-way interactions removed (excluded interactions: species and chlorophyll *a*: $\chi^2 = 1.63$, $df = 3$, $P = 0.6516$; species and bathymetric depth squared: $\chi^2 = 0.38$, $df = 3$, $P = 0.9446$).

§ Estimated coefficients are the same for all four species.

¶ Test statistics refer to the overall effect the interaction between species and temperature (squared and unsquared).

Test statistics refer to the overall effect of the interaction between species, daytime and distance to the coast (squared and unsquared).

|| Test statistics refer to the overall effect of the interaction between species, daytime and diving depth (squared and unsquared).

time periods, in case these were available (630 out of 1934 combinations of grid cell and time period). In case of not a single chlorophyll *a* value being available for a cell, we interpolated it from the other cells, averaged across time periods (247 combinations of grid cell and time period). Interpolation was done with R (R Development Core Team 2009) using the function "interp" with spline interpolation provided by the package "akima" (Akima et al. 2006).

Temperature Data

We obtained temperature and dive depth (pressure data) from the loggers attached to the birds. However, GPS data were stored separately from temperature and depth data. Thus we had to combine both data sets. In a first step, we deleted all data sampled during handling of birds and logger transportation. We then determined for each temperature/pressure data point the GPS position obtained simultaneously. If this position was not available (e.g., during dive), we determined the last GPS position prior to the data point as well as the next succeeding it. This revealed for each temperature/pressure data point either one or two GPS positions. In the latter case, the mean position was calculated. We deleted the temperature/pressure data point in case the two GPS positions were more than 1,000 meters apart or taken at intervals of more than 15 min. Temperature data points were first assigned to a geographical grid cell (see above). Within each grid cell, we binned depth using a bin width of 9 meters (with the first bin beginning at 1 m depth). Furthermore, we binned these data also with regard to time using a bin width of 1 hour. This resulted in temperature values recorded for cubes of 1 min edge length and 9 meters depth, separately for each hour (29,866 combinations of cube and time). We summarized temperature values per cube and hour using the median.

Table A3. Estimated coefficients from the model comparing the diving behavior of two colonies of Rockhopper Penguins at New Island. Indicated are estimates for main effects and significant interactions derived from a GLMM.

Effect	North End colony	Settlement colony	χ^2	*df*	*P*
Intercept	4.176	4.165			†
sin(day time)	−0.253	0.002			†
cos(day time)	−0.313	−0.716			†
Chlorophyll *a*	0.006		3.5	1	0.062‡
Distance to coast	0.140	0.362			†
Distance to coast‡	−0.092	0.114			†
Temperature	0.015	0.007	3.6	1	0.058
Temperature‡	−0.008		4.2	1	0.041‡
Diving depth	−0.461	−0.723			†
Diving depth‡	−0.053	−0.305			†
sin(day time): distance to coast	−0.037	−0.195	10.3	2	0.006§
sin(day time): distance to coast‡	−0.042	−0.070			
cos(day time): distance to coast	0.245	0.520			
cos(day time): distance to coast‡	−0.109	0.251			
sin(day time): Diving depth	0.009	−0.126	28.0	6	<0.001¶
sin(day time): Diving depth‡	0.139	−0.057			
cos(day time): Diving depth	−0.175	−0.359			
cos(day time): Diving depth‡	0.094	−0.039			
Autocorrelation term	0.514				

† Significance test not indicated because it is not meaningful for a term involved in a significant interaction or also occurring squared.

‡ Indicated estimates and test statistics are derived from a model with non-significant interactions removed (these were colony and temperature squared: $\chi^2 = 0.0012$, $df = 1$, $P = 0.9725$; and colony and chlorophyll *a*: $\chi^2 = 0.2017$, $df = 1$, $P = 0.6533$); all other estimates and test statistics are derived from the full model.

§ Test statistics refer to the overall effect of the interaction between colony, daytime and distance to the coast (squared and unsquared).

¶ Test statistics refer to the overall effect of the interaction between colony, daytime and diving depth (squared and unsquared).

Behavioral Data

For each of the cubes defined above we also determined the number of seconds an individual bird was in it as the number of data points (abbreviated as 'NObs' in the model formula below) in the temperature/pressure data. We took this measure as the response variable in subsequent statistical analyses.

Modeling Spatial and Temporal Segregation

To analyze the data we used a General Linear Mixed Model (GLMM; Faraway 2006, Baayen 2008). GLMMs allow for testing several (continuous and categorical) predictor variables while controlling for random effects (due to e.g., different subjects). Into the GLMM we included the following variables as fixed effects: species (as a dummy coded categorical predictor variable) as well as time of day (see below), chlorophyll *a* concentration, bathymetric depth, depth of the cube, distance to coast and temperature (of the cube) as continuous predictor variables ('covariates'). To account for non-linear effects of bathymetric depth, depth of the cube, distance to coast and temperature we also included their squares into the model. To account for effects of covariates being potentially different between species we also included into the model the interactions between species, on the one hand, and time of day, bathymetric depth (squared and unsquared), depth of the cube (squared and unsquared), distance to coast (squared and unsquared) temperature (squared and unsquared), and chlorophyll *a* concentration, on the other hand. Finally, we included the three-way interaction between species, distance to coast (squared and unsquared) and time of day and that between species, depth of cube (squared and unsquared) and time of day into the model, to allow for distance and depth preferences of species to differentially vary with the daytime. Finally, we included the two-way interactions between time of day, on the one hand, and distance to coast (squared and unsquared) as well as depth of cube (squared and unsquared)

Table A4. Estimated coefficients from the model comparing the diving behavior of two colonies of Magellanic Penguins. Indicated are estimates for main effects and significant interactions derived from a GLMM

Effect	Air strip colony	Prion area colony	χ^2	*df*	*P*
Intercept	3.873	3.961			†
sin(day time)	0.084	0.038			†
cos(day time)	0.082	0.071			†
Chlorophyll *a*	0.020		2.1	1	0.147‡,§
Distance to coast	0.055	−0.022			†
Distance to coast‡	0.013	−0.060			†
Temperature	0.119	0.034			†
Temperature‡	−0.010		3.0	1	0.081‡,§
Diving depth	−0.359	−0.214			†
Diving depth‡	−0.005	0.070	5.6	1	0.018‡
sin(day time): distance to coast	−0.014	−0.095	5.4	2	0.066‡,¶
cos(day time): distance to coast	−0.010	0.022			
sin(day time): distance to coast‡	0.020		7.7	2	0.021‡,#
cos(day time): distance to coast‡	0.025				
sin(day time): diving depth	−0.006	−0.052	6.7	2	0.034‡,||
cos(day time): diving depth	−0.186	−0.132			
Autocorrelation term	0.656				

† Significance test not indicated because it is not meaningful for a term involved in a significant interaction or also occurring squared.

‡ Test statistics and estimates derived from model not including non-significant interactions which were those between colony, daytime and cube depth squared ($\chi^2 = 1.23$, $df = 2$, $P = 0.541$), between colony daytime, and distance to coast squared ($\chi^2 = 0.77$, $df = 2$, $P = 0.681$), between, colony, and temperature squared ($\chi^2 = 0.52$, $df = 1$, $P = 0.469$), and between colony and chlorophyll *a* ($\chi^2 = 0.29$, $df = 1$, $P = 0.591$).

§ Estimated coefficients are the same for both colonies because the interaction between colony and the respective term was not significant and excluded.

¶ Test statistics refer to the overall effect of the interaction between colony, daytime and distance to the coast.

Test statistics refer to the overall effect of the interaction between daytime and squared distance to the coast; estimates are the same for both colonies (since the interaction was not-significant and excluded).

|| Test statistics refer to the overall effect of the interaction between colony, daytime and diving depth.

into the model to achieve valid estimation of the effects of the two three-way interactions included.

Hence, the full model with regard to the fixed effects and their interactions was NObs ~ species + DayTime + BathymDepth + BathymDepth^2 + CubeDepth + CubeDepth^2 + DistCoast + DistCoast^2 + Temp + Temp^2 + Chloroph + species × DayTime + species × BathymDepth + species × BathymDepth^2 + species × CubeDepth + species × CubeDepth^2 + species × Temp + species × Temp^2 + species × Chloroph + species × DistCoast^2 × DayTime + species × DistCoast^2 × DayTime + DistCoast × DayTime + DistCoast^2 × DayTime + species × CubeDepth × DayTime + species × CubeDepth^2 × DayTime + CubeDepth × DayTime + CubeDepth^2 × DayTime

In addition to these fixed effects, we included the individual bird as a random effect and also an autocorrelation term (see below). To account for potential individual differences with regard to preferred distances to the coast, daytimes for foraging trips as well as cube and bathymetric depths we also included random slopes for these effects (and their squares except for daytime) into the model (Baayen 2008, Schielzeth and Forstmeier 2009). These random slopes were required because removal of any of the squared terms from them let to a highly significant decrease in model fit (likelihood ratio tests: all $\chi^2 > 71$, all $df = 9$, all $P < 0.001$), as did removal of daytime ($\chi^2 > 308$, $df = 17$, $P < 0.001$).

Time of day actually represents a circular variable (with zero following 23 hs) and, hence, we first transformed the hour to values ranging from zero to 2 × Pi, and then included the sine and cosine of the derived variable as predictor variables into the model (allowing to model daily periodicity with a peak at any time). Hence, 'DayTime' in the above model actually represents two variables. Since the response variable (number of seconds an individual bird was in a cube) was highly right skewed, we log-transformed it revealing an almost normal distribution.

In addition, we squareroot transformed distance to the coast and log transformed chlorophyll *a* concentration and cube depth to achieve

Table A5. Estimated coefficients from the model comparing the diving behavior of two colonies of Gentoo Penguins at New Island. Indicated are estimates for main effects and significant interactions derived from a GLMM.

Effect	North End colony	South End colony	χ^2	*df*	*P*
Intercept	3.532	2.283			†
sin(day time)	−0.077	0.589			†
cos(day time)	0.314	−0.265			†
Chlorophyll *a*	−0.015	0.043	4.9	1	0.028
Distance to coast	0.079	0.015			†
Distance to coast‡	0.113	0.245			†
Temperature	0.330	0.176			†
Temperature‡	0.017	0.061	3.4	1	0.063
Diving depth	0.426	0.035			†
Diving depth‡	0.262	0.124	2.9	1	0.090
sin(day time): distance to coast	−0.176	−0.033	42.6	2	<0.001‡
sin(day time): distance to coast‡	0.060	−0.115			
cos(day time): distance to coast	0.231	0.248			
cos(day time): distance to coast‡	0.190	0.007			
sin(day time): Diving depth	−0.100		3.8	2	0.148§
cos(day time): Diving depth	−0.122				
sin(day time): Diving depth‡	−0.050		3.3	2	0.190
cos(day time): Diving depth‡	−0.258				
Autocorrelation term	0.707				

† Significance test not indicated because it is not meaningful for a term involved in a significant interaction or also occurring squared.

‡ Test statistics refer to the overall effect of the interaction between colony and distance to the coast.

§ Test statistics refer to the overall effect of the interaction between colony, daytime and diving depth (interaction between species, daytime and squared diving depth not included into the model).

more or less symmetric distributions of these predictor variables. Prior to fitting the model we z-transformed all continuous predictor variables (i.e., chlorophyll *a* concentration, bathymetric depth, depth of the cube, distance to coast and temperature) such that their mean equaled zero and their standard deviation equaled one (Aiken and West 1991, Schielzeth 2010).

We also analyzed whether the effects of ecological variables on diving behavior differed between colonies. We ran these analyses separately for the three different penguin species (shags were not analyzed because they all bred in a single colony). The principle procedure and model implemented was exactly the same as in the previous analysis (see above and below) with the following exceptions: the factor species was replaced by the factor colony and all interactions with species were replaced by the respective interaction with colony.

In addition we excluded bathymetric depth from these analyses, since it was highly correlated with distance to coast in all sub-datasets (Pearsons's rho, Rockhopper penguins: $r_P = -0.89$, $n = 6234$, $P < 0.01$; Magellanic penguins: $r_P = -0.63$, $n = 11551$, $P < 0.001$; Gentoo penguins: $r_P = -0.81$, $n = 10423$, $P < 0.001$). Prior to testing we also determined (using likelihood ratio tests; see below) which random slopes were required to be controlled for. Based on this we removed random slopes of cube depth squared and daytime from the rockhopper model and distance to coast from the Magellanic penguin model (all $P > 0.5$), but retained all other random slopes (all $P < 0.05$).

Accounting For Spatio-temporal Autocorrelation

The behavior of the birds studied (i.e., frequency of observation per cell) was likely to be driven also by factors other than those investigated, leading to non-independence of data, i.e., spatio-temporal autocorrelation, potentially devaluating the statistical analysis. Hence, we explicitly incorporated spatio-temporal autocorrelation into the statistical analysis. Including autocorrelation in a valid statistical model is a preferable way to deal with it rather than to attempt to eliminate it by restricting data prior to analysis (Griffith 1992, de Solla et al. 1999). We did this by first running an ordinary model (without considering autocorrelation) and deriving the residuals from it. Then we averaged, for

each cube separately, the residuals of all neighboring cubes, with neighboring cubes being defined as those eight cubes being in the same depth bin in directly neighboring grid cells, those 16 cubes being directly above or below them, the cell itself and the two cells being directly above and below it. However, we included the cell itself only for hours other than the one actually considered. When averaging these residuals we additionally accounted for time by weighting the contribution of residuals by the time lag between the observation for which the neighboring residuals should be averaged and the hours when residuals were derived. Hence, the autocorrelation term for the ith cell at moment k was $ac_{ij} = \Sigma\ (res_{ijkl} \times w_{ijkl}) / \Sigma\ (w_{ikjl})$, with ac_{ij} being the autocorrelation term for the ith cube at hour j, res_{ikjl} being the residual of the kth neighboring cube of cube i at hour l. We defined the weight w_{ijkl} to follow a Gaussian function with

$$w_{ijkl} = \frac{e^{-0.5*((j-l)/\sigma)^2}}{\sigma\sqrt{2\pi}}$$

with w_{ijkl} = weight of the kth residual in the calculation of the ith autocorrelation term, with $\sigma = 3$ and hours j and l at cubes i and k. This leads to the weight being essentially zero (<0.0001) at lags equaling twelve or more hours. The resulting autocorrelation term we included as an additional fixed effect into the model. It was calculated separately for each subject.

Statistical Testing

Significance testing in a GLMM is currently still under development and no generally agreed and accepted standard seems to exist (Bolker et al. 2008). We generally tested significance using Likelihood ratio tests comparing the fit (deviance) of a full with the fit of a reduced model (Faraway 2006). For this we estimated model coefficients using Restricted Maximum Likelihood. Since both the number of subjects and particularly the total number of observations are large, we believe that P-values derived can be trusted. We first established the significance of the full model comprising all effects, squared terms and interactions as well as the autocorrelation term and individual (see above) by comparing it with a reduced model comprising only the autocorrelation term (as derived from the full model) and the random effects (including the random slopes). In case of testing the effect of colony on data comprising only a single species, we compared the fit of the full model with the fit of a model excluding colony and all interactions with it. In the next step we tested the highest order interactions by comparing a model including an interaction with a model excluding it. For all these reduced models the autocorrelation term was that derived from the full model. In case a covariate was included unsquared and squared we tested the interaction of the squared covariate while retaining the interaction with the unsquared covariate. Following this we removed all non-significant interactions and built a new full model for testing interactions and/or main effects being part of non-significant interactions. We tested whether random slopes were significant comparing the fit of a full model and the fit of a corresponding reduced model not comprising the random slope using likelihood ratio tests as well.

Further Considerations

We calculated GLMMs using the function 'lmer' provided by the package 'lme4' (Bates et al. 2008; version 0.999375-28) for R (R Development Core Team 2009; version 2.8.1) using a Gaussian family and an identity link-function. We calculated likelihood ratio tests using the R-function 'anova' (with the argument 'test' set to 'Chisq'). To check the model assumptions (normality and homogeneity of residual variance) we first visually inspected plots of residuals against predicted values. These suggested a moderate deviation from the assumption of homogeneous error variance (with the variance slightly increasing with the predicted value). In addition we correlated absolute residuals with predicted values. This revealed a small though highly significant correlation (*Pearson's rho* = 0.17, n = 30687). However, since the correlation coefficient was actually rather small and the data were already log-transformed (and other transformations like the squareroot were less successful) we kept the model and are confident that the moderate deviation from the assumption does not severely affect its validity, particularly since the sample size was rather large. To check for collinearity, we determined Variance Inflation

Factors (VIF, Quinn and Keough 2002, Field 2005) for each predictor variable (with species being included as a set of three dummy coded variables) using a self-written procedure based on a standard linear model excluding random effects, interactions and squared terms. For the model including all species simultaneously this revealed a largest VIF equaling 4.41 and an average VIF equaling 1.96 and, hence, did not suggest a serious collinearity problem to exist. Nevertheless, we ran also a model not including distance to cost and one not including bathymetric depth, because particularly these two variables were quite correlated. This did not have a strong effect on the estimates revealed for distance to cost and bathymetric depth and the interactions with them, respectively. For the models of the individual species the largest and average VIF equaled 1.63 and 1.33 for Rockhopper, 1.67 and 1.24 for Magellanic 2.10 and 1.46 for Gentoo penguins, respectively (VIF determined after this exclusion of bathymetric depths).

Appendix B

Animation showing space and time segregation of Imperial Shags, Rockhopper, Magellanic, and Gentoo penguins, at New Island, during two contiguous days of the breeding season 2008–2009. Species are color-coded. Each circle denotes a bird. The "tail" of the circles shows the position of the bird during the previous 30 minutes. Empty circles denote diving events. Time of the day is indicated (top left). The contour of the islands surrounding New Island is shown. [doi:10.1890/ES10-00103.2]

Appendix C

Animation showing space and time segregation of two colonies of Rockhopper Penguins, at New Island, during two contiguous days of the breeding season 2008–2009. Colonies are color-coded. Each circle denotes a bird. The "tail" of the circles shows the position of the bird during the previous 30 minutes. Empty circles denote diving events. Time of the day is indicated (top left). The contour of the islands surrounding New Island is shown. [doi:10.1890/ES10-00103.3]

Appendix D

Animation showing space and time segregation of two colonies of Magellanic Penguins, at New Island, during two contiguous days of the breeding season 2008–2009. Colonies are color-coded. Each circle denotes a bird. The "tail" of the circles shows the position of the bird during the previous 30 minutes. Empty circles denote diving events. Time of the day is indicated (top left). The contour of the islands surrounding New Island is shown. [doi:10.1890/ES10-00103.4]

Appendix E

Animation showing space and time segregation of two colonies of Gentoo Penguins, at New Island, during two contiguous days of the breeding season 2008–2009. Colonies are color-coded. Each circle denotes a bird. The "tail" of the circles shows the position of the bird during the previous 30 minutes. Empty circles denote diving events. Time of the day is indicated (top left). The contour of the islands surrounding New Island is shown. [doi:10.1890/ES10-00103.5]

Appendix F

Animation showing space and time segregation of female and male Imperial Shags, at New Island, during two contiguous days of the breeding season 2008–2009. Gender is color-coded. Each circle denotes a bird. The "tail" of the circles shows the position of the bird during the previous 30 minutes. Empty circles denote diving events. Time of the day is indicated (top left). The contour of the islands surrounding New Island is shown. [doi:10.1890/ES10-00103.6]

Appendix G

Three-dimensional animation showing space and time segregation of Rockhopper, Magellanic, and Gentoo penguins, at New Island, during two contiguous days of the breeding season 2008–2009. Species are color-coded. Dive depth profiles are shown for each bird as the foraging trip progresses. Time of the day is indicated (top left). The contour of the islands surrounding New Island is shown. [doi:10.1890/ES10-00103.7]