Trophic Interactions in South West Atlantic Seabird Colonies

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Abstract

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Seabirds act as both predators and as prey. In the marine environment, seabird foraging patterns can reflect ocean conditions. On land, their breeding success reflects constraints placed on seabirds by central-place foraging, as well as aspects of the evolution of coloniality.

In Chapter 1, I investigate whether differences in marine productivity influence foraging and reproductive success at two Magellanic Penguin (*Spheniscus magellanicus*) colonies—New Island (Falkland Islands / Islas Malvinas) and Punta Tombo (Argentina). Magellanic Penguins reflected ocean productivity in both their foraging and breeding patterns. During the late chick stage, ocean productivity was higher at New Island, and foraging areas were smaller. Accordingly, New Island penguins had shorter foraging trips and higher reproductive output. Plasticity in their natural history allows seabirds to balance self-maintenance, foraging and reproductive success under variable ocean conditions.

In Chapter 2, I explore the causes and consequences of albatross chicks off their nests at Steeple Jason Island, Falkland Islands. In Black-browed Albatross (*Thalassarche melanophrys*), chicks that prematurely end up outside their nests typically die. The number of chicks off their nests increased with time, and correlated negatively with adult nest attendance. Off-nest chicks on the colony edge were more likely to be found adjacent to other off-nest chicks. Off-nest chicks with injuries or feathers matted with stomach oil regurgitate occurred primarily on the colony edge and in clusters. These patterns were most consistent with predation or attempted predation by Southern Giant Petrels (*Macronectes giganteus*).

In Chapter 3, I examine resource use overlap between two avian predators at a mixed seabird colony in the Falkland Islands. Striated Caracaras (*Phalcoboenus australis*) and Falkland Skuas (*Stercorarius antarctica antarctica*) are locally on Steeple Jason Island. Both predators ate the same prey types—eggs and chicks of albatross and of penguins. Food was not limiting during the breeding season, and interspecific fights were rare. Both species foraged in similar colony locations, times of day, and stages of the season. Any proportional preferences in their prey preferences appear to derive from behavioral or morphological differences between the two predators.

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Chapter 1

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Chapters 2 & 3

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Dedication

For my mom, who never gives up on me, even though she probably should. And for Angel and Buddy, the reasons I get out of bed every morning.

Chapter 1: Plasticity in foraging and reproduction of two South Atlantic Magellanic Penguin colonies reflects ocean productivity

INTRODUCTION

Behavioral or reproductive flexibility may buffer individuals against the effects of changing environments (Levins 1968, Huey et al. 2003), and often occurs in species with life history traits of high adult survival, longevity, delayed reproduction, slow development, and low fecundity (Stearns 1992). Seabirds—as a group—exhibit these traits and theory predicts that when resources are limited, breeding adults should favor self-maintenance instead of reproduction because they have a high probability of reproducing in the future (Stearns 1989, Ricklefs 1990). However, in locations or years when resources are abundant, seabirds are expected to maximize their reproductive output without compromising their own survival (Suryan et al. 2009). Studies that can explicitly link resource availability, foraging behavior, and breeding success are important to fully establish these predicted relationships.

Seabird reproductive success depends on resources available during the breeding season (Lack 1968, Cury et al. 2011), and reflects variation in ocean productivity (Ashmole 1963). Because their at-sea feeding activity is constrained by their need to return to the nest or colony to provision chicks (Shealer 2001), seabirds are considered ‘central-place foragers’ (Costa 1991). Central-place foraging theory (Orians and Pearson 1979) provides a robust framework to evaluate seabird response to variable food availability. When ocean conditions are favorable (e.g. higher food density at close proximity), this theory predicts that adults will spend more time at the colony and have high survivorship, and that their chicks will grow quickly and have high fledging rates (Cairns 1987).

Empirical evidence supporting central place foraging theory shows many seabird species accurately reflect marine productivity directly through plasticity in diet, behavior (e.g. time budgets), and foraging effort (Montevecchi 1993, Piatt et al. 2007, Parsons et al. 2008, Einoder 2009). Seabirds also respond indirectly to variation in ocean conditions through flexibility in their breeding phenology, chick growth rates, and reproductive output (Furness and Camphuysen 1997; see also Harding et al. 2006). However, because most long-term studies linking environmental conditions to seabird functional responses have been focused at a single breeding location, they are unable to capture the full extent of the plasticity that may occur in a species over space and time (Grémillet and Charmantier 2010).

We examined foraging and breeding plasticity of Magellanic Penguins (*Spheniscus magellanicus*) in response to spatial and temporal variation in ocean conditions. Previous studies on this species along the Argentine coast found that variation in foraging trip patterns among six colonies correlated with indices of local ocean productivity. Penguins from northern colonies with higher sea surface temperatures and lower chlorophyll *a* values (indicating lower productivity) made significantly longer trips than did birds in more southerly colonies with lower sea surface temperatures and higher chlorophyll *a* values (Boersma et al. 2009). In another study of seasonal and latitudinal differences among six south Atlantic Magellanic colonies (five mainland, plus the Falkland Islands), birds from the center of the geographic colonies traveled further during incubation, likely in response to lower local food availability (Wilson et al. 2005).

Additional tracking studies on breeding Magellanic Penguins report within-colony variation in reproductive success between years, related to annual average foraging trip distance and duration. At Punta Tombo, Argentina, trip duration correlated strongly with distance to the foraging area (Boersma et al. 2007). Multiple years of tracking at this colony showed the annual probability of fledging chicks decreased as a function of increasing foraging trip distance, and longer trips equated with decreased average reproductive success through reduced chick provisioning rates (Boersma and Rebstock 2009). Within the Falkland Islands, penguins making shorter trips had higher apparent reproductive success (Boersma et al. 2002, Putz et al. 2002, Otley et al. 2004).

We investigated whether foraging and reproductive success reflect ocean productivity at two Magellanic Penguin colonies—New Island (Falkland Islands / Islas Malvinas) and Punta Tombo (Argentina). Limited regional estimates of chlorophyll concentrations suggest that ocean productivity at New Island is about 30-50% higher than at Punta Tombo (Moreno et al. 2012). Using central-place foraging theory as a conceptual framework, we predicted that higher local productivity at New Island would correlate with: (1) shorter trips (both distance and duration) and proportionately more foraging relative to transit; and (2) heavier chicks at fledging, higher fledging rates, and greater nest attendance. Because egg volumes may influence chick growth and fledging (O'Connor 1984, Williams 1994), and because adult body size or condition may contribute to variation in egg size and chick survival (Reid and Boersma 1990), we examined these additional variables as potential alternate drivers of reproductive or foraging patterns. Punta Tombo and New Island are the only Magellanic Penguin sites having both satellite tracking and concurrent breeding data. Thus, these datasets enable us to test the plasticity of foraging and breeding patterns—within species, between locations—resulting from variation in ocean productivity.

METHODS

Study species and locations

We satellite tracked Magellanic Penguins and followed their nesting success during five breeding seasons (1997-2001) at two locations: New Island, Falkland Islands (51˚42'S, 61˚17'W) and Punta Tombo, Argentina (44˚3'S, 65˚13'W) (Fig. 1.1). New Island and Punta Tombo are at the south-eastern and north-western edges (respectively) of the south-west Atlantic Patagonian continental shelf and experience different oceanographic regimes. The marine environment surrounding Punta Tombo features seasonally and annually variable tidal mixing fronts (Acha et al. 2004) with prominent spring and fall phytoplankton blooms (Romero et al. 2006) and a narrow band of tidal coastal front adjacent to the colony (Piola and Rivas 1997). The Falkland Islands are strongly influenced by the Falklands Current, a branch of the Antarctic Circumpolar Current that splits around the islands and flows northward (Piola and Rivas 1997). In addition, a clockwise gyre to the west/south-west introduces nutrients to the system via upwelling, contributing to summer phytoplankton blooms (Garcia et al. 2008). Like Punta Tombo, the area surrounding New Island features a tidal coastal front (Rivas and Dell'Arciprete 2000).

Magellanic Penguins breed during the Austral summer in colonies along the coastlines of Argentina, Chile, and the Falklands archipelago (Williams 1995). The breeding season comprises three stages: (1) incubation, when adults are on eggs; (2) early chick (also called the brood/guard stage), when adults continuously attend the nest to brood and protect young chicks; and (3) late chick, when parents no longer continuously attend chicks, but before chicks are old enough to fledge (Boersma et al. *in press*). Females lay two eggs per year, and both members of a pair incubate eggs and rear chicks (Boersma et al. 1990). Following molt (which occurs after the breeding season), birds from Punta Tombo and the Falkland Islands migrate northward along the South American continental shelf as far as Brazil (Ruoppolo et al. 2012), a journey of over 800 km (Stokes and Boersma 1998, Garcia-Borboroglu et al. 2010), and 1800 km, respectively (Pütz et al. 2000, Pütz et al. 2007). With 200,000 breeding pairs, Punta Tombo is the world's largest colony of this species, although this population is declining (22% decrease between 1987 and 2006; Boersma 2008). Reliable estimates do not exist for the Falkland's Magellanic population, but the archipelago may have about 100,000 breeding pairs (range 76,000-142,000; Woods and Woods 1997). A 2002 census of the southern half of New Island found approximately 2000 adult birds and 220 active nests in late January (A. N. Van Buren unpubl. data).

Device deployment and location data processing

To track penguins over their foraging journeys, we attached (with epoxy) Platform Transmitter Terminal (PTT) 'satellite' tracking devices (see Boersma et al. 2002) to the lower backs of 26 birds (n = 6 females, n = 20 males) at New Island, and 121 birds (n = 56 females, n = 65 males) at Punta Tombo. The 90-gram devices comprised model ST-10 electronic components (Telonics, Mesa, Arizona, USA) encased within waterproof epoxy resin (Sirtrack Ltd., Havelock North, New Zealand), and transmitted locations every 45 s. At Punta Tombo, tracked birds were marked with permanent numbered stainless-steel flipper bands (Lambournes-Porzana Ltd., East Sussex, UK) and their mates with numbered mouse eartags (#1005–3, 2 × 10 mm; National Band and Tag Company, Newport, Kentucky, USA) attached to the outer webbing of the left foot (Boersma and Rebstock 2010). At New Island, both tracked birds and mates were marked (as above) with numbered mouse eartags. We checked nests for eggs/chicks and adult attendance 1 to 3 times daily during PTT deployment, and every 2 to 10 days before or after deployment. Using dial calipers, we measured egg maximum length and width. Every 5-10 days we weighed chicks (hand-held spring scales) and measured their bill length, bill depth, flipper length and foot length (dial calipers or plastic metric ruler). We weighed and measured tracked birds when we attached the transmitter.

Penguin at-sea locations were determined through the Argos satellite network (Service Argos, Largo, Maryland, USA). Using location classes 0-3 (≥ 4 messages; Argos 2006), we filtered data (Matlab R2010a, MathWorks) to remove unreasonable locations, based on point-to-point distances, times, and traveling speeds (see Boersma and Rebstock 2009). We assigned consecutive trip numbers to individual birds, where each assigned trip required at least 3 locations over 5 km from the colony. For birds tracked in multiple years, we used data only from the first tracking year. We excluded incomplete trips, where departure or arrival times could not be confirmed with nest checks. Because we had actual lay dates for Punta Tombo birds only, we excluded the first incubation trip (see below) for all birds.

We coded trips by breeding season stage (incubation, early chick, or late chick) based on the type and age of nest contents on the date a tracked bird departed on a foraging trip. We designated trips as ‘incubation’ after egg-laying but before hatching, and as ‘early chick’ after at least one egg hatched, up to 29 days chick age. At Punta Tombo, where parents attend chicks until age 29+/-4 days (Boersma et al. 1990), we coded trips as ‘late chick’ ≥ 30 days after the first chick hatched (when actual hatch date was known ± 1 day), or ≥ 30 days after the median hatch date (when actual hatch date was not known). Median hatch date for tracked birds at Punta Tombo was 22 November (range 14 November to 6 December, n = 78), with late chick beginning on 22 December. Because New Island parents rarely left chicks unattended even during the late chick period (median % attendance for January: New Island 93% of nest checks, n = 25 nests; Punta Tombo 25% of nest checks, n = 64 nests; $p < 0.0001$, $\chi^2 = 467.59$, df = 1), we used the 21-day brood/guard period found for another Falkland Islands Magellanic Penguin colony, Volunteer Point (Otley et al. 2004). For New Island, the median hatch date was 29 November (range 22 November to 10 December, n=9), with late chick beginning 22 days post-hatching, or on 22 December.

Foraging trip patterns

To compare foraging trip patterns between colonies and stages of the breeding season, we used General Linear Mixed Models (GLMMs) on (1) average trip distance (km), (2) maximum trip distance (km), and (3) average trip duration (days) for each bird. Data were positive (right) skewed, so we transformed data to natural logarithms (ln). All models included Colony, Sex, Stage, and Year as fixed factors. For average trip duration and average trip distance, multiple trips (nested within bird) was included as a random factor; maximum trip distance comprised a single trip per bird.

We used two approaches to characterize relative amount of transit versus foraging per trip, the ‘meander ratio’ and the number of locations by proportional distance from the colony (see Boersma et al. 2009). For each trip, the meander ratio is the straight-line maximum trip distance (out and back) as a proportion of the summed point-to-point distances; higher values represent a straighter track. Because low number of locations (per trip) distorts the accuracy of the meander ratio metric (Seuront et al. 2004), we excluded trips with fewer than nine locations (the maximum that still enabled running the full model). We arcsine square-root transformed proportions and used a GLMM that included Colony, Sex, Stage, and Year as fixed factors, and multiple trips (nested within bird) as a random factor.

To identify the proportional distance at which foraging begins, we adapted the method from Boersma et al. (2009), which assumes that for a given foraging trip, higher location densities reflect greater foraging activity. For each at-sea location (within trip) we calculated its linear distance from the colony as a proportion of the maximum distance for that trip, and plotted the proportional distances (frequency histograms with equal size bins). Under the null hypothesis (e.g. foraging occurs throughout the trip), the expected frequencies will be uniformly distributed. Bins in which the observed frequencies exceed those expected represent the proportional distances that correspond to foraging. We used the median number of at-sea locations per trip to set the bin size and then qualitatively compared New Island to Punta Tombo.

Reproductive output

To compare chick mass between New Island and Punta Tombo, we used nests of tracked birds that hatched two chicks, and fledged at least one chick. We used established fledging criteria for Magellanic Penguins: chick weight greater than 1800 g when last seen, after January 10 (Boersma et al. 1990). We log-transformed individual chick weights at fledging and compared New Island to Punta Tombo using an ANOVA on Colony, Sex, Year, and Number Fledged (i.e. brood size at fledging), plus two-way interactions. For nests that fledged two chicks, we used an ANOVA on Colony, Year, and Colony*Year to compare total brood weights at fledging. We used separate two-sample *t*-tests to compare (1) colony hatching dates; and (2) colony fledging dates (approximated by date last seen) for two-chick nests. Because of small sample sizes, the comparisons for hatching date and fledging date were restricted to a single factor, Colony. To evaluate reproductive output for nests that hatched two chicks, we used ordinal logistic regressions on fledging rates to compare (1) New Island to Punta Tombo by Year and Colony*Year, and (2) within-colony variation by Year.

Body size, body condition, and clutch (egg) volume

To evaluate alternate explanations for differences in foraging and breeding patterns between New Island and Punta Tombo, we examined adult size and body condition (measured when the tracking device was applied) and clutch (egg) volumes. To index adult body size, we analyzed the first principal component from measurements of bill length, bill depth, flipper length, and foot length (see Yorio and Boersma 1994, Hood et al. 1998). This component explained 76% of the variance. We compared PC1with an ANOVA on Colony, Sex, and Year, plus two-way interactions.

To compare body condition of adults from both populations, we first corrected for negative PC1 values by adding a constant (5) to all PC1 values. We then log-transformed both PC1 and mass, and regressed mass on PC1 ($\ln[\text{mass}] = 1.0421 + 0.2176*\ln[\text{PC1}+5]$, $R^2 = 0.41$) to obtain the standardized residuals (Schulte-Hostedde et al. 2005). We then used an ANOVA (Colony, Sex, Year, plus two-way interactions) to compare body condition between colonies. To calculate clutch volumes (2-egg nests only), we followed Boersma and Rebstock (2010) and computed individual egg volume as $5.5101 + 0.4837L*B^2$, summed volumes by nest, and then used a two-sample *t*-test to compare populations. Because of small sample sizes, the comparison for clutch volume was restricted to a single factor, Colony.

Ocean productivity and foraging area size

To estimate ocean productivity during the breeding season, we used January chlorophyll *a* concentrations (g m^{-3}) from SeaWiFS monthly composite 9-km grid data for all five years of the study. Chlorophyll *a* is often used as a proxy for primary production, and higher chlorophyll *a* values should correspond with greater food abundance (Behrenfeld et al. 2006). We plotted late-chick foraging locations (derived from the proportional distance analysis described above), and intersected location minimum convex polygons (ArcGIS 9.3, Esri) with the corresponding year's chlorophyll raster data to select grid cells for analysis. Because chlorophyll *a* values were positive (right) skewed, we log-transformed data, and then used a GLMM that included Colony as a fixed factor and repeated chlorophyll measures (nested within Year) as a random factor. In addition, we used the foraging location minimum convex polygons to estimate the average size of the yearly foraging areas during January. We used a Wilcoxon rank-sum test to compare New Island to Punta Tombo these late-chick stage foraging areas.

Data analysis

Unless otherwise noted, all statistical analyses were performed using Jmp (version 9.0, SAS). To evaluate whether distributions were normal, we used Shapiro-Wilk goodness of fit tests and visually inspected residuals for the most general (i.e. full) model. GLMMs comprised standard least squares (REML) with unbounded variance components. We began with a complete factorial model (single and interaction effects) and then used a backward stepwise selection process and the lowest AICc value to identify the best model (separated by 2 or more units). GLMMs and ANOVAs included post-hoc Tukey HSD or Students *t* tests to identify significant pairwise differences in means. We back-transformed means and standard errors (SE's) for reporting in results and figures, and all means or estimated marginal means (Searle et al. 1980) are given ± SE.

RESULTS

Foraging trip patterns

Average trip distance was 125% shorter at New Island (Fig. 1.2a; 21.2 ± 3.2 km, n = 27 birds, 271 trips) than at Punta Tombo (91.9 ± 11.9 km, n = 90 birds, 421 trips; $p < 0.0001$, $t_{589} = 9.94$). Within Stage, New Island trip distance was 158% shorter during incubation ($p < 0.0001$, $t_{672} = 17.70$), and 105-106% shorter during early ($p < 0.0001$, $t_{671} = 12.11$) and late chick ($p < 0.0001$, $t_{607} = 15.92$). Both colonies exhibited similar trends between stages: foraging trips were longest during incubation (61.8 ± 12.5 km, n = 33 birds, 45 trips), shortest during early chick (34.4 ± 4.5 km, n = 54 birds, 280 trips) and intermediate during late chick (40.5 ± 4.6 km, n = 57 birds, 367 trips; ANOVA $p < 0.0001$, $F_{2,652} = 14.59$). However, within colony, New Island trip distances were similar between stages, whereas Punta Tombo trip distances varied based on stage (Tukey HSD, $p < 0.05$). Trends between sexes were similar for both colonies: average trip distance for females was 14% shorter compared to males (females: 41.1 ± 5.6 km; n = 47 birds, 256 trips; males: 47.4 ± 5.8 km; n = 70 birds, 436 trips; $p < 0.02$, $t_{663} = 2.52$). Two models for average trip distance had the best fit (lowest AICc values), and included the factors Colony, Stage, and Colony*Stage, plus Sex (Table 1.1, Fig. 1.2a); Year and its interactions were not significant.

Maximum trip distance was 113% shorter at New Island (Fig. 1.2b; 39.6 ± 8.3 km, n = 37) than at Punta Tombo (143.3 ± 22.5 km, n = 107; $p < 0.0001$, $t_{136} = 11.78$). Both colonies exhibited similar trends between stages: maximum trip distances for early chick (49.4 ± 9.7 km, n = 54) were 65% shorter compared to incubation (97.3 ± 20.6 km, n = 33) and 57% shorter compared to late chick (89.0 ± 15.6 km, n = 57; ANOVA $p < 0.0001$, $F_{2,139} = 23.37$). A single model for maximum trip distance had the lowest AICc value, and included the factors Colony and Stage (Table 1.1, Fig. 1.2b); Sex and Year (plus their interactions) were not significant.

Average trip duration was 121% less at New Island (Fig. 1.2c; 0.60 ± 0.09 days, n = 27 birds, 271 trips) than at Punta Tombo (2.44 ± 0.32 days, n = 90 birds, 421 trips; $p < 0.0001$, $t_{619} = 12.76$). Within Stage, New Island trip duration was 157% less during incubation ($p < 0.0001$, $t_{685} = 7.64$), 79% less during early chick ($p < 0.0001$, $t_{480} = 6.27$), and 111% less during late chick ($p < 0.0001$, $t_{226} = 11.64$). Both colonies exhibited similar trends between stages: compared to incubation (2.32 ± 0.56 days, n = 33 birds, 45 trips), early chick was 102% less (0.75 ± 0.09 days, n = 54 birds, 280 trips) and late chick was 79% less (1.01 ± 0.09 days, n = 57 birds, 367 trips; ANOVA $p < 0.0001$, $F_{2,523} = 27.09$). However, within colony, New Island trip durations were similar between stages, whereas Punta Tombo trip durations varied based on stage (Tukey HSD, $p < 0.05$). A single model for average trip duration had the lowest AICc value, and included the factors Colony, Stage, and Colony*Stage (Table 1, Fig. 1.2c); Sex and Year (and their interactions) were not significant) .

Penguins from New Island meandered more (Fig. 1.2d; 0.60 ± 0.04, n = 27 birds, 271 trips) than birds from Punta Tombo (0.66 ± 0.03, n = 90 birds, 421 trips; $p < 0.001$, $t_{399} = 3.47$). Both colonies exhibited similar trends between stages: the meander ratio was smallest during incubation (0.54 ± 0.06, n = 33 birds, 45 trips), intermediate during late chick (0.62 ± 0.03, n = 57 birds, 367 trips), and largest during early chick (0.71 ± 0.04, n = 54 birds, 280 trips; ANOVA $p < 0.0001$, $F_{2,399} = 23.69$). A smaller proportion indicates more meandering (i.e. higher foraging relative to transit). A single model for meander ratio had the lowest AICc value, and included the factors Colony and Stage (Table 1, Fig. 1.2d); Sex and Year (and their interactions) were not significant).

The proportional distance at which foraging began was 40% of maximum trip distance for New Island, and 70% for Punta Tombo (Fig. 1.3). The median number of locations per trip was 11. The mean number of locations per trip for New Island was 9.3 ± 0.5, and for Punta Tombo the mean was 29.9 ± 1.9.

Reproductive output

Chicks fledging at New Island (3663 ± 541 g, n = 35) weighed 36% more than chicks at Punta Tombo (2536 ± 103 g, n = 58; ANOVA $p < 0.0001$, $F_{6,86} = 23.35$; Colony $p < 0.0001$; Sex, Year, Number Fledged, and interactions were not significant). For nests fledging two chicks, the mean total brood weight at fledging (last check) was 38% greater at New Island (7381 ± 150 g, n = 17 nests) than at Punta Tombo (5002 ± 186 g, n = 10 nests; ANOVA $p < 0.0001$, $F_{5,21} = 22.19$; Colony $p < 0.0001$, Year and Colony*Year were not significant). On average, New Island chicks hatched 7 days later (November 29 ± 2.3 days, n = 9) than did Punta Tombo chicks (November 21 ± 0.6 days, n = 78; $p < 0.05$, $t_9 = 3.14$). New Island chicks fledged 7 days earlier (January 29 ± 1.3 days, n = 34) than did Punta Tombo chicks (February 5 ± 1.9 days, n = 20; $p < 0.005$, $t_{37} = 3.04$).

Reproductive success of pairs (nests of tracked birds) was much higher at New Island than at Punta Tombo, and this pattern held at all stages of the breeding season and in all years. New Island birds lost fewer eggs than did Punta Tombo birds (4%, n = 52; 13%, n = 225, respectively; $p < 0.05$, $\chi^2 = 3.72$, df = 1). Similarly, New Island birds lost fewer chicks than did Punta Tombo birds (2%, n = 50; 69%, n = 192, respectively; $p < 0.0001$, $\chi^2 = 72.65$, df = 1). For pairs that hatched two chicks, their average fledging success was 98 ± 2% at New Island (n = 24 nests) compared to 31 ± 4% at Punta Tombo (n = 87 nests; $p < 0.0001$, $\chi^2 = 93.83$, df = 5; Colony $p < 0.0001$, Colony*Year $p < 0.001$). New Island fledging rates were similar between years ($p = 0.57$, $\chi^2 = 2.91$, df = 4); Punta Tombo fledging rates were significantly different among years ($p < 0.001$, $\chi^2 = 21.62$, df = 4). No nests at New Island were abandoned (by tracked birds or their mates) during the breeding season (n=26 nests). In 9.5% of nests at Punta Tombo (11 of 116), either the tracked bird or the mate (8 females and 3 males) abandoned the nest ($p = 0.10$, $\chi^2 = 2.67$, df = 1). None of these birds were seen again during the current season, and they were presumed to have died as none were seen in any subsequent breeding season.

Body size, body condition, and clutch (egg) volume

Body size index (PC1) was similar between colonies; however, mean female size index was significantly smaller (-1.72 ± 0.19, n = 62) than for males (1.27 ± 0.12, n = 84) at both colonies (ANOVA $p < 0.0001$, $F_{15,130} = 28.94$; Sex $p < 0.0001$; Colony, Year, and interactions were not significant). New Island and Punta Tombo penguins had similar body condition, regardless of Colony, Sex, or Year (ANOVA $p = 0.11$, $F_{15,130} = 1.51$). Clutch (egg) volumes were also similar between colonies (New Island: 227.7 ± 7.5 cm^3, n = 19; Punta Tombo: 234.8 ±

1.9 cm^3, n = 89; $p = 0.39$, $t_9 = 0.91$).

Ocean productivity and foraging area size

Average chlorophyll *a* values of foraging areas for the month of January (late chick stage) were about 24% higher at New Island (3.2 ± 0.1 g m^3, n = 5 years, 322 chlorophyll values) than at Punta Tombo (2.4 ± 0.5 g m^3, n = 5 years, 1705 chlorophyll values; ANOVA $p < 0.0001$, $F_{1,2025} = 32.55$). Both colonies exhibited significant variation among years. Geospatial analysis of at-sea locations showed that Punta Tombo penguins foraged in an area about five times larger than New Island birds (New Island: 3770 ± 1010 km^2, range 1940-7620 km^2, n = 5 years; Punta Tombo: 21470 ± 6730 km^2, range 6760-39360 km^2; n = 5 years; Wilcoxon 2-sample test, normal approximation, S=39, Z=2.29, $p<0.03$; Fig. 1.1).

DISCUSSION

Penguins at New Island travelled shorter distances on their foraging trips, and were gone for shorter periods than were penguins at Punta Tombo. Furthermore, New Island penguins spent a greater proportion of their trips actively feeding, as indicated by lower meander ratio values and proportionately more locations closer to the colony. These colony foraging patterns held at all stages of breeding but were most different during the incubation and late chick stages. In addition, foraging distance and duration were much less variable among stages at New Island than at Punta Tombo.

These differences in foraging are reflected in the breeding patterns of the two colonies.

On New Island, broods of two chicks just prior to fledging had masses that were almost double those of Punta Tombo penguins. Moreover, New Island chicks at fledging were over 35% larger than Punta Tombo chicks and were more than twice as likely to fledge. Overall, New Island penguins appear to have expended less energy in rearing more chicks than did Punta Tombo birds. In addition, fledging rates were almost 100% on New Island, but were much lower (31%) and more variable among years at Punta Tombo.

Does ocean productivity drive these colony differences in foraging and reproduction? As estimated by the SeaWiFS chlorophyll *a* values during January, ocean productivity was 24% higher overall in the area used by New Island penguins than that used by Punta Tombo birds. These values are comparable to previously published spring/summer chlorophyll *a* estimates for the Patagonian Shelf: 5-8 g m^{-3} reported north-west of the Falkland Islands, versus 1-2 g m^{-3} north-east of Punta Tombo (Rivasa et al. 2006). Although the ocean productivity differed among years at both colonies, Punta Tombo had greater inter-annual variation in chlorophyll *a* values. Furthermore, the foraging areas at Punta Tombo were about five times larger than at New Island, and the size of the areas between years was more variable. Magellanic Penguins are generalist feeders with regional diet differences (Gandini et al. 1999, Boersma et al. *in press*). Thus the foraging areas at New Island and Punta Tombo likely contain different prey types and abundance. New Island penguins eat seasonally abundant non-migratory prey such as squid and krill (Thompson 1993, Pütz et al. 2001). Punta Tombo birds primarily eat seasonally migratory schooling fish (Wilson et al. 2005, Boersma et al. *in press*).

Food availability generally increases during the breeding season, corresponding to elevated rates of primary productivity during high-latitude summers (Bunt 1975). Penguin foraging patterns at by breeding stage reflect both this seasonal food increase and the type (egg or chick) or age of nest contents. For both Punta Tombo and New Island, adults made their longest foraging trips during incubation and their shortest during the early chick stage. Long trips during incubation are feasible as adults are foraging for self-maintenance and return to the nest only to relieve their mates (Williams 1995). However, adults with young chicks must return to the nest every 1 to 3 days to feed their offspring (Boersma et al. *in press*), limiting the distance and duration of their foraging trips. These constraints are common among species that are central-place foragers during breeding, and in areas where food abundance is cyclical or seasonal (Stephens and Krebs 1986). Surprisingly, we did not find any differences in foraging among years, (see Boersma et al. 2009), likely because the extreme differences between colonies and stages far exceeded any inter-annual variation.

Overall, females and males had similar foraging trip patterns, with the exception of average trip distance. Although females made significantly shorter trips (~41 km) than males (~47 km), the difference was relatively minor given that average trip distances ranged from 21 to 143 km. Sex-based foraging differences have been documented for other penguin species, including Adélie Penguins (*Pygoscelis adeliae*; Watanuki et al. 2004), Little Penguins (*Eudyptula minor*; Kato et al. 2008), and Macaroni Penguins (*Eudyptes chrysolophus*; Hart et al. 2010). Diving patterns for Magellanic penguins were similar between the sexes, although bigger penguins tended to dive deeper (Walker and Boersma 2003). Body size may explain the longer average trip distances of males compared to females. At both New Island and Punta Tombo, females were smaller than males, a pattern typical for Magellanic Penguins (Williams 1995, Boersma et al. *in press*). In many bird species, the smaller individuals have higher mass-specific metabolic rates and energetic demands (Speakman 2005), which might decrease their foraging range (Harestad and Bunnell 1979). Alternatively, females may simply have smaller guts and fill up more quickly, enabling shorter trips (Andersson 1978).

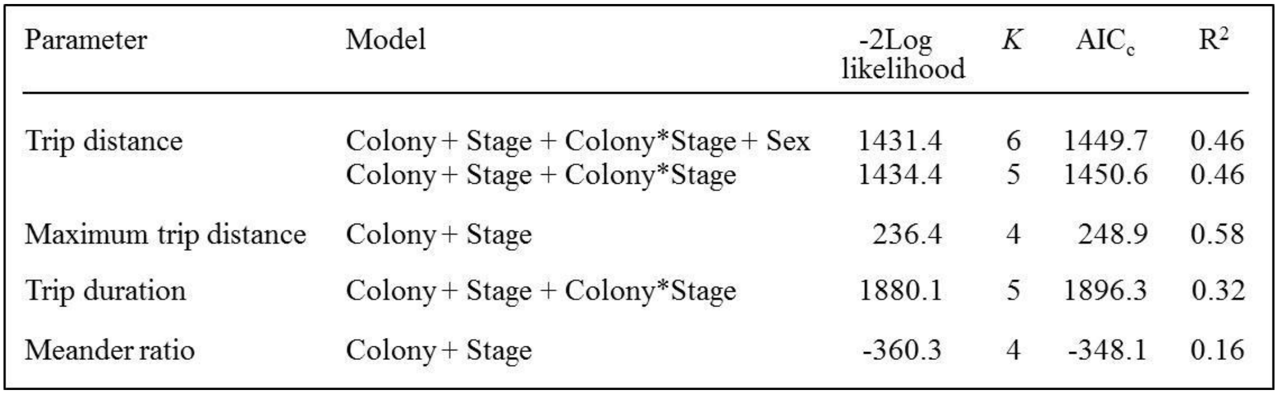
Adult body size did not explain the between-colony variance in foraging trip patterns because New Island and Punta Tombo penguins were similar in size. Thus, the longer foraging trips made by Punta Tombo birds is not a function of increased energy requirements associated with large body size (McNab 1963). Additionally, New Island and Punta Tombo penguins had similar body condition, which likewise cannot explain foraging trip length. Seabirds (in general) have a life history strategy that favors self-maintenance over reproduction (Ricklefs 1990). This tradeoff is evident in the shorter trips corresponding to greater reproductive output at New Island, and the longer trips corresponding to lower reproductive output at Punta Tombo. In both sites, adult body condition was constant, but reproductive success varied depending on food availability.

Clutch (egg) volumes did not explain differences in breeding success between colonies. Large eggs hatch larger chicks, potentially contributing to higher chick mass at fledging and greater reproductive success (O’Connor 1984, Williams 1994). In Magellanic Penguins, larger eggs also produce chicks with bigger feet (Reid and Boersma 1990), which may allow chicks to become mobile at a younger age. However clutch (egg) volumes were similar between colonies, perhaps because penguins from these colonies share a common environment during much of their winter migration (Ruoppolo et al. 2012). The development of the yolk takes several weeks so females would be making eggs while returning to their breeding colonies (Astheimer and Grau 1985). Birds from both colonies migrate north along the continental shelf, with Falklands birds travelling about twice as far (Stokes and Boersma 1998, Pütz et al. 2000, Pütz et al. 2007, Garcia-Borboroglu et al. 2010). If Magellanic Penguin egg volumes reflect ocean conditions encountered during migration prior to the breeding season (Rafferty et al. 2005, Boersma and

Rebstock 2009), we would expect little difference in egg or clutch volumes between colonies. Alternatively, because New Island penguins must expend more energy migrating further to reach their breeding grounds, their egg/clutch volumes should potentially be less than for birds at Punta Tombo.

In summary, compared to Punta Tombo, New Island Magellanic Penguins forage in an ocean environment of high local productivity and food availability, as evidenced by their short foraging trips and increased reproductive output. As a species, these penguins thus exhibit plasticity in their foraging patterns in response to local ocean productivity. Furthermore, Magellanic Penguins accurately reflect ocean productivity in both their foraging patterns and breeding success. Inter-colony comparisons like the current study can contribute to our understanding of the constraints placed on seabirds by central-place foraging, and how plasticity in their natural history allows them to survive under a variety of challenges.

Table 1.1. Corrected Akaike’s information criterion (AICc) values for Magellanic Penguin foraging trip pattern GLMMs. Only best models (lowest AICc values within 2 units) are presented. *K*: number of model parameters.



Parameter	Model	-2Log likelihood	K	AIC_c	R^2
Trip distance	Colony + Stage + Colony*Stage + Sex	1431.4	6	1449.7	0.46
	Colony + Stage + Colony*Stage	1434.4	5	1450.6	0.46
Maximum trip distance	Colony + Stage	236.4	4	248.9	0.58
Trip duration	Colony + Stage + Colony*Stage	1880.1	5	1896.3	0.32
Meander ratio	Colony + Stage	-360.3	4	-348.1	0.16

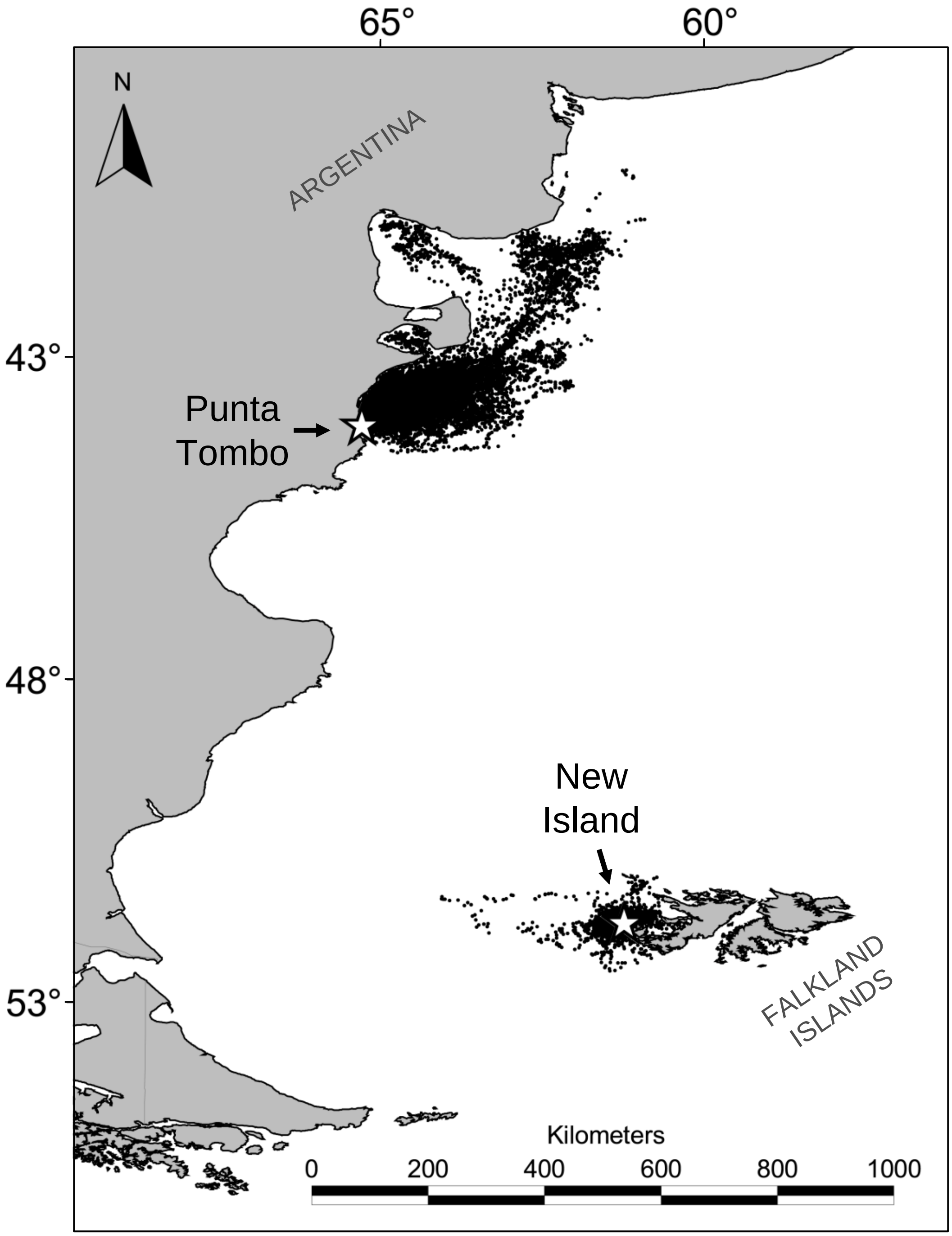


Fig. 1.1. Map of at-sea locations for Magellanic Penguins tracked during the breeding season, 1997-2001. Stars indicate the breeding colonies at New Island (Falkland Islands) and Punta Tombo (Argentina).

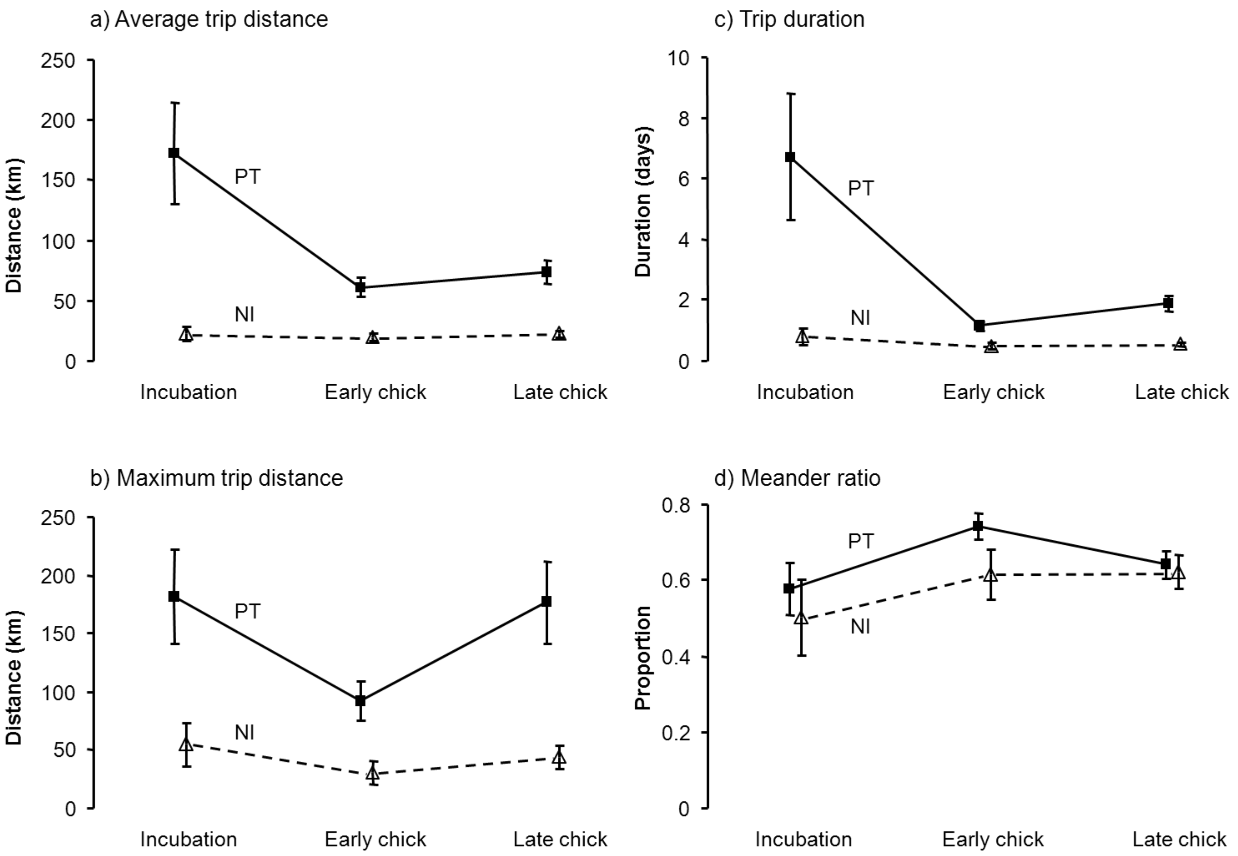


Fig. 1.2. NI: New Island; PT: Punta Tombo. Estimated marginal mean (± 1 SE) trip patterns for each colony by stage of the breeding season. Sample sizes for (a) average trip distance (km), (c) trip duration (days), and (d) meander ratio (proportion) are: NI incubation n = 8 birds, 20 trips; NI early chick n = 8 birds, 70 trips; NI late chick n = 21 birds, 181 trips; PT incubation n = 25 birds, 25 trips; PT early chick n = 46 birds, 210 trips; PT late chick n = 36 birds, 186 trips. Sample sizes for (b) maximum trip distance (km) are: NI incubation n = 8 birds/trips; NI early chick n = 8 birds/trips; NI late chick n = 21 birds/trips; PT incubation n = 25 birds/trips; PT early chick n = 46 birds/trips; PT late chick n = 36 birds/trips.

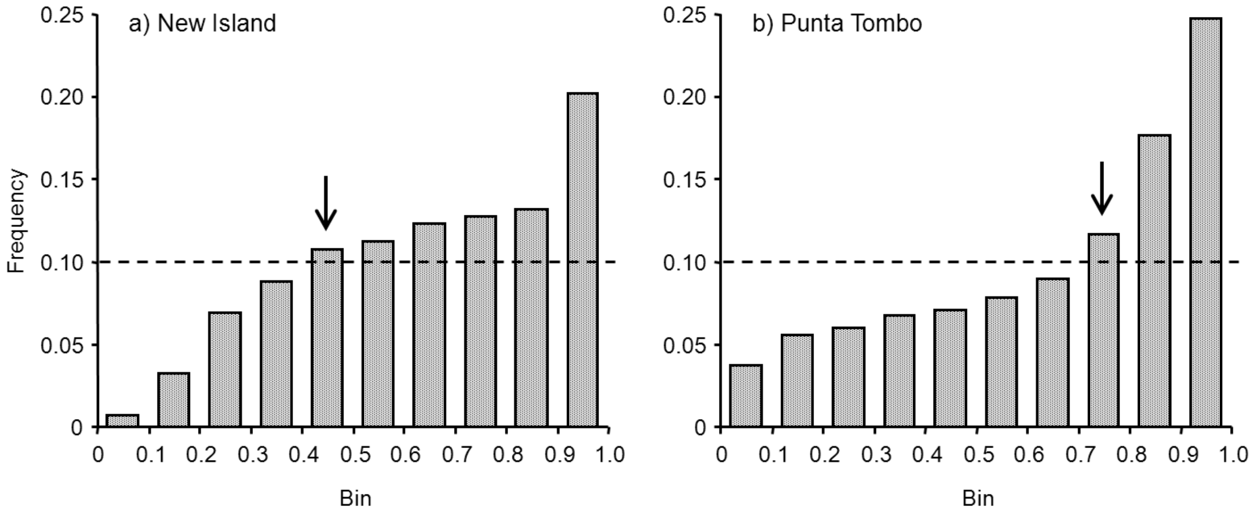


Fig. 1.3. Frequency histograms of Magellanic Penguin at-sea location distance from colony expressed as a proportion of maximum trip distance from colony (by trip). The dashed lines represent expected frequencies under the null hypothesis of a uniform distribution. Arrows indicate where observed frequencies exceed the expected, and represent the proportional distance at which foraging begins: (a) New Island 40% of the maximum trip distance (n = 26 birds, 271 trips), and (b) Punta Tombo 70% of the maximum trip distance (n = 121 birds, 420 trips).

Chapter 2: The mysterious case of albatross chicks off their nests

INTRODUCTION

In birds, the nest serves as a confining refuge that helps protect eggs and chicks from predators and the elements. Black-browed Albatross (*Thalassarche melanophrys*), a medium-sized Procellariiform that lives on islands in the southern ocean, build cylindrical raised nests of mud, using their bills to move and spread the material, much like a mason spreading plaster. Inter-annual nest site fidelity is very high (Tickell and Pinder 1975), and pairs continue to build and repair their nests through successive breeding seasons (Brooke 2004). Over time some nests can reach almost a meter in height, although the average height is about 0.5 m (Warham 1990, AVB pers. obs.).

The nest cup of Black-browed Albatross is a shallow bowl with raised sides, which allows albatross chicks to move radially using a rocking motion, but effectively prevents them from tumbling out of the nest. Aside from restraining the chick, these raised nests likely serve a thermoregulatory function (Kim and Monaghan 2005) by keeping chicks out of puddles. Raised nests may also facilitate defense (Gilchrist and Gaston 1997): like other Procellariiforms, albatross chicks can projectile vomit stinky orange stomach oil (Warham 1996), and the raised nest may provide them a platform from which they can regurgitate down upon invaders.

In Black-browed Albatross, the chicks generally remain confined to their elevated nests until they fledge. Chicks that end up on the ground are unable to climb back into the nest, and they are vulnerable to weather and predators (Warham 1990, AVB pers. obs.). Also, parents do not feed a chick that is on the ground, even if it is next to its own nest (N. Huin, pers. comm.). Similar to other altricial bird species (Lack 1968), Black-browed Albatross chicks that prematurely end up out of their nests and on the ground typically do not survive.

In January 2006, while conducting field work in the mixed seabird colony at Steeple Jason Island (Falkland Islands / Islas Malvinas), my field crew and I began noticing some Black-browed albatross chicks on the ground, off of their nests. In the colony, adults were just starting to leave their chicks unattended, and initially we attributed the few chicks we observed on the ground as isolated incidents. But as the season progressed, we noted more and more albatross chicks off their nests, especially in the mornings. Except in rare cases (described below), we did not see chicks actually coming off their nests, and so the cause of the phenomenon was a mystery. We hypothesized two possible causes: 1) chicks were accidentally knocked off their nests; 2) chicks were pulled out of their nests during failed predation attempts. This paper summarizes the trends we found for albatross chicks off their nests, explores evidence and likely explanations, and discusses the implications for Black-browed Albatross populations.

METHODS

The Falkland Islands are home to the world's largest population of Black-browed Albatross (~ 530,000 pairs), distributed across 12 breeding sites (Wolfaardt 2012). Within the Falklands, Steeple Jason Island (51° 02′ S, 61° 12′ W) has the largest concentration of breeding birds, with ~ 214,000 pairs (Wolfaardt 2012) that nest in a mixed-species colony along most of the western coast. Here the albatross exhibit strong coloniality, and nest densities in the mixed colony ranged from 0.46 to 0.75 breeding pairs per square meter (Huin and Reid 2006; Huin 2007). Like other Procellariiform species, the Black-browed Albatross has delayed maturity, and individuals typically do not breed until age 8 to14 years (ACAP 2009). Pairs lay a single egg in early October, hatching occurs in mid-December, chicks are left unattended except for feeding visits (e.g. “post-guard” stage) starting around the first week of January (Catry et al. 2011), and fledging occurs in April (K. Chater. pers. comm.).

During January 2006, in the course of conducting other field work, we made opportunistic observations of albatross chicks off their nests. To assess the influence of adult nest attendance, we counted the number of albatross chicks alone on the nest, or with a parent. Using stratified random transects in the mixed colony, we made weekly counts in circular quadrats (3 m radius, area 28.3 m^2) from 20 December through 2 February (n = 205 total quadrats). A simple linear regression was used to compare nest attendance (weekly average) and the number of chicks observed off nest per hour (weekly count divided by weekly person-hours).

For each chick we found off the nest, we noted time, general location, whether the chick was on the edge or interior of the colony, whether it was in close proximity to other chicks off the nest (cluster) or surrounded only by other chicks on the nest (solitary), and its condition (e.g. wounded or stained with its own regurgitated stomach oil). Chi-squared analyses were used to compare chicks off the nest based on chick condition (damaged or healthy), location (colony interior or edge), and grouping (clustered or solitary).

Because we seemed to find most off-nest chicks in the morning, we exploited the full moon on the night of 18 January 2006 to do overnight observations at the mixed colony. In addition, three to four days per week we censused the number of albatross chick carcasses along the wide colony margin in the North section of the mixed colony, searching specifically for fresh kills. This area was commonly used by predators as a stopover place to eat prey or pick at carcasses removed from the colony (AVB pers. obs.).

RESULTS

During 200 hours in the mixed-species colony, we counted 235 albatross chicks off the nest (via opportunistic observations). We found the majority (85%, n = 200) in the North colony section, likely because our other research activities were concentrated there. The numbers of off-nest chicks found in each colony section were proportional to the time we spent there ($R^2 = 0.57$, $P = 0.012$); thus, the phenomenon was not restricted to a certain area.

The number of chicks found off their nests (per person-hour in the colony) increased between 20 December (first observed) and 18 January, then decreased slightly through early February (Fig. 1). This trend was inversely related to nest attendance: as the season progressed, the proportion of chicks attended decreased until 18 January, then remained constant (ANOVA $F_{1,5} = 120.13$, $R^2 = 0.95$, $P < 0.001$; Fig. 1). Albatross on Steeple Jason began leaving their chicks unattended during the last week of December, and by 10 January more than 50% of chicks were no longer being continuously guarded.

Similar proportions of chicks were found off their nests in the colony interior (39%, n = 92) versus on the colony edge (43%, n = 100; for 18% the location was not recorded). We found more chicks off their nests in clusters (66%, n = 155) than solitary (34%, n = 80). However, off-nest chicks on the edge were more likely to be found in clusters (76%, versus 58% for interior) and off-nest chicks in the colony interior were more likely to be solitary (42%, versus 24% for edge; $\chi^2 = 7.35$, df = 1, $P = 0.007$).

Most chicks found off their nests were in good condition (80%, n = 187). About 14% (n = 33) had evidence of physical trauma such as lacerations on the head, face or back, neck or chest wounds, swollen or crusted eyes, or damaged bills. Half of the injuries (n = 17) were severe, and included torn throats, punctured eyes, or broken bills or jaws. Of the injured chicks, 15% (n = 5) also had feathers matted with stomach oil regurgitate; an additional 15 chicks (6% of total) had matted feathers but no injuries.

Damaged off-nest chicks (either injuries or matted feathers) were more likely to be found on the edge of the colony (25%, versus 13% for interior; $\chi^2 = 4.40$, df = 1, $P = 0.036$). They were also more likely to be found in clusters (35%) rather than solitary (13%; $\chi^2 = 4.69$, df = 1, $P = 0.030$; Fig. 2). From 3-28 January, we noted an additional 13 damaged chicks still on their nests, three with severe wounds and 11 with oil-matted feathers. Of these, 10 were at the edge of the colony, and 10 were near another albatross chick off of its own nest.

On one occasion, we observed an albatross chick with a deformed leg (likely a developmental anomaly) push itself out of the nest as it was turning to face an approaching intruder. Between 11 January and 2 February we noted nine chicks with similarly deformed legs, all still on their nests. For three healthy chicks found on the ground, the nest itself was broken or insubstantial (i.e. low and without a defined nest cup). Albatross chicks may also be knocked off their nests by adult albatross attempting to land. We frequently observed adult albatross crash-landing in the colony, but only one instance when a tumbling adult knocked a chick out its nest. On two separate occasions we witnessed Striated Caracaras (*Phalcoboenus australis*) capturing and killing albatross chicks on the nest; on three occasions we saw caracaras dismantling bloody albatross chick carcasses, which we presumed they obtained via predation. In all cases, the caracaras first removed the chick's head, then began feeding on the remainder of the carcass starting at the top (head end) of the body.

On 15 January, shortly after sunrise, we surprised a Southern Giant Petrel (*Macronectes giganteus*) in the tussac, feeding on a bloody albatross chick carcass. We noticed unusual drag marks leading to the carcass—an erratic path stained with splotches of albatross chick stomach oil—that led back to an albatross nest (Fig. 3). The nest had prominent and fresh splashes of oily regurgitation around the base and covering one side. The chick carcass was turned inside-out via the cloaca and the head was wet-looking, as if it had been slobbered on. The following morning we encountered another petrel feeding on a freshly-killed albatross chick in the tussac, again with drag marks leading from the nest to the carcass, which was also inside-out with a "wet head". We found 12 similar drag trails between 15 January and 3 February, eight of them with fresh albatross chick remains at the end.

Suspecting we were arriving at the colony too late in the morning to catch the petrels in the act of predation, we returned to the colony on 18 January before sunrise. At 0450, we witnessed a giant petrel approach an albatross chick, grasp it by the back of the head, and pull it off the nest (Fig. 4). The petrel chewed on the chick's head until the chick stopped moving, and then grasped the chick by the cloaca and began vigorously thrashing it. That same day, we took advantage of a full moon and monitored part of North colony section overnight, from 2130 to 0530. When we arrived at the colony just after sunset, we surprised four giant petrels waiting along the margin. Petrels flew low over the colony throughout the night, something we never saw during the day. Around 0100, we observed one petrel on the ground, walking along the colony margin. Around 0115, we heard albatross chicks popping their bills, which they do when threatened, and saw the giant petrel walking through the colony among the albatross nests. In the morning (0530), we found three albatross chicks off their nest in this same area: one had a "wet head" and feathers matted with fresh stomach oil; the other two appeared undamaged.

For the carcass censuses along the colony margin, we counted about 7 (± 0.23 SE) obviously new fresh carcasses per census-day (13 days). For fresh (bloody) carcasses, we noted two distinctive types: (1) missing the head, and apparently eaten from the top down (n = 22); and (2) head intact but often wet-looking, turned inside-out, and apparently eaten from the bottom up (n = 68). At least nine of the chicks found off their nests also had wet heads, similar to what we observed on the petrel-killed carcasses.

DISCUSSION

For solitary interior chicks, the lack of obvious wounds or stomach oil stains suggests that some of these chicks may have come off their nests accidentally. Albatross are called "gooney birds" for a reason—they are almost infamous for crash-landing in their colonies. In other seabird species such as the Common Murre (*Uria aalge*), adults may knock eggs or chicks out of the nest, especially when disturbed (Ainley et al. 2002). For adult albatross knocking chicks out of the nest, one would expect the frequency of unintended collisions to decline as the season progressed because chick provisioning rates decrease as the chicks get older (Huin et al. 2000). As causes for chicks coming off their nests, deformed legs or faulty nests are stochastic in nature, and they should occur randomly in space and time. Thus, none of these accidental events support the increasing trend we observed in the frequency of albatross chicks off their nests during the breeding season.

The number of chicks off the nest was strongly and inversely related to adult nest attendance. In many seabird species, adults at the nest deter predators, as unguarded chicks are more vulnerable to predation (Mallory and Forbes 2011). The presence of wounds and stomach oil regurgitations strongly suggests that damaged chicks were pulled off their nests during failed predation attempts. We initially presumed the most likely culprits were Striated Caracaras, a bird of prey common at seabird colonies in the Falklands (Strange 1996, Meiburg 2006). Caracaras are scavengers and predators on albatross chicks (Catry et al. 2008), and they were ubiquitous at the mixed colony on Steeple Jason. The island supports a population of about 150 caracaras (Woods 2007; AVB unpubl. data), which we encountered every day, and on every visit. Carcasses that had missing heads and had been eaten from the top down were consistent with Striated Caracara predation. This type of feeding is common in raptors (Slagsvold et al. 2010).

Carcasses that were turned inside-out and that had “wet heads” were more consistent with Southern Giant Petrel predation. At the Crozet Islands, giant petrels (*Macronectes* spp.) captured King Penguin (*Aptenodytes patagonicus*) chicks by grabbing an individual by the head/neck, waiting for the chick to become weak, and then tearing the chick open from the cloaca (Le Bohec et al. 2003). Northern Giant Petrels (*M. halli*) captured Northern Rockhopper Penguin (*Eudyptes moseleyi*) adults at sea, also by grabbing them by the back of the head (Ryan et al. 2008). In this case, the petrels held the penguins under the water until they stopped moving, then began eating them from the front of the neck or the belly. Southern Giant Petrels captured and killed adult Magellanic Penguins (*Spheniscus magellanicus*) and fledgling Southern Rockhopper Penguins (*E. chrysocome*) in a similar manner (AVB pers. obs.). The petrel held the penguins under the water as described above, then began eviscerating the birds via the cloaca. For petrels attacking Northern Rockhopper Penguins, only 18% of the penguins caught were actually killed; the remainder were released, presumably because they were not grabbed and held correctly (Ryan et al. 2008). Our observations of albatross chicks off the nest were consistent with multiple attempts and releases per actual capture/kill.

Despite having a local population of about 1400 breeding pairs (Reid and Huin 2008) Southern Giant Petrels were extremely rare in the mixed colony on Steeple Jason—at least during daylight hours. From mid-December through early February, we observed them on only five different days. Giant petrels are notoriously skittish (Brooke 2004, Patterson et al. 2008), so our presence in the mixed colony may have artificially limited their day-time activity there. However, we likely underestimated petrel presence in the colony, especially if they were primarily active at night. At the Crozet Islands some petrels engaged in nocturnal predation, and researchers there hypothesized that this behavior facilitated the capture of sleeping King Penguin chicks (Le Bohec et al. 2003). The first documented record for Southern Giant Petrel predation on Black-browed Albatross involved a sub-adult albatross at sea (Cox 1978). Several subsequent sources mention giant petrel predation on albatross chicks (Warham 1990, Catry et al. 2006, Forster and Phillips 2009, Catry et al. 2010), although as unpublished observations or without citations. Based on direct observation and indirect inference, we conclude that attempted predation by Giant Petrels was the most likely explanation for the majority of live albatross chicks we found off their nests during the post-guard stage.

Whether this attempted predation by petrels has a major impact on albatross populations is debatable. Black-browed Albatross are currently IUCN listed as Endangered (BirdLife International 2012). However, a recent report shows that the Falklands populations have increased dramatically (from 350,000 to 530,000 pairs) since 2005 (Wolfaardt 2012). In small or vulnerable populations, predation has the potential to cause complete reproductive failure (Young 1994, Parrish et al. 2001). But in large or increasing seabird populations, predation, parasitism, and disease (especially on chicks) probably have very little effect on population demography (Croxall and Rothery 1991). On Steeple Jason, approximately half of the affected albatross chicks were on the edge of the colony. In colonial seabirds, edge nests typically have lower reproductive success than do interior nests (e.g., Tenaza 1971, Pierotti 1982). At Steeple

Jason, petrel predation (and attempted predation) may be just one of many factors that contribute to lower success for edge nests. Thus, although the attempted predation by Giant Petrels was unfortunate for the albatross chicks involved, the overall impact on the Steeple Jason Black-browed Albatross population was likely minimal.

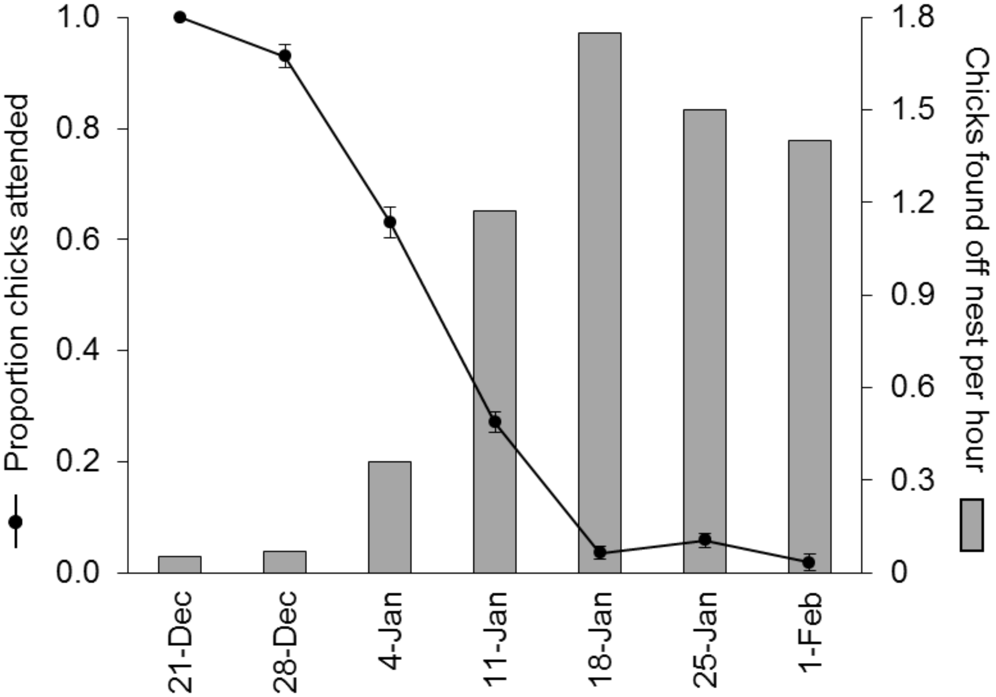


Fig. 2.1. Significant negative relationship between nest attendance and number of chicks found off the nest. Weekly counts of chicks off the nest (found per person-hour in the colony; n = 216 chicks) were regressed on the average weekly percentage of chicks being attended by a parent (n = 205 quadrats).

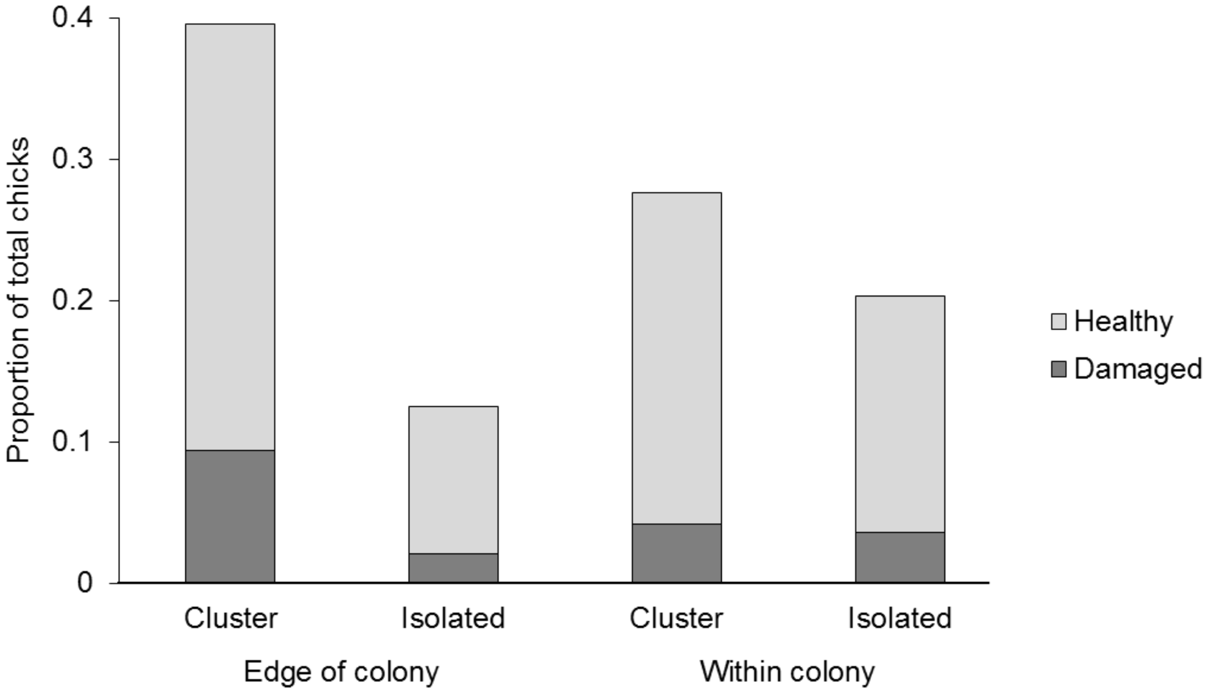


Fig. 2.2. Proportions of chicks off the nest that were damaged versus healthy, located on the colony edge or interior the colony, or were found in clusters versus solitary (n = 192 chicks).

Fig. 2.3. Typical petrel drag trail stained with splotches of stomach oil regurgitate, and leading from an albatross nest to an albatross chick carcass in the tussac.

Fig. 2.4. Albatross chick carcass, freshly killed by a Southern Giant Petrel in the pre-dawn hours (0450) on the morning of 18 January 2006.

Chapter 3: Resource use overlap among avian predators in a mixed seabird colony in the Falkland Islands

INTRODUCTION

The concepts of niche differentiation and resource partitioning were originally conceived as mechanisms by which evolutionary divergence among closely related species occurs in response to interspecific competition (c.f., Walter 1991). More recently, the predictions of resource partitioning have been applied in community ecology to examine how species differ in their resource use (Schoener 1986). For intra-guild (Root 1967) suites of organisms (functional groups comprising species that may not be closely related), niche theory provides a useful framework for exploring how species having similar resource requirements can co-exist (e.g. African apex predators, Hayward and Kerley 2008).

In this context, spatial or temporal partitioning among members of a community (Schoener 1974) may result from various factors (Shmida and Ellner 1984, Strong 1982), including—but not limited to—interspecific competition (Ross 1986). Morphological or behavioral differences between species may promote co-existence if these differences enable each to be more successful, relative to other species within the same guild, at capturing specific types of prey (Pyke 1982, Kohda et al. 2008, Schreier et al. 2009). Factors such as predation, parasitism, or migration mortality can also limit populations of potential competitors within a community (Hulsmann et al. 2011, Gorman and Haas 2012), allowing for dietary overlap. In cases where resource overlap is high, species may co-exist without apparent partitioning if the resource is not actually limiting (Strong 1982, de Iongh et al. 2011).

In this paper, I adopt an intra-guild approach and use the predictions of niche differentiation to examine resource use overlap among avian predators at a mixed seabird colony. Striated Caracaras (*Phalcoboenus australis*, Falconidae) and Falkland Skuas (*Stercorarius antarctica antarctica*, Stercorariidae) are locally abundant predators at seabird colonies in the Falkland Islands (Islas Malvinas). Striated Caracaras are a comparatively large bird of prey, with feet and legs that are long relative to their body size (Strange 1996). Unlike true falcons, they spend considerable time on the ground as scavengers, and they are infamous for their bold, curious, and often destructive behavior (Meiburg 2006). Falkland Skuas are similar to the largest gulls in size, wingloading, and flight capabilities (Furness 1996). A putative subspecies of the Brown Skua, Falkland Skuas are sometimes called "seabirds of prey" for their hooked beaks, which are well suited to tearing flesh (Woods and Woods 1997). Both species are opportunistic generalists, feeding on carrion, seabird eggs and chicks (penguins, albatross, cormorants, and small petrels), seabird regurgitations or spilled food, goose eggs and chicks, and pinniped faeces (Lamey 1995, Strange 1996, Woods and Woods 1997, Liljesthröm et al. 2008, Anderson et al. 2009, Catry et al. 2011a, Silva et al. 2011).

I quantified the extent of resource use overlap between the two predators, including diet and the degree to which predators co-occur spatially and temporally. If resource use overlap is high, one would expect to find either (1) evidence of interspecific competition, or (2) that food is not limiting. If resource use overlap is low, one can assess potential morphological or behavioral characteristics that might account for differences in the predators' resource use (diet). Few published studies exist for either Striated Caracaras or Falkland Skuas. Thus, this research contributes to the limited body of knowledge on these predators, while exploring the intersection between classical niche theory and community ecology.

METHODS

Study area

Steeple Jason Island (51°02′ S, 61°12′ W), which lies on the north-western margin of the Falkland Islands archipelago, is 8 km long and up to 1.5 km wide (Thompson and Rothery 1991; Fig. 1). The Falkland's largest population of Black-browed Albatross (*Thalassarche melanophrys*; 171,000 pairs; Huin and Reid 2006) and its second largest population of Rockhopper Penguins (*Eudyptes chrysocome chrysocome*; 59,000 pairs; Huin 2007) breed at Steeple Jason—primarily in a mixed colony—that extends along most of the western coast of the island (Fig. 1).

The northern colony section lies in a broad plain between uplifted coastal rock ridges and a wide inland band of tussac (*Poa flabellata*), and ranges in width from 25-170 m. The western colony section varies between broad sloping plains and deep narrow valleys, and ranges in width from 20-200 m. The southern colony section is a long narrow valley nestled between uplifted coastal rock ridges and a steep inland hill with fringing tussac vegetation, and ranges in width from 15-65 m. Both the West and The South sections have multiple large and prominent boulders within the mixed colony. The area of the northern section is 57,000 m^2, with the highest nest densities for both albatross (0.75 m^{-2}) and penguins (0.26 m^{-2}); the western section area is 85,000 m^2, with intermediate albatross (0.61 m^{-2}) and penguin (0.16 m^{-2}) nest densities; the southern section area is about 26,000 m^2, with the lowest nest densities for both albatross (0.46 m^{-2}) and penguins (0.13 m^{-2}) (Huin and Reid 2006; Huin 2007).

Study species

Two predatory bird species—Striated Caracaras (“caracara”) and Falkland Skuas (“skua”)—are locally abundant on Steeple Jason and are important predators during the austral summer (Strange 1996, Woods and Woods 1997). The caracara population in summer is about 63 pairs, most of which nest in tussac along the inland margin of the mixed colony, where nests and territories are spaced approximately every 100 m (Woods 2007). An additional 15 to 20 sub-adult birds also forage in the mixed colony (AVB, unpubl. data). Skuas number about 110 pairs that nest in “clubs” on gentle slopes away from the mixed colony; about 250 non-breeding floaters congregate near the breeding areas or in sheltered coastal flats (AVB, unpubl. data). The largest club, located adjacent to the northern section of the mixed colony, comprises about 40 breeding pairs; the other four clubs range from two to 25 pairs (AVB, unpubl. data). The breeding seasons for both species coincide with those of their seabird prey (Strange 1993, Woods and Woods 1997, Catry et al. 2008, Catry et al. 2011a, AVB, pers. obs.). In winter, when the seabird colonies are empty, caracaras migrate east toward West Falkland (Woods and Woods 1997, Meiburg 2006). Skuas have a pelagic migration in winter (Strange 1993), likely in deep sub-Antarctic waters near the central Patagonian shelf-break (Phillips et al. 2007).

Data collection and analysis

Caracaras and skuas were observed in three sections of the mixed colony during two stages of the penguin/albatross breeding season in 2005-2006 : “hatching/brood-guard” when parents continuously attend the nest (4-26 December) and “post-guard” when chicks are unattended except during feedings (5-29 January). Observations were rotated among colony sections and time blocks to equalize coverage. Within each colony section and time block, I randomly assigned observation start times and locations (1.5 hours duration; 216 hours total).

Predator characteristics and behavior

Using instantaneous scan sampling at five-minute intervals, I recorded predator behaviors in six categories—perching, feeding, searching in the air, searching on the ground, transit, and territorial—and compared the relative frequencies of behaviors between the two predators (chi-squared test). I recorded every instance of skua or caracara territorial behavior that occurred during each observation session, including whether the dispute was between individuals of the same or different species (intra, inter), and whether the fight was over food (food, territorial). I tested for interference competition (chi-squared tests) by comparing relative frequencies of (1) inter- or intra-specific disputes over food versus over territory (e.g. not related to food), and (2) the proportions of food versus territorial fights by predator.

The morphology of the two predators was contrasted with measurements taken from a sample of 27 caracaras (19 adults, 8 sub-adults > 1 year old) and 11 skuas. I used separate Student's two-sample *t*-tests to compare wing chord length, tail length, and weight.

Resource use and foraging

To examine resource use overlap, I recorded every instance of skua or caracara feeding that occurred during each observation session. For each feeding event, I identified the predator (skua, caracara) and prey type (albatross egg, albatross chick, penguin egg, penguin chick, or regurgitation). In addition, I determined whether the predator took live prey from an active nest (predation); abandoned live prey and dead prey were both classified as scavenging. Colony section (North, West, South) and location within the colony (edge, interior) were recorded as spatial variables. Stage of the season (hatching/brood-guard, post-guard) and time (morning: 0500-1000h; midday: 1000-1600h; evening: 1600-2100h) were recorded as temporal variables. To examine differences in foraging behavior between caracaras and skuas, I recorded whether the predator approached prey from the air or on the ground (air, ground), and whether the predator ate at the capture site or removed the food item from the colony (dine-in, take-out).

Temporal, spatial, and foraging behavior patterns

I characterized general temporal, spatial, and foraging behavior patterns for caracaras and skuas—independent of diet—using 2*2 and 2*3 chi-squared tests. Analyses compared the relative frequencies of the two predators by colony section, colony location, stage, and time of day, and general foraging behavior by approach and consume locations.

Dietary overlap and resource partitioning

I quantified overall dietary overlap between predators. Then, as a test for the effect of spatial or temporal factors on dietary overlap, prey type was crossed with each of the other factors—colony section, colony location, stage, and time—to create four interaction effects that represented spatial or temporal resource partitioning at two scales. As a test for the effect of foraging behavior on dietary overlap, prey type was crossed with each of the other factors—approach location and consume location—to create two interaction effects intended to reflect innate predator characteristics (i.e. morphological differences).

To assess dietary overlap, including the interactions described above, I used an ecological null model (the niche overlap module in Ecosim; Gotelli and Entsminger 2001) which compares an observed data matrix to pseudo-matrices generated via Monte Carlo randomizations (Pianka 1986). I used Pianka's (1973) niche overlap index and Randomization Algorithm 3 (Winemiller and Pianka 1990), in which the niche breadth is retained and zero states are reshuffled. I assumed resource states were equally probable, and used 5000 iterations for the simulations. The output is an observed overlap index that ranges from zero to one: lower values represent minimal overlap; higher values represent maximal overlap (Gotelli and Graves 1996). The probability of the observed overlap being higher than expected by chance is determined directly as the proportion of the simulated matrices that have a higher overlap index than the observed matrix (Gotelli and Entsminger 2001). Thus, “significant” overlap is indicated by $p \leq 0.05$, which is equivalent to fewer than 250 of the 5000 random iterations having a higher overlap index than the observed. For each simulation, I used post-hoc contingency analyses (Jmp version 10.0, SAS) to compare the observed and expected frequencies across categories.

Food availability

I used two approaches to assess food availability: direct counts of uneaten dead eggs/chicks of albatross or penguins, and an energetic model to estimate the total number of live albatross or penguin chicks the two predators (plus their chicks) would require. I counted the number of available dead prey items (eggs or chicks of albatross and penguins) using stratified random transects in the North section of the mixed colony. Weekly counts were made in circular quadrats (3 m radius, area 28.3 m^2) from 16 December through 29 January (n = 864 total quadrats). Using these counts and the total areas of the North, West, and South sections of the mixed colony, I estimated the weekly quantity of dead prey available for scavenging. On 13 and

15 December, during peak hatching, I surveyed two 20*20 m plots (one in the North colony section, and one in the West) and counted the number of penguin eggs abandoned outside of the nest.

To assess availability of live prey, I calculated the numbers of albatross and penguin chicks necessary to meet predator dietary needs from penguin hatching (10 December) through albatross fledging (18 April). For predator food requirements during the breeding season, I used previously published estimates on Striated Caracaras from New Island, Falkland Islands (Catry et al. 2008), and on Great Skuas (*Stercorarius skua*) from St. Kilda, Outer Hebrides (Phillips et al. 1999). Great Skuas are the northern hemisphere equivalent of the Brown Skua. The daily food requirement for adult caracaras was 125 grams, and for skuas the daily value was 228 grams.

I estimated daily food requirements for predator chicks by manually fitting total food for the chick-rearing period to growth curves for Falconidae and Stercorariidae (Ricklefs 1968; Fig. 2), integrated from hatching until fledging. For caracaras I used a seasonal requirement of 3286 grams (Catry et al. 2008), with a chick-rearing period of 65 days and a median hatch date of 15 December (AVB unpubl. data). For skuas I used 4193 grams for the 47-day period from hatching to fledging, 1692 grams for the 18-day period from fledging to departure (Phillips et al. 1999), and a median hatch date of 25 December (AVB unpubl. data).

I estimated the number of predator chicks by using published values for reproductive success: 1.67 chicks per pair for Striated Caracaras at New Island (Catry et al. 2008), and 1.52 chicks per pair for Brown Skuas at Bird Island, South Georgia (Phillips et al. 2004). Thus, at Steeple Jason, the caracara breeding population of 63 pairs was estimated to have 105 chicks, and the skua breeding population of 110 pairs to have 167 chicks.

For albatross and penguin chicks as prey items, I used existing growth curves for Black-browed Albatross at Bird Island (Huin et al. 2000) and for Rockhopper Penguins at New Island (Poisbleau et al. 2008) to estimate daily mass, manually interpolated from hatching to fledging (Fig. 2). For albatross, median hatch date was 15 December (AVB unpubl. data), and the duration of the chick-rearing period is about 125 days (Huin et al. 2000). For penguins, the median hatch date was 10 December, with a chick-rearing period of about 65 days (AVB unpubl. data).

Not all of a killed chick carcass is digestible, so I used a conversion factor of 65% previously estimated for seabirds as prey (Votier et al. 2004) and a caloric content for seabird meat of 10.9 kJ per gram (Phillips et al. 1999). I assumed albatross and penguin chicks were captured at rates corresponding to their relative abundance, so I applied the observed ratio of 2.9 albatross nests per penguin nest, or 1.45 albatross chicks per penguin chick.

I used the following equation to calculate the daily numbers of albatross and penguin chicks required to feed the combined population of caracaras and skuas:

> [(n caracara adults) * (grams food)] + [(n skua adults) * (grams food)] + [(n caracara chicks) * (interpolated grams food)] + [(n skua chicks) * (interpolated grams food)] = [(n penguin chicks) * (interpolated penguin chick mass) * 0.65] + [1.45 * (n penguin chicks) * (interpolated albatross chick mass) * 0.65]

I then manually solved for n penguin chicks (days 1-65) or n albatross chicks (days 66-125), and summed the daily prey numbers to estimate the total albatross and penguin chicks required by caracaras and skuas.

RESULTS

Predator characteristics and behavior

Skuas spent more than half (56%) of their time in the air, either searching for prey (42%) or in transit (14%; Fig. 3). In contrast, caracaras spent the majority of their time on the ground (77%) either perching (73%) or searching on foot (4%; Fig. 3). Predators differed in the frequency and type of their territorial behaviors (Fig. 4). Most (59%) skua disputes (both intra-specific and interspecific) were over food, whereas only 12% of caracara disputes were food-related. Most fights ($n = 232$) occurred between individuals of the same species: 82% of food fights and 83% of territorial (non-food) fights were within species. For fights between species ($n = 17$), caracaras and skuas were each the aggressors in about half of both food and non-food disputes.

For caracaras, adult and sub-adult weights ($t_{13} = 0.45$, $p = 0.65$), wing lengths ($t_{18} = 1.13$, $p = 0.27$), and tail lengths ($t_{9} = 1.96$, $p = 0.08$) were similar, so I pooled age classes for analysis. Skuas weighed about 325 g less than caracaras ($t_{20} = 5.48$, $p < 0.0001$), and their wings ($t_{28} = 6.70$, $p < 0.0001$) and tails ($t_{35} = 17.32$, $p < 0.0001$) were also relatively short (Appendix 1, 2). Skua beaks were long and narrow, similar to gulls, whereas caracaras had short, deep beaks, typical of larger raptors.

Skuas were agile fliers, adept at hovering directly over the colony, even in very light or strong wind conditions. We frequently observed them floating almost stationary, looking downward toward the albatross and penguin nests, then rapidly dropping down into the mixed colony after prey without actually landing. Skuas were less mobile on the ground, comparable to their congeners in the gull family. Skuas were able to easily pick up and carry penguin eggs and small, brood-size penguin chicks, which they typically swallowed whole in flight, but they could carry only the smallest albatross chicks. Some individual skuas seemed to specialize on albatross regurgitation, eating it by scraping their lower bills horizontally against the ground.

Caracaras were able to fly in most wind conditions, but they rarely hovered. Most of their flights were short transits from perch to perch, or dropping down from a vantage point after prey. In contrast to skuas (and other falcons), caracaras were extremely mobile on the ground, capable of sprinting through the colony among the albatross nests by using their wings to assist in making sharp turns. Caracaras were not able to pick up and carry penguin eggs using their beaks unless the egg was pipped (that is, had a hole made by the hatching chick) or broken. They were able to easily carry the smaller post-guard penguin and albatross chicks, but not the larger chicks later in the season. As a result, caracara pairs that killed an albatross or penguin chick that was too large to carry took turns guarding their kill and transporting pieces back to the nest or to hidden food caches in the tussac.

Temporal, spatial, and foraging behavior patterns

Independent of diet, both predators foraged in all colony sections (Fig. 5). However, predators differed proportionately in the colony sections in which they captured prey (Pearson $\chi^2 = 15.88$, df = 1, $p < 0.001$; Table 1). Although caracaras foraged mostly in the North (70%), they also captured prey in the West (12%) and South (18%); skuas concentrated almost exclusively in the North (85%). Both predators captured prey on the colony edge and in the colony interior (Fig. 6). However, the predators differed proportionately in the locations from which they took their prey (Pearson $\chi^2 = 20.10$, df = 1, $p < 0.001$; Table 1). Caracaras took most of their prey from the interior (92%), whereas skuas took prey from both the colony edge (44%) and interior (56%).

Independent of diet, predators were similar in the stage of the season in which they captured their prey (Pearson $\chi^2 = 0.09$, df = 1, $p = 0.75$; Table 1, Fig. 7). Both fed more in the post-guard stage: caracaras 74%, skuas 75%. Both predators foraged throughout the day (Fig. 8). However, the predators differed proportionately in the time of day during which they captured most of their prey (Pearson $\chi^2 = 10.19$, df = 2, $p < 0.01$; Table 1). Whereas caracaras captured prey almost exclusively in the midday (84%, versus 66% for skuas), skuas also foraged partly in the morning (22%) or evening (12%).

Independent of diet, predators were similar in their foraging behavior in approaching prey (Pearson $\chi^2 = 2.54$, df = 1, $p = 0.11$; Table 1, Fig. 9). Both caracaras and skuas approached prey from the ground most of the time (86% and 77%, respectively). Both predators primarily consumed their prey on-site (Fig. 10). However, the predators differed proportionately in where they consumed their prey (Pearson $\chi^2 = 7.87$, df = 1, $p < 0.01$; Table 1). Caracaras ate 66% on-site and removed 34%; skuas ate 80% on-site and removed 20% of their prey.

Dietary overlap and resource partitioning

For all dietary overlap and resource partitioning comparisons, an observed overlap index significantly higher than would be expected by chance is indicated by $p \leq 0.05$. Caracaras and skuas had very high (0.94) overlap in their diet ($p = 0.026$; Fig. 11). Both predators scavenged more than they captured live prey, but skuas scavenged about 92% of the time compared to 82% for caracaras (Pearson $\chi^2 = 7.26$, df = 1, $p < 0.01$). Dead albatross chicks (61% overall) were the most common prey item for both caracaras (63%) and skuas (60%). For caracaras, the next most common prey item was live penguin chicks (17%); for skuas, regurgitations comprised about 23% of their diet.

Caracaras and skuas had very high (0.92-0.96) overlap in their diet both spatially and temporally, except for colony location (0.63). For both predators, the most common prey was dead albatross chicks in the North (Fig. 5). Both predators also scavenged the most prey types in the North (caracaras four, skuas five). In the North caracaras took about 6% more live penguin chicks than expected, and scavenged regurgitations 12% less than expected; in the South caracaras took 7% more dead albatross chicks than expected (Pearson $\chi^2 = 63.81$, df = 17, $p < 0.001$; Table 2). Predators did not significantly overlap (0.63, $p = 0.13$) in their diet based on colony location (Fig. 6). The most common prey for caracaras was dead albatross chicks in the colony interior; for skuas the most common was regurgitations along the colony edge. In the colony interior caracaras took about 25% more dead albatross chicks than expected; caracaras scavenged regurgitations less than expected both within the colony (-5%) and on the colony edge (-20%); skuas took 16% fewer dead albatross chicks than expected from the colony interior, and 13% more regurgitations than expected from the edge of the colony (Pearson $\chi^2 = 46.93$, df = 12, $p < 0.001$; Table 2).

When partitioned by stage of the season, the most common prey item for both predators was dead albatross chicks, eaten during the post-guard stage (Fig. 7). During hatching/brood-guard, caracaras took about 8% more live penguin chicks than expected, and scavenged regurgitations less than expected during both hatching (-7%) and the post-guard stage (-6%; Pearson $\chi^2 = 42.07$, df = 12, $p < 0.001$; Table 2). For time of day, the most common prey item for both predators was dead albatross chicks, eaten during the middle of the day (Fig. 8). In the evening caracaras took about 9% more live penguin chicks than expected, 9% more dead albatross chicks than expected, and 7% fewer regurgitations than expected (Pearson $\chi^2 = 52.94$, df = 18, $p < 0.001$; Table 2).

Caracaras and skuas had very high (0.94-0.97) overlap in their diet based on foraging behavior. The most common approach behavior for both predators was on the ground, to scavenge dead albatross chicks (Fig. 9). Caracaras scavenged more prey types (four) by approaching on the ground; skuas scavenged more prey types (four) by approaching from the air. Skuas approached from the air exclusively when capturing live prey (predation). Caracaras approached dead penguin chicks from the ground 10% more than expected, and approached regurgitations from the air (-8%) and ground (-7%) less than expected (Pearson $\chi^2 = 36.81$, df = 13, $p < 0.001$; Table 2). The most common consume behavior for both predators was to scavenge dead albatross chicks on site (dine-in) (Fig. 10). For live chicks or eggs (predation) skuas always removed their prey (take-out). Caracaras captured and removed (take-out) live penguin chicks (9%) and dead albatross chicks (7%) more than expected, and ate dead albatross chicks (-6%) and regurgitations (-11%) on-site (dine-in) less than expected (Pearson $\chi^2 = 59.17$, df = 13, $p < 0.001$; Table 2).

Food availability

Food availability in the North colony section was mostly constant, with daily densities of uneaten dead items ranging from 0.02 to 0.03 per square meter during the first five weeks and 0.01 per square meter during the last two weeks. Extrapolated to the entire area of the North section, the weekly availability was approximately 1500 dead items in the first five weeks, and about 800 in the last two weeks. Extended to the other colony sections and adjusting for densities, the weekly availability was 1700 (decreasing to 900) for the West, and 400 (decreasing to 200) for the South. Combining all areas, an estimated 21,800 dead albatross or penguin eggs/chicks were available for scavenging across the seven-week period. In the two plots (North and West) I found a total of 30 penguins eggs abandoned outside the nest, or about 0.04 eggs per square meter.

Predator food requirements (in kg of meat) increased during chick-rearing, then decreased at post-fledging (Fig. 12). For the corresponding live prey required by the two predators (plus their offspring), the number of penguin and albatross chicks was highest very early in the season, when prey chicks were small (Fig. 12). The total number required for the season—from penguin chick hatching through albatross chick fledging—was 19,300 penguin chicks plus 11,400 albatross chicks.

DISCUSSION

Caracaras and skuas had high general overlap in both diet and co-occurrence (spatial and temporal). Both predators ate the same prey types—eggs and chicks of albatross and penguins—although skuas also relied heavily on regurgitations. Spatially, both species foraged in similar colony sections and locations within the colony. Temporally, the activity peaks of both predators were during the same time of day and stage of the season. Given overlap in diet and co-occurrence, I expected to find either: (1) evidence of interference competition, in cases where both predators were active in the same areas at the same time; or (2) that food was not limiting, such that both predators had access to ample resources.

I found little evidence of interference competition between the two predators. Both food and territorial fights were much more likely to happen within species, rather than between species. Within species, skuas fought over food. At Cape Bird in the Antarctic, skuas nest adjacent to penguin colonies and pairs may hold and defend territories that are used for both breeding and feeding (Young 1994). At King George Island on the Antarctic Peninsula, territorial Brown Skuas (*S. antarctica lonnbergi*) were dominant (on their own territory) to all other conspecific skuas, which resulted in the territory owners having higher foraging and fledging success (Hahn and Bauer 2008). On Steeple Jason, skuas nest away from the mixed colony, thus their breeding and feeding areas are separate. Thus, skuas foraging within the mixed colony only need to defend their feeding rights, resulting in higher frequencies of food fights and kleptoparasitism.

In contrast to the skuas, caracaras fought mostly over territory. Caracaras on Steeple Jason nest in tussac along the colony margin, and aggressively defend their breeding territories against intruders (Strange 1996). However, their aggression appears to primarily target other Striated Caracaras, especially sub-adults and juveniles. A study on social hierarchies among four Falkland Island scavenging raptor species (Dwyer and Cockwell 2011) found that Striated Caracaras were least likely to be the aggressor toward the other three species (Variable Hawk, *Buteo polyosoma*; Southern Caracara, *Caracara plancus*; Turkey Vulture, *Cathartes aura jota*); however adult Striated Caracaras were the aggressors 97-100% of the time against conspecific sub-adults or juveniles. In an avian predator assemblage at Rockhopper Penguin colonies on Staten Island (Tierra del Fuego), observers did not report aggressive interactions between Striated Caracaras and the other species, and the most common activity for all predators was searching (Liljesthröm et al. 2008). Caracaras do cannibalize each other's nests/chicks (Meiburg 2006), so aggressive defence against other caracaras likely helps increase a pair's reproductive success.

I found no direct evidence that food was limited. In fact, food limitation is unlikely given that potential prey (150,000 eggs or chicks) vastly outnumber the predators (620 birds). A crude estimate for the numbers of live prey required by both predators and their chicks was 11,400 albatross chicks plus 19,300 penguin chicks. These values are well below the number of live chicks likely available. Black-browed Albatross lay a single egg, which is largely inaccessible to both predators (AVB, pers. obs.). However, with a population of 171,000 pairs and a likely fledging success of about 0.6 chicks per nest with egg (reported for Black-browed Albatross at New Island, Falkland Islands; Catry et al. 2011b), at least 100,000 albatross chicks were available as prey during the season. Rockhopper Penguins lay two eggs, although in most locations the smaller first egg (or just hatched chick) is lost during the hatching period (Lamey 1993, St. Clair and St. Clair 1996). With a population on Steeple Jason of 59,000 pairs and a likely fledging success of about 0.8 (the average reported for Rockhopper Penguins from multiple locations in the Falkland Islands; Clausen and Pütz 2002), at least 47,000 penguin chicks were available as prey.

Not all of these prey were equally—or easily—accessible to predators; large, healthy Rockhopper Penguin chicks can escape from or fend off predators (AVB pers. obs.; see also Young 1994 for Adélie Penguins, *Pygoscelis adeliae*). Black-browed Albatross chicks use projectile vomit of stinky orange stomach oil as a deterrent to predators (Warham 1996). However, in the North section of the colony, I estimated that 800-1500 uneaten albatross or penguin carcasses were available each week of the study. Extrapolated to the West and South sections, a total of 21,800 dead eggs or chicks were available between late December and early February. The maximum adult predator population for the entire island was about 470 skuas and 150 caracaras, some of which did not forage in the mixed colony (AVB, pers. obs.).

Additionally, for both predators scavenging on dead prey for food was much more common than killing live prey. Caracaras and skuas are both migratory in winter, and food shortages during the non-breeding period likely limit total abundance (Meiburg 2006). As a consequence, the summer population of these predators is probably well below carrying capacity—for food, at least—in a seabird colony as large as the one on Steeple Jason.

Given apparently ample food supplies, I expected that caracaras and skuas would exhibit high spatial and temporal overlap in their diet. Indeed, they had very similar diets based on time of day, a result consistent with previous studies in various taxa (e.g. Huey and Pianka 1983, Kronfeld-Schor and Dayan 2003). The two predators did not appear to be specializing exclusively on different prey types in different stages of the season, although some preferences may have existed. For example, during the hatching/brood-guard stage, only skuas captured live penguin eggs (predation) and removed them from the colony, but both predators scavenged dead penguin eggs. At New Island (Falkland Islands), skuas were the main cause of egg loss in Rockhopper Penguins; however only 35% of eggs taken came from beneath an incubating parent (St. Clair and St. Clair 1996). Rockhopper eggs commonly get displaced from the nest (Lamey 1993). In mid-December during peak hatching, I found a total of 30 eggs (in two 20*20 m plots) abandoned outside of the nest, thus I likely over-estimated skua predation (versus scavenging) on penguin eggs. In comparison, during the hatching/brood-guard stage caracaras took mostly live penguin chicks (predation), also removing them from the colony. On Staten Island (Tierra del Fuego) caracaras were the main predator in Rockhopper Penguin colonies, and were responsible for 93% of predation on chicks (Liljesthröm et al. 2008). In another Falkland Island mixed seabird colony, caracaras rarely captured live penguin chicks, and instead stole them from skuas or scavenged dead chicks (Catry et al. 2008).

During the post-guard stage, both caracaras and skuas targeted albatross chicks. Caracaras fed on dead chicks, but some pairs captured and killed live albatross chicks. Skuas almost exclusively scavenged on dead chicks, and I observed as many as six individuals congregated at caracara kills sites, awaiting opportunities to steal pieces from a carcass. Similar resource use patterns exist among sympatric Brown Skuas and South Polar Skuas (*S. maccormicki*) breeding near the Antarctic Peninsula; like the current study, niche overlap was high (both fed on penguins), but one species captured chicks and the other scavenged on dead adults, allowing the two species to co-exist (Grilli and Montalti 2012). In contrast, skuas at New Island were the main predators on albatross chicks, whereas caracaras acted as scavengers (Catry et al. 2011b). At Steeple Jason, differences in prey type likely resulted from the physical (or prey-handling) capabilities of the two predators: skuas lack the force necessary to subdue and kill large albatross chicks, and caracaras lack the bill structure to grab and carry penguin eggs.

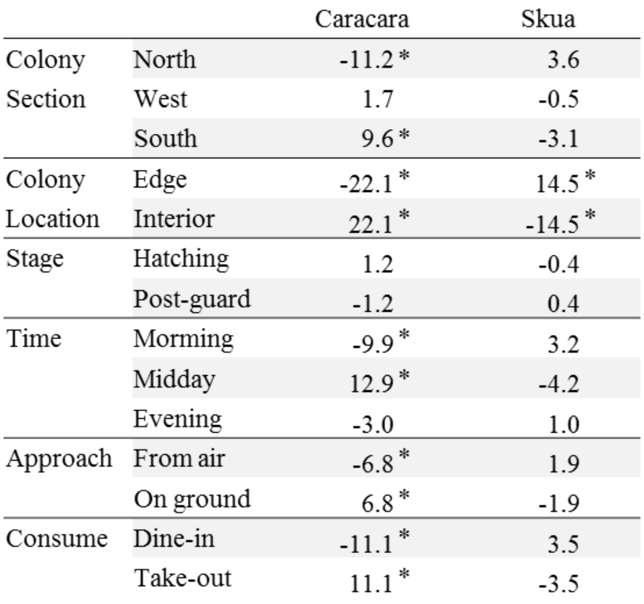
Spatially, caracaras and skuas captured similar prey types in similar colony sections, but not in the same areas within the colony. Both predators took more prey—and more prey types—from the North colony section. Caracaras captured a variety of prey in all three colony sections, which reflects the uniform distribution of their nest sites along the inland margin of the mixed colony (Woods 2007). Skuas were virtually absent in the South and West, which may be related to distance from the main skua breeding areas. The largest skua club was located adjacent to the North colony section, presumably because it afforded easy access to a preferred foraging area. Caracaras took more prey in the colony interior, mostly scavenging dead albatross chicks; skuas foraged in both the interior (dead albatross chicks) and along the colony edge (regurgitations). Adult albatross commonly used the open areas along the colony edge to rest, preen, and vomit up boluses of undigested food matter (AVB, pers. obs.). Brown skuas at King George Island on the Antarctic Peninsula also concentrated their feeding at the colony edge, targeting penguin chicks (Emslie et al. 1995).

Caracaras spent the majority of their time at the colony perching, which reflected their superior agility on the ground versus in the air. They approached prey from the ground and primarily from within the colony. At Rockhopper Penguins colonies on Staten Island, Striated Caracaras captured prey from tussac perches surrounding penguin nesting areas, or from “central tussacs” which acted as functional edges (Liljesthröm et al. 2008). I observed a similar strategy, in which caracaras seemed to use the steep sides and narrow valleys of the South and West colony sections—or boulders, ridges, and vacant albatross nests within all colony sections—as convenient perching locations from which to attack potential prey. In contrast, skuas spent the majority of their time at the colony in-flight, hovering above the breeding albatross and penguin nests, searching for prey. *Stercorarius* skuas typically nest and forage in flat open areas, which enables them to maximize their flight capabilities (Furness 1987, 1996). At Steeple Jason, skuas seemed to be exploiting the broad plain of the North colony section, which facilitated prolonged and almost effortless search flights.

The resource use patterns of caracaras and skuas at Steeple Jason appear unrelated to interspecific interference competition: despite having extensive dietary, spatial, and temporal overlap, the two species rarely fought. On the few occasions when the two predators did fight, each species was equally likely to be the aggressor. However, the extent of resource overlap and the type of interactions between caracaras and skuas may depend on local conditions. A study from New Island (Catry et al. 2011a) tentatively attributed the rapid decline in the local skua population to a concurrent increase in the caracara population. The numbers of caracaras and skuas on New Island are the largest found in the Falkland Islands; caracaras are dominant over skuas and they exclude skuas from carrion or kleptoparasitize their prey (Catry et al. 2008). At New Island, higher densities of predators may influence interspecific interactions and foraging, whereas at Steeple Jason behavioral or morphological attributes better accounted for any observed foraging preferences.

In conclusion, although caracaras and skuas were dissimilar in how they hunted, they ate the same prey. Any preferences in prey types between the two predators likely derived from behavioral or morphological attributes, and not from food limitation during the breeding season. This study found that caracaras and skuas shared non-limiting resources with minimal competition; however, interactions between these two Falkland Island apex predators in other locations are likely context-dependent. Applying the predictions of niche theory provided a functional framework for explaining species co-existence among caracaras and skuas at Steeple Jason Island, and a similar approach could inform studies on these species at other locations.

Table 3.1. Difference between the observed and expected values (expressed as percentages) by predator for (1) spatial variables: colony section and colony location; (2) temporal variables: stage and time of day; (3) foraging behaviors: approach location and consume location (*asterisks denote differences ≥ 5%).



		Caracara	Skua
Colony Section	North	-11.2 *	3.6
	West	1.7	-0.5
	South	9.6 *	-3.1
Colony Location	Edge	-22.1 *	14.5 *
	Interior	22.1 *	-14.5 *
Stage	Hatching	1.2	-0.4
	Post-guard	-1.2	0.4
Time	Morming	-9.9 *	3.2
	Midday	12.9 *	-4.2
	Evening	-3.0	1.0
Approach	From air	-6.8 *	1.9
	On ground	6.8 *	-1.9
Consume	Dine-in	-11.1 *	3.5
	Take-out	11.1 *	-3.5

Table 3.2. Difference between the observed and expected values (expressed as percentages) by predator for interaction effects between prey types and (1) spatial variables: colony section and colony location; (2) temporal variables: stage and time of day; (3) foraging behaviors: approach location and consume location. Regu = regurgitation; *asterisks denote differences ≥ 5%.

			Predation				Scavenge				
			Albatross		Penguin		Albatross		Penguin		
			Egg	Chick	Egg	Chick	Egg	Chick	Egg	Chick	Regu
Diet		Caracara		0.6	-2.9	9.8	1.1	1.7	2.3	0.1	-12.7
		Skua		-0.2	0.9	-3.2	-0.4	-0.5	-0.7	0.0	4.1
Colony Section	North	Caracara	----	----	-2.4	5.6*	-0.5	-1.4	-0.5	-0.4	-11.6*
	West		----	0.6	-0.5	4.2	1.7	-4.3	0.3	0.6	-0.8
	South		----	----	----	----	----	7.3*	2.5	----	-0.3
	North	Skua	----	----	0.8	-1.8	0.2	0.4	0.2	0.1	3.7
	West		----	-0.2	0.2	-1.3	-0.5	1.4	-0.1	-0.2	0.3
	South		----	----	----	----	----	-2.4	-0.8	----	0.1
Colony Location	Edge	Caracara	----	----	----	1.6	----	-2.3	-0.8	-0.8	-19.8*
	Interior		----	1.2	-1.5	4.7	1.2	25.0*	1.6	-4.6	-5.3*
	Edge	Skua	----	----	----	-1.0	----	1.5	0.5	0.5	13.1*
	Interior		----	-0.8	1.0	-3.1	-0.8	-16.4*	-1.0	3.0	3.5
Stage	Hatching	Caracara	----	-0.3	-2.9	8.1*	----	----	2.6	0.7	-6.9*
	Post-guard		----	0.8	----	1.7	1.1	1.7	-0.3	-0.5	-5.7*
	Hatching	Skua	----	0.1	0.9	-2.6	----	----	-0.8	-0.2	2.2
	Post-guard		----	-0.3	----	-0.5	-0.4	-0.5	0.1	0.2	1.8
Time	Morning	Caracara	----	----	-0.3	-0.5	----	-3.0	-0.3	-1.1	-4.8
	Midday		----	----	0.1	0.2	----	1.0	0.1	0.3	1.5
	Evening		----	0.6	-2.7	8.7*	1.1	8.6*	1.4	2.3	-7.0*
	Morning	Skua	----	-0.2	0.9	-2.8	-0.4	-2.8	-0.5	-0.7	2.3
	Midday		----	----	----	1.7	----	-3.9	1.1	-1.1	-0.8
	Evening		----	----	----	-0.5	----	1.3	-0.4	0.3	0.3
Approach	From air	Caracara	----	1.1	-1.9	3.6	1.1	-2.3	1.3	-2.2	-7.5*
	On ground		----	----	----	2.2	0.8	10.0*	0.8	-0.3	-6.7*
	From air	Skua	----	-0.3	0.5	-1.0	-0.3	0.7	-0.4	0.6	2.1
	On ground		----	----	----	-0.6	-0.2	-2.8	-0.2	0.1	1.9
Consume	Dine-in	Caracara	----	0.9	----	1.7	1.5	-5.9*	1.5	----	-10.7*
	Take-out		----	-0.3	-3.1	8.8*	-0.3	7.3*	0.3	-0.1	-1.6
	Dine-in	Skua	----	-0.3	----	-0.6	-0.5	1.9	-0.5	----	3.4
	Take-out		----	0.1	1.0	-2.8	0.1	-2.3	-0.1	0.0	0.5

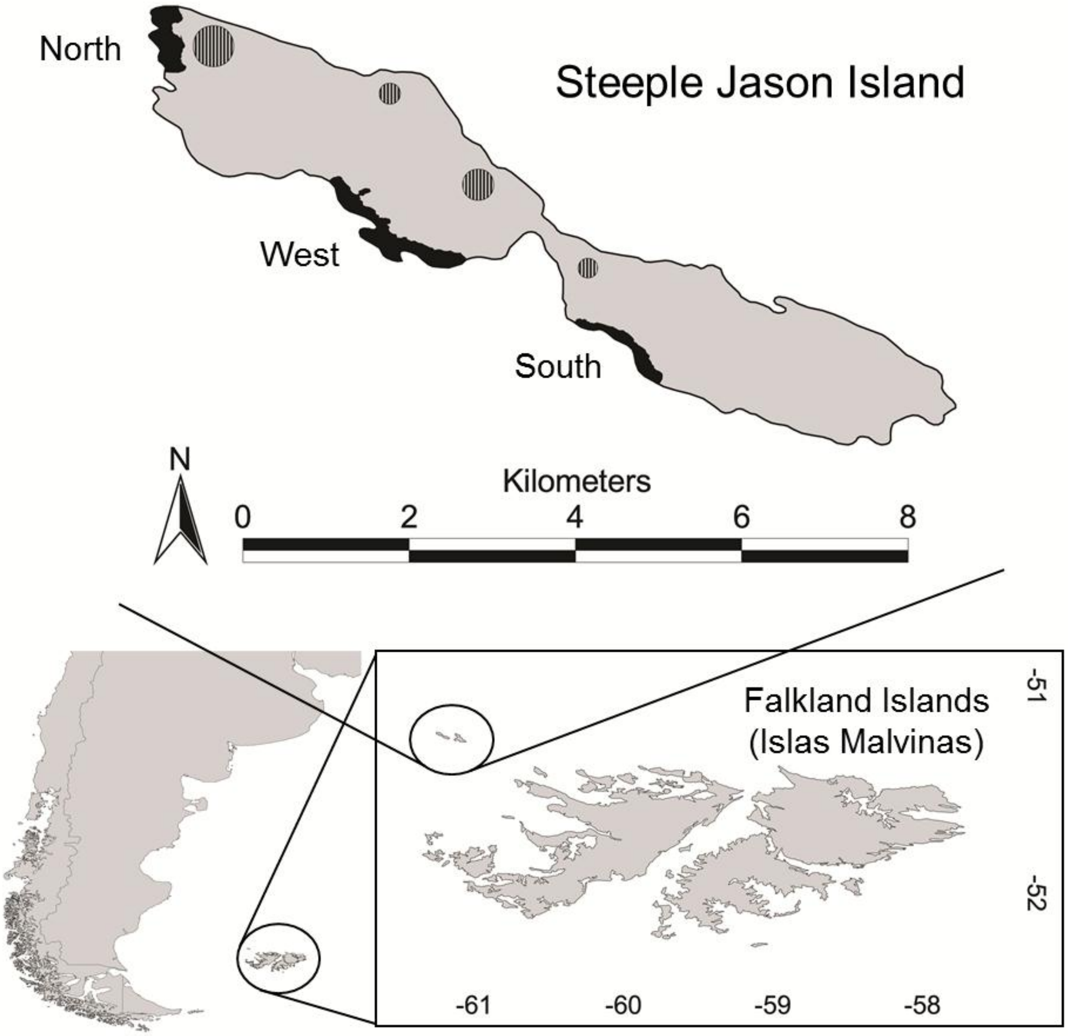


Fig. 3.1. Steeple Jason Island is on the north-western margin of the Falklands archipelago. Observations were made in the black shaded areas that represent the sections of the mixed colony. Circles show the major skua breeding areas (clubs).

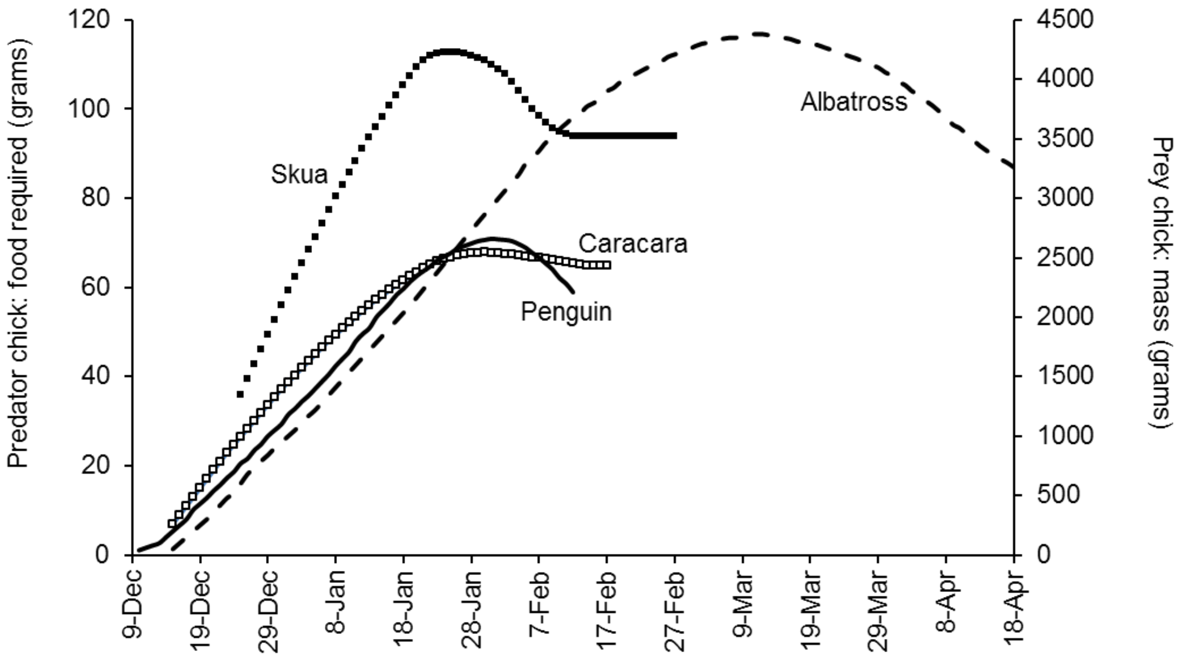


Fig. 3.2. Interpolated curves from hatching through fledging for (1) caracara (□□□) and skua (■■■) food requirements (per chick, extrapolated using data from Catry et al. 2008, Phillips et al. 1999, and Ricklefs 1968); and (2) albatross (‒ ‒) and penguin (—) chick growth (per chick, modified from Huin et al. 2000 and Poisbleau et al. 2008, respectively).

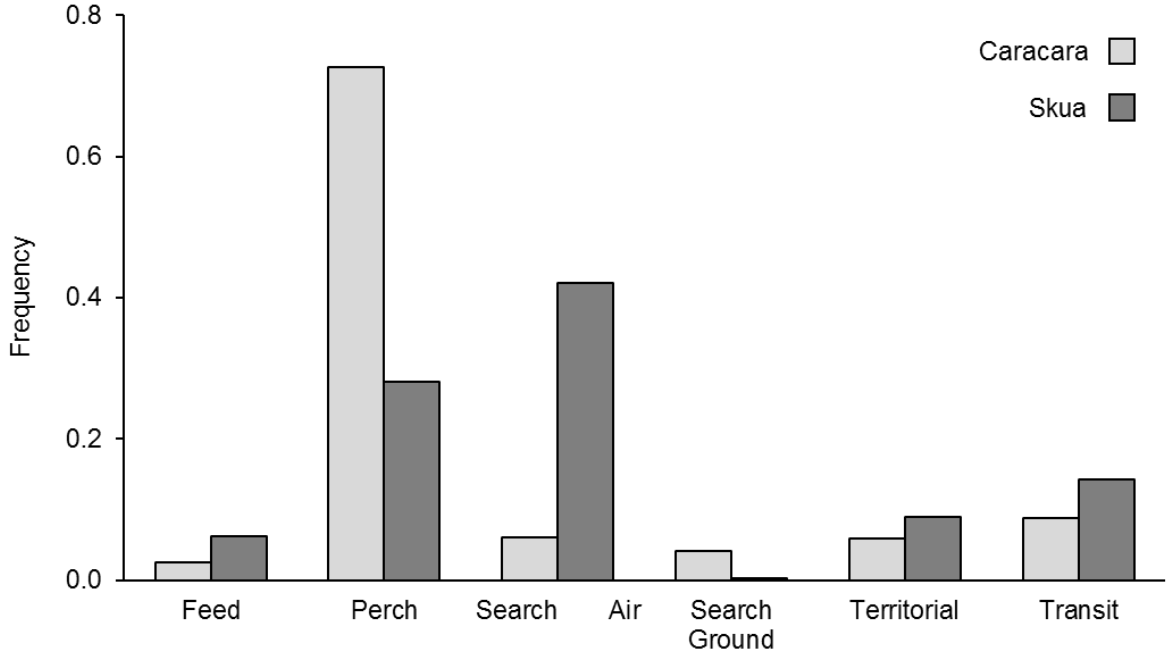


Fig. 3.3. Relative behavior frequencies for caracaras and skuas from instantaneous scan sampling. Caracaras perched more than expected (+25%) and searched from the air less than expected (-20%). Skuas did the opposite: they perched less than expected (-19%) and searched from the air more than expected (+16%). N = 1135 caracara observations, n = 1474 skua observations; Pearson $\chi^2 = 672.68$, df = 5, $p < 0.0001$.

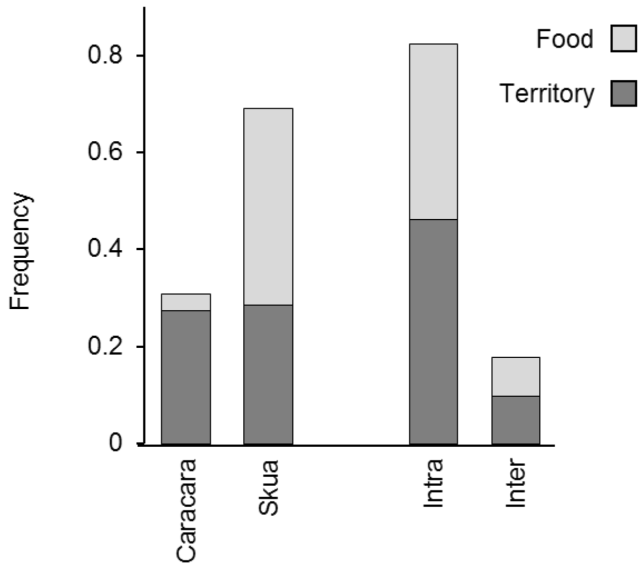


Fig. 3.4. Frequency and type of territorial behavior. Most caracara disputes were not related to food, whereas most skua disputes were food-related (Pearson $\chi^2 = 47.71$, df = 1, $p < 0.001$; n = 77 caracaras observations, n = 172 skua observations). Most disputes, whether over food or not food-related, occurred primarily between individuals of the same species (Pearson $\chi^2 = 0.04$, df = 1, $p = 0.85$; n = 110 food, n = 139 territorial).

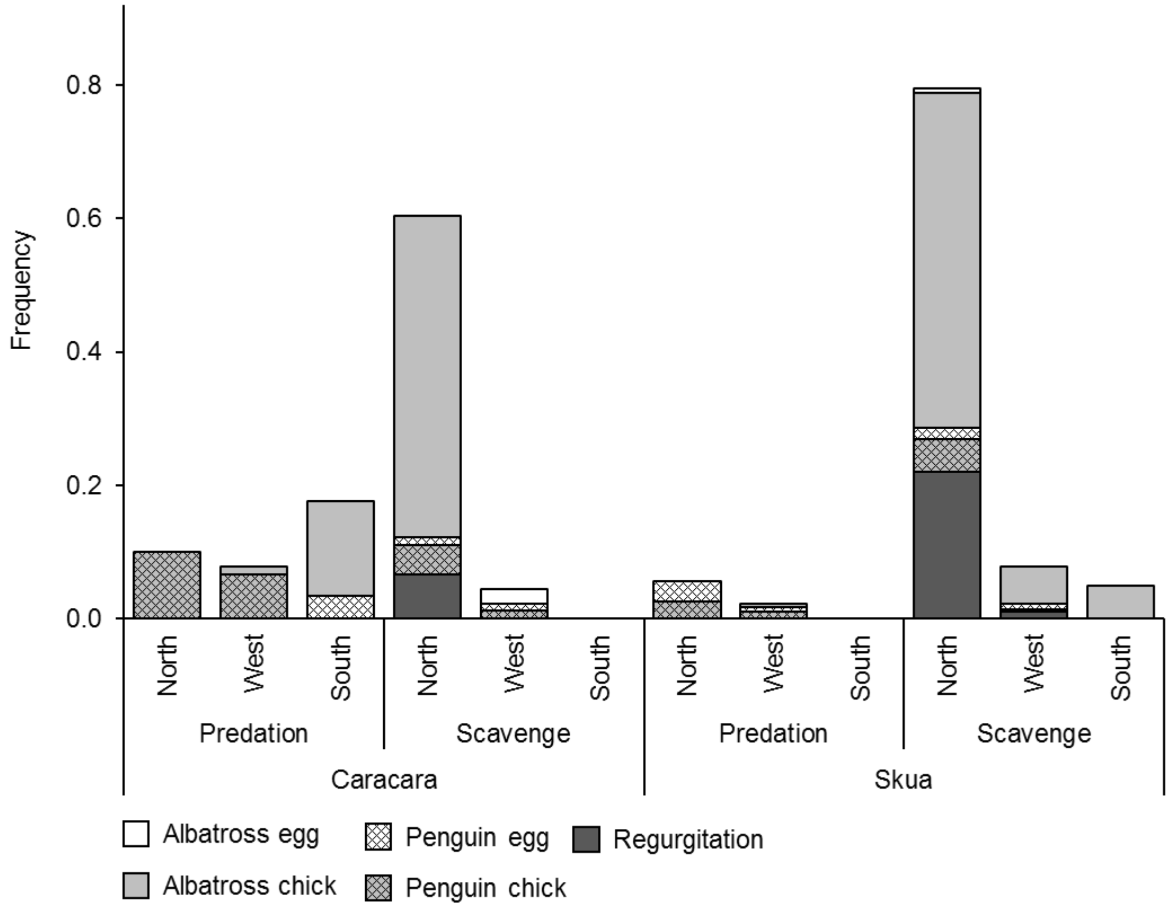


Fig. 3.5. Independent of diet, both predators foraged in all colony sections. However, predators differed proportionately in the colony sections in which they captured prey (Pearson $\chi^2 = 15.88$, df = 1, $p < 0.001$). Based on colony sections, caracaras and skuas had high overlap in their diet (observed overlap index = 0.92, mean of simulated indices = 0.19 ± 0.003 SE, $p = 0.008$). Three cases had observed values that were more than 5% different from expected: in the North caracaras took about 6% more live penguin chicks than expected, and scavenged regurgitations 12% less than expected; in the South caracaras took 7% more dead albatross chicks than expected. N = 91 caracara observations, n = 283 skua observations.

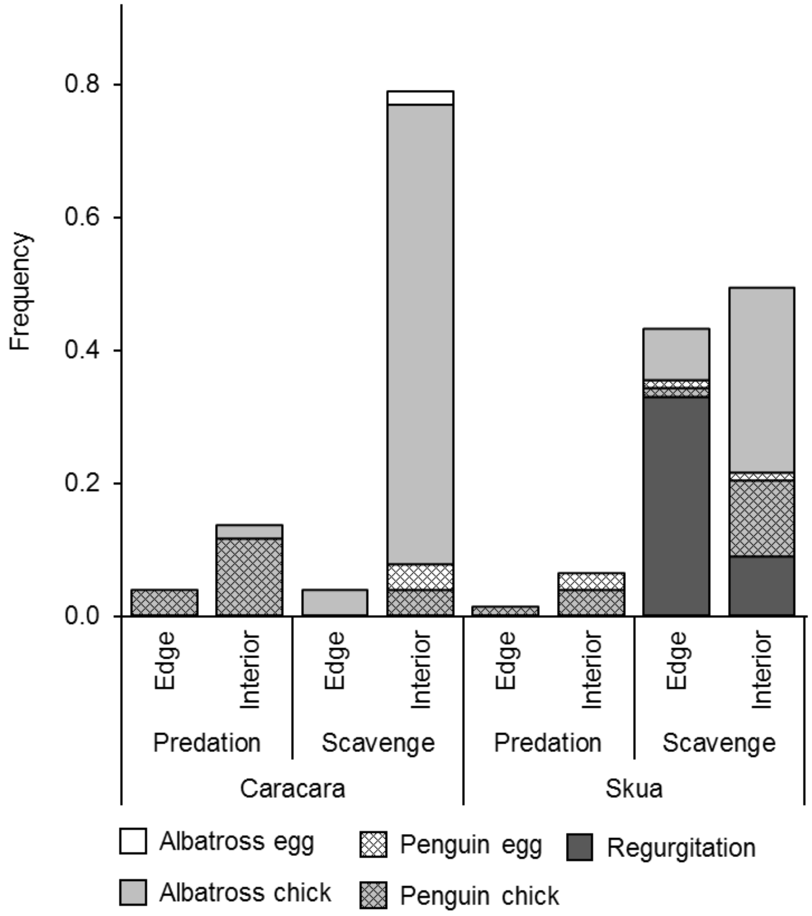


Fig. 3.6. Independent of diet, both predators captured prey on the colony edge and in the colony interior. However, the predators differed proportionately in the locations from which they took their prey (Pearson $\chi^2 = 20.10$, df = 1, $p < 0.001$). Based on colony location, caracaras and skuas did not significantly overlap in their diet (observed overlap index = 0.63, mean of simulated indices = 0.23 ± 0.003 SE, p = 0.13). Five cases had observed values that were more than 5% different from expected: in the colony interior caracaras took about 25% more dead albatross chicks than expected; caracaras scavenged regurgitations less than expected both within the colony (-5%) and on the colony edge (-20%); skuas took 16% fewer dead albatross chicks than expected from the colony interior, and 13% more regurgitations than expected from the edge of the colony. N = 52 caracara observations, n = 79 skua observations.

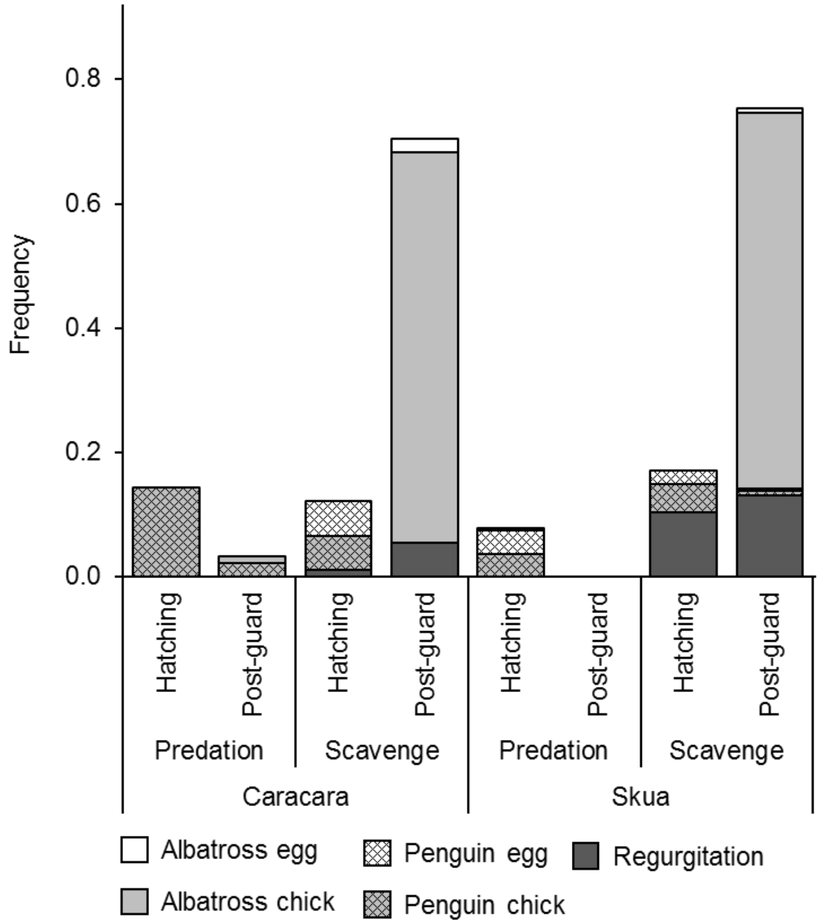


Fig. 3.7. Independent of diet, both predators fed more in the post-guard stage (Pearson $\chi^2 = 0.09$, df = 1, p = 0.75). Based on stage of the breeding season, caracaras and skuas had high overlap in their diet (observed overlap index = 0.96, mean of simulated indices = 0.19 ± 0.003 SE, p = 0.017). Three cases had observed values that were more than 5% different from expected: during hatching caracaras took about 8% more live penguin chicks than expected; caracaras scavenged regurgitations less than expected during both hatching (-7%) and the post-guard stage (-6%). N = 91 caracara observations, n = 283 skua observations.

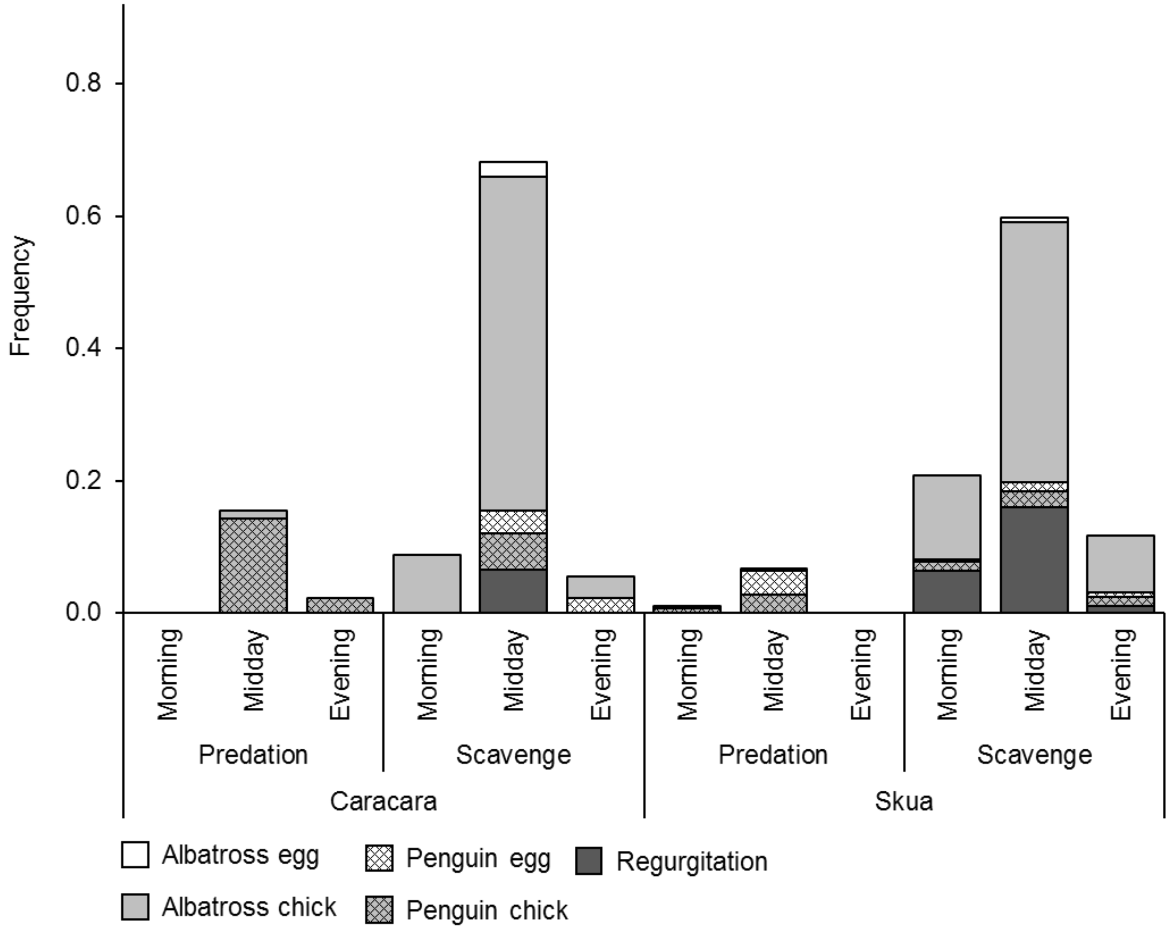


Fig. 3.8. Independent of diet, both predators foraged throughout the day. However, the predators differed proportionately in the time of day during which they captured most of their prey (Pearson $\chi^2 = 10.19$, df = 2, $p < 0.01$). Based on time of day, caracaras and skuas had high overlap in their diet (observed overlap index = 0.92, mean of simulated indices = 0.22 ± 0.003 SE, $p = 0.005$). Three cases had observed values that were more than 5% different from expected: in the evening caracaras took about 9% more live penguin chicks than expected, 9% more dead albatross chicks than expected, and 7% fewer regurgitations than expected. N = 91 caracara observations, n = 283 skua observations.

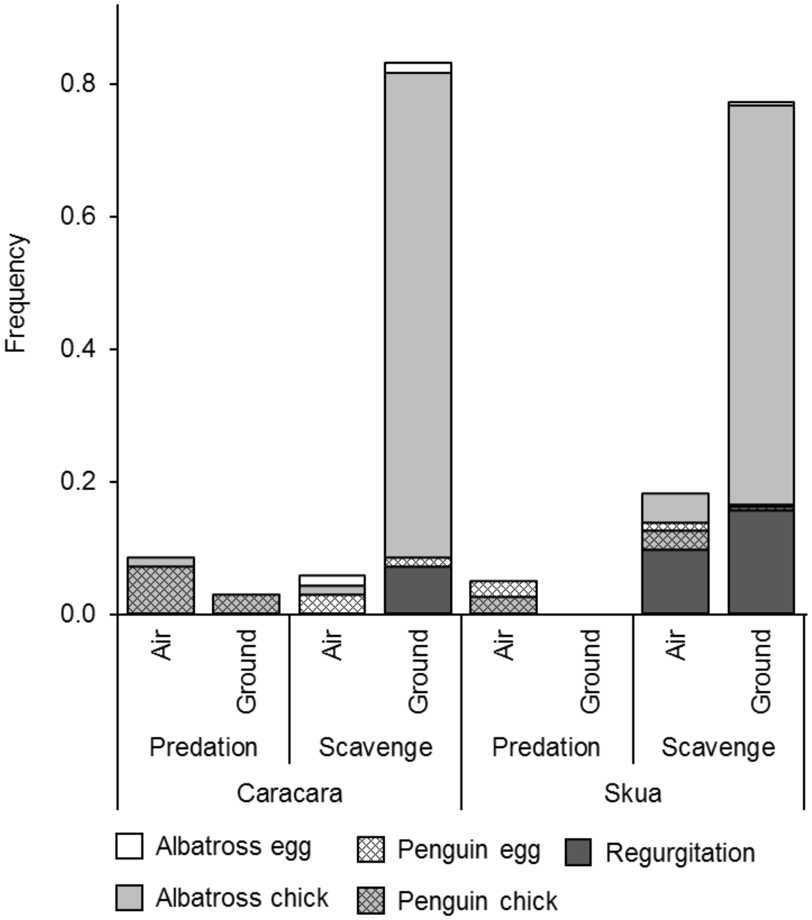


Fig. 3.9. Independent of diet, both predators approached prey from the ground most of the time (Pearson $\chi^2 = 2.54$, df = 1, $p = 0.11$). Based on their approach behavior, caracaras and skuas had high overlap in their diet (observed overlap index = 0.97, mean of simulated indices = 0.15 ± 0.003 SE, $p = 0.008$). Three cases had observed values that were more than 5% different from expected: caracaras approached dead penguin chicks from the ground 10% more than expected, and approached regurgitations from the air (-8%) and ground (-7%) less than expected. N = 71 caracara observations, n = 250 skua observations.

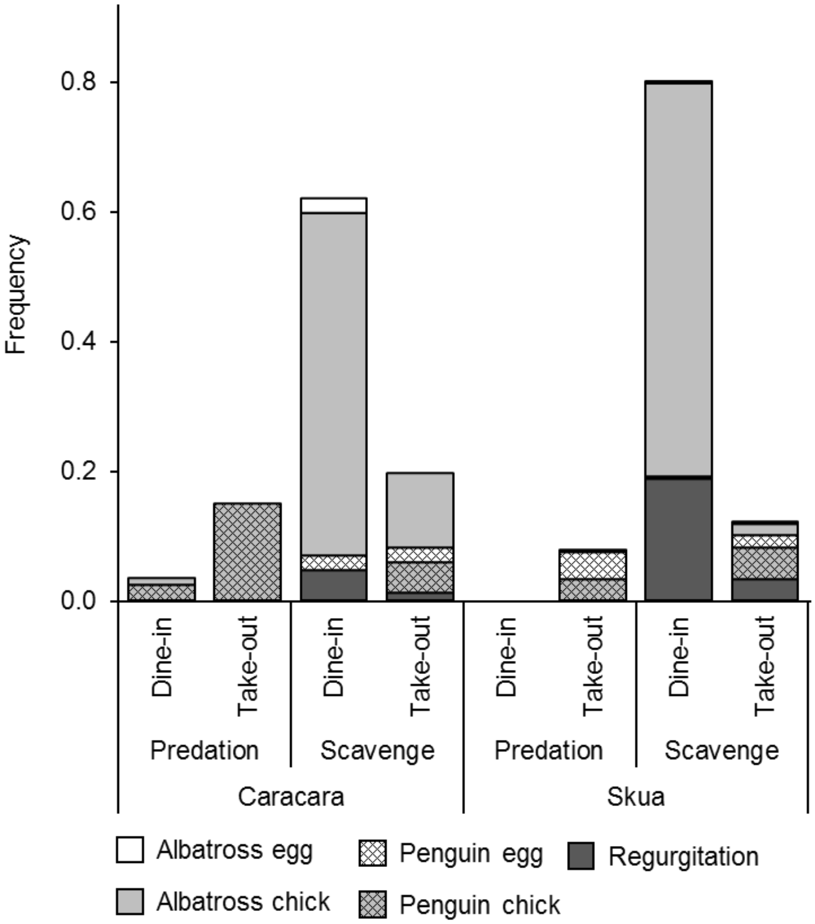


Fig. 3.10. Independent of diet, both predators primarily consumed their prey on-site. However, the predators differed proportionately in where they consumed their prey (Pearson $\chi^2 = 7.87$, df = 1, $p < 0.01$). Based on where they consumed their prey, caracaras and skuas had high overlap in their diet (observed overlap index = 0.94, mean of simulated indices = 0.20 ± 0.003 SE, p = 0.011). Three cases had observed values that were more than 5% different from expected: caracaras captured and removed (take-out) live penguin chicks (9%) and dead albatross chicks (7%) more than expected, and ate dead albatross chicks (-6%) and regurgitations (-11%) on-site (dine-in) less than expected. N = 87 caracara observations, n = 272 skua observations.

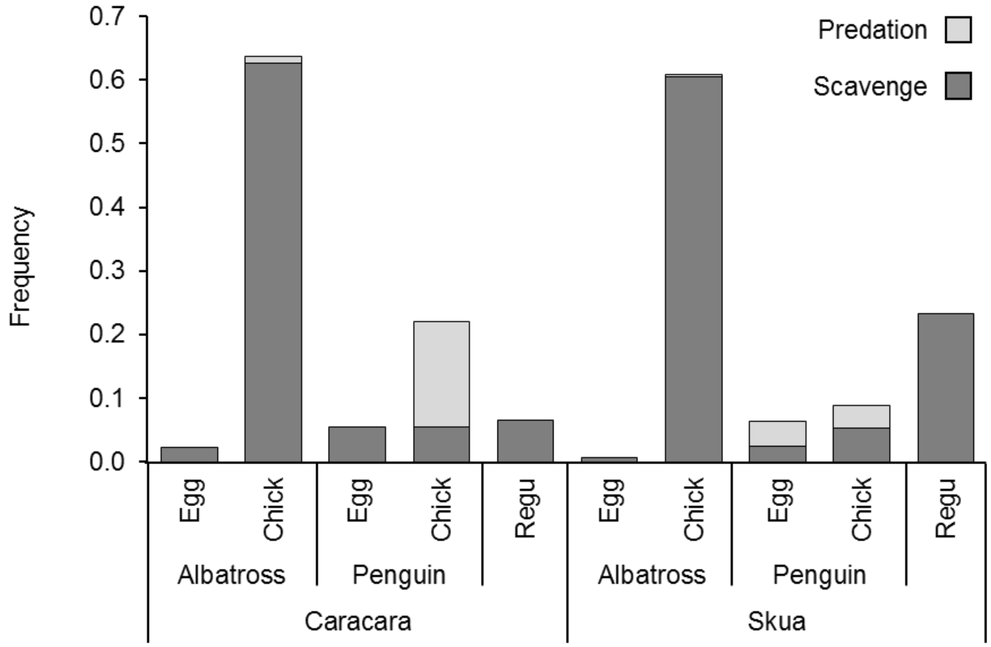


Fig. 3.11. Overall, caracaras and skuas had high overlap in their diet (observed overlap index = 0.94, mean of simulated indices = 0.29 ± 0.004 SE, p = 0.026). Two cases had observed values that were more than 5% different from expected: caracaras took about 10% more live penguin chicks than expected, and ate about 13% fewer regurgitations than expected. N = 91 caracara observations, n = 283 skua observations.

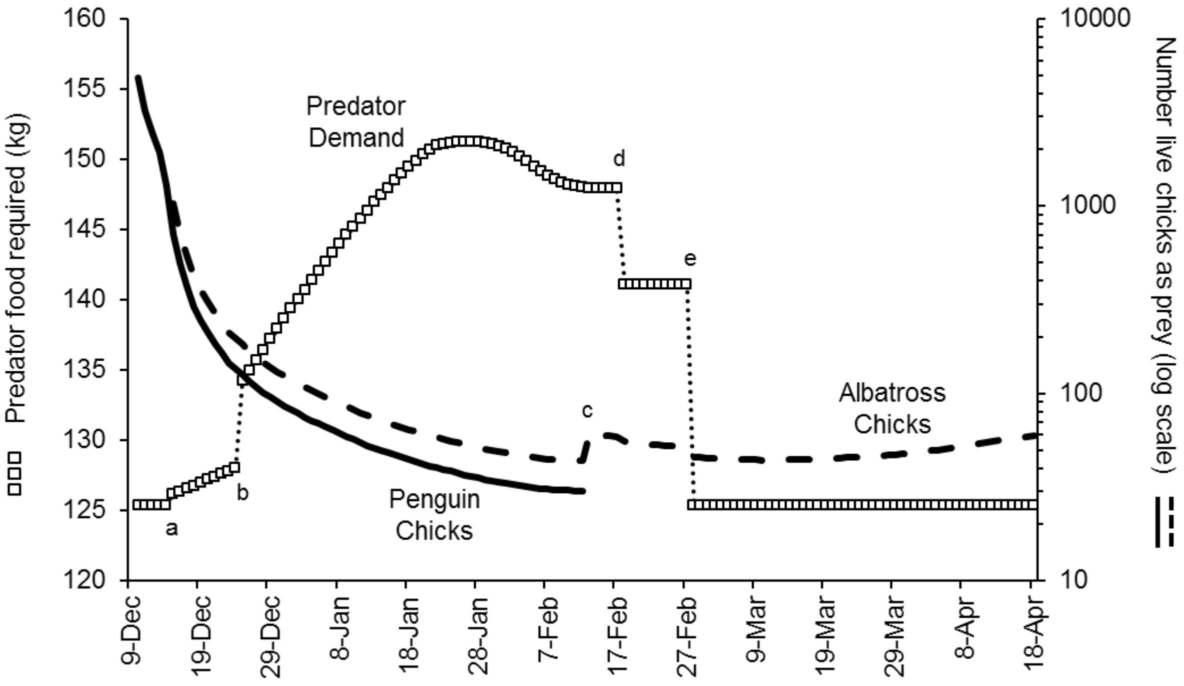


Fig. 3.12. Total predator food requirements in kg of seabird meat (□□□), and in the corresponding numbers of live albatross (– –) and penguin (—) chicks. Marked events correspond to (a) caracara chick median hatching; (b) skua chick median hatching; (c) end of penguin chick-rearing; (d) end of caracara chick-rearing; (e) skua fledgling departure. K = constant 4825, n = number of chicks.

Appendix 3.1. Measurements for adult and sub-adult (> 1 year old) Striated Caracaras on Steeple Jason Island, Falkland Islands, December 2005.

	Tail (mm)	Wing (mm)	Bill length (mm)	Bill depth (mm)	Weight (g)
Caracara	216	378	33.5	23.0	1275
(adult)	251	427	34.8	24.5	1825
	252	418	33.0	25.1	1650
	245	410	32.2	24.1	1525
	241	405	33.2	23.3	1475
	228	400	32.4	24.4	1425
	268	432	32.2	23.9	1675
	254	428	33.8	24.6	1625
	250	405	32.8	24.2	1500
	247	416	34.0	24.3	1600
	245	420	35.0	24.8	1775
	245	417	36.7	25.6	2000
	231	405	33.6	23.1	1525
	258	438	35.1	23.5	1600
	210	407	34.1	23.7	1650
	246	438	34.4	23.1	1800
	231	385	32.8	23.1	1325
	242	421	35.0	24.6	1775
	230	411	33.6	23.2	1500
Mean ± SE	242 ± 3	414 ± 4	33.8 ± 0.3	24 ± 0.2	1607 ± 41
Caracara	230	405	30.9	22.5	1325
(sub-adult)	200	395	33.1	22.7	1525
	246	424	34.3	24.1	1900
	236	419	32.4	24.5	1575
	232	402	31.1	22.3	1350
	224	410	34.4	24.3	1625
	246	415	35.0	24.9	1625
	178	389	33.1	23.9	1650
Mean ± SE	224 ± 8	407 ± 4	33 ± 0.5	23.7 ± 0.4	1572 ± 64

Appendix 3.2. Measurements for adult Falkland Skuas on Steeple Jason Island, Falkland Islands, December 2005.

	Tail (mm)	Wing (mm)	Bill length (mm)	Bill depth (mm)	Weight (g)
Skua	155	365	46.9	18.5	1275
(adult)	173	392	47.1	19.5	1525
	157	378	50.7	18.4	1100
	150	382	47.5	19.7	1200
	148	380	46.1	19.1	1125
	157	388	45.6	18.4	1325
	158	400	47.4	18.2	1150
	160	385	44.7	18.0	1300
	173	397	48.6	18.0	1175
	146	377	45.6	17.8	1600
	162	380	48.2	19.0	1200
Mean ± SE	158 ± 3	384 ± 3	47.1 ± 0.5	18.6 ± 0.2	1270 ± 49

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