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FORAGING-NICHE SEPARATION OF BREEDING GENTOO AND CHINSTRAP PENGUINS, SOUTH SHETLAND ISLANDS, ANTARCTICA

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Abstract. The realized niches of closely related species must differ if these species are to co-exist stably. The Gentoo (*Pygoscelis papua*) and Chinstrap Penguins (*P. antarctica*) breed concurrently in the Scotia Sea and Antarctic Peninsula regions. To identify species- and site-specific foraging niches, we compared the two species' foraging niches, including diet and foraging locations, at two sites in the South Shetland Islands with contrasting marine habitats. Both species fed primarily on Antarctic krill (*Euphausia superba*), though fish was also a component of the Gentoo Penguin's diet. Gentoo Penguins foraged closer to shore than did Chinstrap Penguins. Gentoo Penguins foraged during the day, while Chinstrap Penguins foraged throughout the diel cycle, sometimes traveling farther from shore on overnight foraging trips. In most cases, these species-specific foraging patterns were consistent with trends seen elsewhere in the region. However, within each species, site-specific differences in foraging niches were still evident. Overall, we observed that Gentoo Penguins traveled within consistent and limited distances from their colonies, but their diets varied by site in both meal mass and content. Chinstrap Penguins, in contrast, had a uniform diet of krill at both sites but varied the distance from shore and times at which they foraged.

Key words: Gentoo Penguin, Chinstrap Penguin, Pygoscelis papua, Pygoscelis antarctica, *niche, foraging ecology.*

Separación de Nicho de Forrajeo durante el Periodo de Cría en los Pingüinos *Pygoscelis papua* y *P. antarctica,* en las Islas Shetland del Sur, Antártica

Resumen. El nicho realizado de especies próximamente relacionadas debe diferir para que estas especies puedan coexistir de forma estable. Los pingüinos *Pygoscelis papua* y *P. antarctica* crían simultáneamente en las regiones del Mar de Scotia y de la Península Antártica. Para identificar los nichos específicos de cada especie en cada sitio, comparamos los nichos de forrajeo de las dos especies, incluyendo la dieta y las localidades de forrajeo, en dos sitios con hábitats marinos contrastantes en las Islas Shetland del Sur. Las dos especies se alimentaron principalmente de krill (*Euphausia superba*), a pesar de que los peces también fueron un componente de la dieta de *P. papua*. Los individuos de *P. papua* forrajearon más próximos a la costa que los de *P. antartica* Los individuos de *P. papua* forrajearon durante el día mientras que los de *P. antartica* forrajearon durante todo el ciclo diario, y a veces viajaron lejos de la costa durante la noche para forrajear. En la mayoría de los casos, estos patrones de forrajeo específicos para cada especie fueron consistentes con las tendencias observadas en la misma región. Sin embrago, dentro de cada especie, las diferencias particulares en los nichos de forrajeo para cada sitio fueron aún evidentes. De modo general, observamos que los individuos de *P. papua* viajaron a distancias consistentes y limitadas desde sus colonias, pero que sus dietas variaron entre sitios en términos de masa y de contenido. De modo contrastante, los individuos de *P. antartica* tuvieron una dieta uniforme de krill en los dos sitios, pero variaron en la distancia de forrajeo desde la costa y en los momentos en que forrajearon.

INTRODUCTION

Closely related species often share similar life-history traits and similar potential niches. When these species have overlapping ranges, they may compete for similar resources. Theory predicts that a complete overlap of niches should lead to an unsustainable level of competition (Lack 1945, MacArthur 1958, Hardin 1960). Ultimately, one of the populations should fail. It is therefore necessary for closely related species to differ in their realized niches if they are to continue to co-exist in overlapping ranges.

The Gentoo (*Pygoscelis papua*) and Chinstrap (*P. antarctica*) Penguins have overlapping breeding distributions in the Antarctic Peninsula region (Woehler 1993). Here, both species consume primarily Antarctic krill (*Euphausia superba*; Volkman et al. 1980, Lishman 1985), share nesting habitat,

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and the timing of their breeding is similar (Trivelpiece et al. 1987). While breeding during the austral summer, both species are central-place foragers, with males and females returning to shore regularly to switch incubation duties with their mates and to feed their chicks (Williams 1995). Their foraging areas during this time are, therefore, locally constrained. These patterns indicate that there is substantial overlap in the ecological niches of these two species; however, there are documented differences in their foraging behaviors and diets. Gentoo Penguins consume more fish than do Chinstrap Penguins (Volkman et al. 1980, Karnovsky 1997) and feed on larger krill and a higher percentage of female krill (Miller and Trivelpiece 2007). Gentoo Penguins tend to dive deeper than Chinstrap Penguins, but they forage closer to shore (Trivelpiece et al. 1986, Miller and Trivelpiece 2008, Miller et al. 2009, Kokubun et al. 2010, Wilson 2010). This separation of foraging locations may maximize the efficiency of both species. Gentoo Penguins are larger and are most efficient diving at deeper depths, while Chinstrap Penguins are more efficient with relatively shallow dives (Kokubun et al. 2010, Wilson 2010). Small differences in the characteristics of foraging of Chinstrap and Gentoo Penguins (dive depth, location, and time of day) can lead to a substantial distinction in their multidimensional niches (Wilson 2010).

Studies of the foraging niches of these species have been limited to single sites, leaving in question whether the differences observed could be generalized for the Gentoo and Chinstrap Penguins throughout the region or whether the realized niche of each species is particular to the study site. Similarly, studies that have directly compared the foraging niches of these two species have been limited to one season, yet their diet and foraging behaviors are known to vary over time. In this study, we examined the foraging niches of the Chinstrap and Gentoo Penguins at two sites and over multiple years in order to develop our understanding of how these two species partition their foraging niches.

The foraging ecology of the Chinstrap and Gentoo Penguins is an important component of ecosystem monitoring in the Southern Ocean (CCAMLR 2004). To develop the potential of these species as tools in adaptive-management planning fully, the differences in their foraging ecologies must be defined. Determining differences in their niches is of interest, furthermore, because Chinstrap Penguin populations in the Scotia Sea region have been declining in recent decades, while Gentoo Penguin populations are stable or increasing (Forcada et al. 2006, Hinke et al. 2007).

In order to determine how much niche partitioning is fundamental to the species and how much is determined by spatial and temporal effects, we compared the foraging niches of Chinstrap and Gentoo Penguins at two sites with contrasting habitats, where they breed sympatrically, over 4–11 years. We looked specifically at diet composition and meal sizes, as well as foraging locations. By comparing results at our two study sites, as well as the results of earlier studies, we were able to identify both region-wide and site-specific characteristics of the foraging niches of these two species of *Pygoscelis*.

MATERIALS AND METHODS

STUDY SITE AND SPECIES

We studied the diet and foraging locations of breeding Gentoo and Chinstrap Penguins at two locations in the South Shetland Islands, Antarctica, where the ecosystem is monitored over the long term by the U.S. Antarctic Marine Living Resources (AMLR) program: Cape Shirreff (62° 28′ S, 60° 46′ W), Livingston Island, and Admiralty Bay (62° 10′ S, 58° 30′ W), King George Island. Cape Shirreff is on the northern side of the South Shetland Islands and faces the open ocean; a shallow inshore area is wide here, and the shelf break lies 25–30 km offshore. Admiralty Bay is on the southern side of the South Shetland Islands, and most surrounding marine habitat, both inside and outside of the bay, is deeper than 200 m. The number of penguins nesting at these sites changed considerably over the study period. At Cape Shirreff the population of the Gentoo Penguin was relatively stable from 1997–1998 to 2007–2008, with 812 ±101 nests, but that of the Chinstrap Penguin declined from 7617 to 3022 nests (Chisholm et al. 2008). At Admiralty Bay, the number of Gentoo Penguin nests increased from 1489 to 2907, while the number of Chinstrap Penguin nests decreased from 2122 to 1128 (Hinke et al. 2007, WZT unpublished data).

DIET SAMPLES

We collected samples of the penguins' diet during the chick-rearing period, early January to mid-February, in the austral summers of 1997–1998 through 2003–2004 for the Gentoo and through 2007–2008 for the Chinstrap. Each year, we collected a total of 20 to 40 diet samples from each species, with the exception of 2000–2001, when Gentoo Penguin diet samples were not collected at Admiralty Bay. Samples were collected from five individuals once every 5 days for the Chinstrap Penguins and once a week for the Gentoo over a 4- to 6-week period annually. We took samples at the same time of day (afternoon) since diet composition can be affected by time of day (Jansen et al. 1998). We followed adults returning from foraging trips to their nest sites to confirm that they were breeding and captured them before they fed their chicks. We recorded the number and approximate age of the chick(s) (±0.5 weeks), as well as the sex of the returning adult, determined by a visual comparison of both members of a pair; the larger bird was considered the male and the smaller the female. Roughly equal numbers of adult males and females were sampled.

We sampled stomach contents by the water-offloading technique (Wilson 1984). Stomach contents naturally separated into a fresh component from the top of the stomach, in which most prey were still intact, and a digested component

toward the bottom of the stomach, where prey were highly digested. Digested material in the stomach is concentrated and so is likely to have an energetic or nutritional content higher than that of the fresh component (WZT, unpubl. data). Therefore we separated the fresh and digested components, then sieved each of these components to drain off excess water and weighed them to determine the total mass of each individual's meal (±1 g), as well as the proportion of fresh and digested matter in each sample.

We sorted and panned all samples for evidence of Antarctic krill, fish (e.g., fish flesh, otoliths, lenses, fish scales), or other prey items such as other crustaceans and squid. Otoliths were reserved for future lab analysis. To determine percent composition of the diet, we separated and weighed krill and fish remains; when samples were highly mixed, we estimated the proportions. Digested fish material was difficult to separate from the rest of the sample, and in many cases where we found otoliths or other evidence of fish, we identified no measurable mass of fish material.

FORAGING LOCATIONS

We located foraging penguins by satellite telemetry, tracking them through the austral summers at both Cape Shirreff and Admiralty Bay; these studies started in different years but were consistent for both species at both sites from 2004–2005 to 2007–2008. The number of individuals tracked per site per year ranged from 3 to 17. Average sample size from 2004–2005 to 2007–2008 (years used in statistical analysis; see below) was 10.4 ± 3.6 SD. Like the diet sampling, these studies were conducted during chick rearing, but we used different individuals for satellite tagging and diet studies. All individuals selected were first confirmed to be breeding. Only one member of a pair was tagged, and the sample sizes of males and females were approximately equal. We attached Kiwisat satellite tags (130 × 35 × 20 mm, 100g; Sirtrack, New Zealand) and SPOT tags (90 × 20 × 15 mm, 70 g; Wildlife Computers, Redmond, WA) to the penguin's feathers with cable ties and either epoxy or super glue. Instruments were attached to the lower dorsal region in order to minimize drag (Bannasch et al. 1994). In 90% of all cases the penguins bore the tags for 1 to 2 weeks (range 2–24 days).

We downloaded the satellite locations from ARGOS and processed them in Matlab (The Mathworks, Natick, MA). We included only locations with an ARGOS quality of 1, 2, or 3, which indicate accuracy to <1 km; in practice, however, the accuracy may sometimes be poorer (Rodary et al. 2000). Therefore, to eliminate poor-quality locations, we filtered the locations further by calculating the distance between consecutive locations and excluding any location that would have required a travel speed >12 km hr^{-1} (following Clarke et al. 2006). We determined the water depth at each location with ETOPO2v2 gridded 2-min depths (www.ngdc.noaa.gov/mgg/gdas). Locations within 1 km of the colony were not included in analyses since they were within the expected error of the location data.

For each penguin, we determined its average distance from shore, maximum distance from shore, and the percent of uplinked locations at various depths. Because uplinks were infrequent, we could not identify foraging trips routinely, so we quantified these variables per deployment of a tag rather than per foraging trip. The frequency of uplinks was not consistent, requiring that we standardize the number of locations used in our analysis. Commonly this is done by interpolating location data, but there were not enough uplinks in our dataset to confirm the direction of travel. Therefore, interpolation was inappropriate. Instead, we subsampled one random location per day per penguin from our dataset when calculating the values. In preliminary analysis, we used *t*-tests to compare basic values calculated from the subsampled data to the complete dataset for both species at both sites. There were no significant differences between the subsampled and complete datasets for any variable for any of the groups.

Penguins' foraging behavior is known to vary between day and night, so we analyzed the differences between day and night foraging locations, defining daytime as sunrise to sunset (http://aa.usno.navy.mil/data).

STATISTICAL ANALYSES

We studied the diet and foraging locations of penguins for different lengths of time at the two sites and for the two species. For comparing sites and species, we used only data recorded concurrently (1997–1998 to 2003–2004 for diet and 2004–2005 to 2007–2008 for foraging locations). We used the complete time series on diet and foraging distributions only when looking at trends within species across years.

Variability in total meal mass, the proportion of digested material in the diet, distances from shore, and percent of time spent on the shelf vs. slope/deep-water regions were assessed with ANCOVAs, brood size and chick age included as covariates in each model. Variability in the percent frequency occurrence of fish was assessed with chi-squared tests for independence. The relationship between meal mass and chick age was assessed with linear regression, and the differences between the sexes in diet and measures of foraging location were assessed with unpaired *t*-tests. We used paired *t*-tests to compare measures of foraging by night and day within an individual. We used Pearson product-moment correlations to assess inter-annual correlations of measures of diet and foraging location by species and site. Statistical tests were performed with NCSS (NCSS, Inc., Kaysville, UT). All data were examined for normality, and nonparametric tests were used when necessary. All proportional data were transformed by either arcsine square-root or logit transformations. All *P*-values were two-tailed, and the level of significance was set at $P = 0.05$. Data are presented as means ± SD.

RESULTS

CHICK DIET

Antarctic krill was present in 100% of the diet samples, and it dominated the diet by weight for both the Gentoo and Chinstrap Penguins at both Cape Shirreff and Admiralty Bay (Table 1). Fish was a substantial part of the diet by weight only for Gentoo Penguins at Cape Shirreff, accounting for 29% of the diet. The amount of fish in the diet of Gentoo Penguins at Admiralty Bay and of all Chinstrap Penguins was <2%. Nonetheless, evidence of fish in diet samples was common for both species and at both locations. The frequency of occurrence of fish in diet samples was higher for the Gentoo Penguin at both sites (Cape Shirreff: $\chi^2_1 = 96.5$, $P < 0.001$; Admiralty Bay: $\chi^2_1 = 21.9$, $P < 0.001$). The frequency of fish in the diet of Chinstrap Penguins at Cape Shirreff and Admiralty Bay was similar ($\chi^2_1 = 3.0$, $P = 0.09$), while the number of samples from the Gentoo Penguin with fish was significantly fewer at Admiralty Bay than at Cape Shirreff ($\chi^2_1 = 25.4$, $P < 0.001$). Other prey items (other euphausiids, primarily *Thysanoessa macrura*; amphipods; squid; and unidentified invertebrates) were present but contributed less than 4% to the diet by weight for either species at either site.

The mass of the penguins' meals significantly differed by species (ANCOVA: $F_{1,247} = 15.9$, $P < 0.001$), with the Gentoo bringing back larger meals, on average, than the Chinstrap (Table 1). Meal mass was not significantly affected by site alone, but it was by the interaction of site and species (ANCOVA: $F_{1,247} = 10.0$, $P = 0.002$). At Cape Shirreff masses of the two species' meals were similar (Table 1), whereas at Admiralty Bay the Gentoo Penguin's meals were larger than the Chinstrap's or than those of either species at Cape Shirreff (Table 1).

Using average weights of Chinstrap and Gentoo Penguins from Volkman et al. (1980), we calculated meal mass as a percentage of adults' body mass. Although Gentoo Penguins provided larger absolute meal masses to their chicks, their meals were proportionately smaller in relation to their body size than Chinstrap Penguin meals. At both sites Chinstrap Penguins carried approximately 15% of their body mass, while Gentoo Penguins carried 11% of their body mass at Cape Shirreff and 13% at Admiralty Bay.

The amount of fresh versus digested material in diet samples varied significantly by species, as did the species × site interaction (ANCOVA species: $F_{1,247} = 47.5$, $P < 0.001$; species × site: $F_{1,247} = 16.3$, $P < 0.001$). Chinstrap Penguins delivered significantly more digested material to their chicks than did Gentoo Penguins at Admiralty Bay but not at Cape Shirreff (Table 1).

Effects of brood size and chick age. Meal mass significantly covaried with both brood size and chick age, although the proportion of digested material in the meals did not (ANCOVA, brood size: $F_{1,274} = 16.9$, $P < 0.001$; chick age: $F_{1,274} = 88.0$, $P < 0.001$). At Cape Shirreff, both Chinstrap and Gentoo Penguins increased their meal masses with increasing chick age (Fig. 1; Chinstrap: $F_{1,174} = 57.5$, $P < 0.0001$, $R^2 = 0.25$; Gentoo: $F_{1,64} = 20.74$, $P < 0.0001$, $R^2 = 0.24$). At Admiralty Bay this relationship did not apply to either the Chinstrap or the Gentoo, but at this site sample sizes for very young chicks were relatively small, which may have obscured any relationships between chick age and meal mass.

Sexual differences. At neither study site did meal mass differ significantly by sex for the Gentoo Penguin (Table 2). For the Chinstrap Penguin, males carried significantly heavier meals than did females (Cape Shirreff: $t_{278} = 3.3$, $P = 0.001$; Admiralty Bay: $t_{191} = 2.0$, $P = 0.05$). However, male and female penguins of both species carried meal masses similar in relation to their average body weight (weights from Volkman et al. 1980). There were no sex differences in the proportion of digested matter in the diet of either the Chinstrap or Gentoo Penguin. At both sites male Gentoo Penguins tended to have more fish mass in their diet than did females (Table 2; Cape Shirreff: $z = 2.0$, $P = 0.05$, Admiralty Bay: $z = -3.2$, $P = 0.001$).

TABLE 1. Characteristics of the diets of Gentoo and Chinstrap Penguins at Cape Shirreff and Admiralty Bay, South Shetland Islands, Antarctica. Means (±SD) are for 1997–1998 to 2003–2004 for the Gentoo and 1997–1998 to 2007–2008 for the Chinstrap.

	Gentoo		Chinstrap	
	Cape Shirreff ($n = 130$)	Admiralty Bay ($n = 120$)	Cape Shirreff ($n = 428$)	Admiralty Bay ($n = 300$)
Diet composition by mass (%)				
Antarctic krill	70.8	98.4	99.4	96.7
Fish	28.8	1.6	0.6	0.1
Other	0.4	0.0	0.0	3.3
Meal mass (g)	596 (±197)	682 (±227)	610 (±204)	580 (±171)
Meal mass/adult weight (%)	10.7 (±3.7)	12.3 (±4.2)	14.6 (±5.3)	14.2 (±4.4)
Digested material in diet (%)	39.2 (±31.2)	30.1 (±19.7)	43.0 (±12.7)	44.9 (±14.0)
Frequency occurrence of fish (%)	79.2	48.3	30.1	24.3
Brood size	1.5 (±0.5)	1.5 (±0.5)	1.6 (±0.5)	1.5 (±0.5)
Chick age (weeks)	3.3 (±1.5)	4.3 (±1.5)	3.7 (±1.7)	4.5 (±1.8)

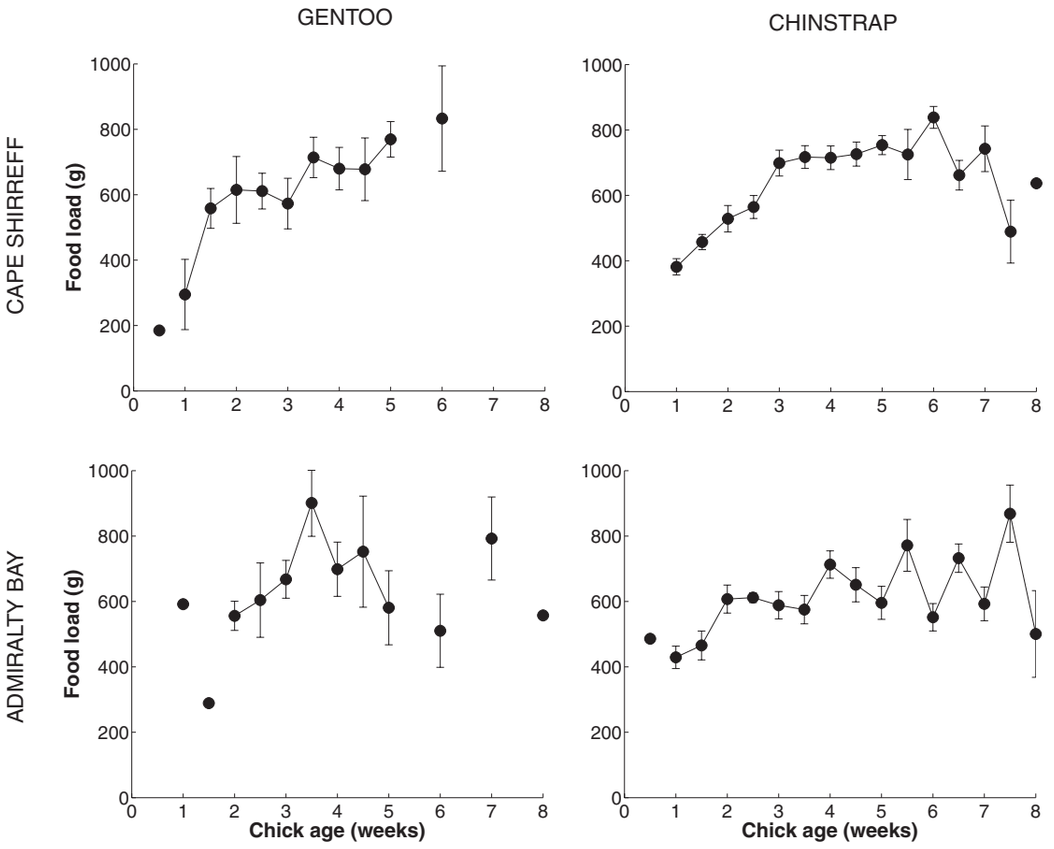

FIGURE 1. Meal mass (± SE) in relation to chick age for Chinstrap and Gentoo Penguins at Cape Shirreff and Admiralty Bay, South Shetland Islands, Antarctica, from 1997–1998 to 2003–2004. Only nests with two chicks are included.

Similarly, at Admiralty Bay, though not at Cape Shirreff, male Gentoo Penguins ate fish more frequently than did female Gentoo Penguins (Table 2; $\chi^2_1 = 10.3$, $P = 0.001$). At both sites, the frequency of occurrence of fish in the diet of male and female Chinstrap Penguins was similar, and neither sex had significant masses of fish in its stomach contents.

FORAGING LOCATIONS

At both study sites Chinstrap and Gentoo Penguins foraged in distinct areas (Fig. 2). At Cape Shirreff, both Gentoo and Chinstrap Penguins consistently traveled to the north or northeast of the colony, generally moving between two submarine canyons. Gentoo Penguins generally traveled no farther than the shelf break, while Chinstrap Penguins sometimes continued to the slope region or farther offshore. At Admiralty Bay, the Gentoo Penguin colony is located inside of the bay, while the Chinstrap Penguin colony is located at the mouth of the bay; both the bay and the nearest open waters are much deeper than around Cape Shirreff. Chinstrap Penguins consistently traveled out of the bay, into the less protected waters of Bransfield Strait. Gentoo Penguins often traveled in the same direction but also regularly foraged within Admiralty Bay.

Chinstrap Penguins at Cape Shirreff traveled farther offshore than did Gentoo Penguins at Cape Shirreff or either species at Admiralty Bay (Table 3). As compared by ANCOVA, the maximum distance penguins traveled from their colonies differed significantly by site ($F_{1,160} = 27.4$, $P < 0.001$), by species ($F_{1,160} = 26.8$, $P < 0.001$), and by the interaction of site and species ($F_{1,160} = 30.3$, $P < 0.001$). The average distance penguins traveled also differed significantly by site ($F_{1,160} = 13.7$, $P < 0.001$), species ($F_{1,160} = 11.2$, $P = 0.001$), and the interaction of site and species ($F_{1,160} = 17.9$, $P < 0.001$).

The percentage of time penguins spent on the shelf region (waters <200 m deep) differed significantly by species and site (ANCOVA, species: $F_{1,160} = 15.5$, $P < 0.001$; site: $F_{1,160} = 140.1$, $P < 0.001$). At both sites, Gentoo Penguins spent more time in shallower water than did Chinstrap Penguins. Not surprisingly, from the local bathymetry, at Admiralty Bay penguins spent more time in deep water than did their conspecifics at Cape Shirreff.

Neither the distance from shore nor the amount of time spent on the shelf covaried significantly with chick age or brood size. However, at Admiralty Bay Gentoo Penguins did significantly increase their maximum and average distances

TABLE 2. Differences in diet between male and female penguins at Cape Shirreff and Admiralty Bay, South Shetland Islands, Antarctica, from 1997–1998 to 2003–2004. Presented as means (±SD); significant differences ($P < 0.05$) indicated by an asterisk.

	Cape Shirreff				Admiralty Bay			
	Gentoo		Chinstrap		Gentoo		Chinstrap	
	Male ($n = 65$)	Female ($n = 65$)	Male ($n = 139$)	Female ($n = 141$)	Male (n=63)	Female ($n = 57$)	Male ($n = 107$)	Female ($n = 114$)
Meal mass (g)	608 (±213)	584 (±181)	646 (±214)	564 (±201)*	717 (±227)	645 (±224)	607 (±179)	562 (±169)
Meal mass/adult weight (%)	10% (±4%)	11% (±4%)	15% (±6%)	14% (±5%)	12% (±4%)	12% (±4%)	14% (±5%)	14% (±5%)
Digested material in diet (%)	38% (±35%)	40% (±28%)	41% (±12%)	41% (±14%)	27% (±15%)	34% (±24%)	45% (±15%)	46% (±14%)
Fish in diet (% by weight)	37% (±40%)	21% (±34%)*	1% (±5%)	1% (±3%) NA	3% (±12%)	<1%*	<1%	<1% NA
Frequency of occurrence of fish (%)	83%	75%	27%	28%	62%	33%*	26%	22%

from shore as chicks aged (maximum: $F_{1,34} = 9.3$, $P = 0.004$, $R^2 = 0.22$; average: $F_{1,34} = 4.5$, $P = 0.04$, $R^2 = 0.12$), while at Cape Shirreff there were no differences in distance traveled as Gentoo chicks aged. At Admiralty Bay Chinstrap Penguins also did not change their foraging distances with chick age, but at Cape Shirreff there was a weak but significant negative correlation between the average and maximum distance from shore and chick age (maximum: $F_{1,52} = 5.1$, $P = 0.03$, $R^2 = 0.09$; average: $F_{1,52} = 4.6$, $P = 0.04$, $R^2 = 0.08$).

Sexual differences. Male and female Chinstrap Penguins traveled similar distances from shore (maximum, Cape Shirreff females: $n = 27$, mean = 26.0, SD = 10.1; Cape Shirreff males: $n = 27$, mean = 26.4, SD = 13; Admiralty Bay females: $n = 13$, mean = 13.8, SD = 8.8; Admiralty Bay males: $n = 16$, mean = 13.3, SD = 8.8) and spent similar amounts of time on the shelf at both sites (Cape Shirreff females: $n = 27$, mean = 82%, SD = 20%; Cape Shirreff males: $n = 27$, mean = 82%, SD = 20%; Admiralty Bay females: $n = 13$, mean = 52%, SD = 30%; Admiralty Bay males: $n = 16$, mean = 42%, SD = 24%). Surprisingly, at Admiralty Bay female Gentoo Penguins traveled farther from shore than did males (females: $n = 19$, mean = 17.4, SD = 10.6; males: $n = 17$, mean = 12.4, SD = 7.7), while at Cape Shirreff males traveled farther from shore (females: $n = 23$, mean = 11.3, SD = 5.3; males: $n = 24$, mean = 17.4, SD = 6.4), although the amount of time the sexes spent on the shelf at both sites was similar (Cape Shirreff females: $n = 23$, mean = 99%, SD = 2%; Cape Shirreff males: $n = 24$, mean = 97%, SD = 6%; Admiralty Bay females: $n = 19$, mean = 50%, SD = 28%; Admiralty Bay males: $n = 17$, mean = 56%, SD = 26%).

Diel patterns in foraging. Only Chinstrap Penguins spent time at sea both during the day and at night. At Cape Shirreff Chinstrap Penguins ranged farther from shore at night than during the day (Fig. 2, Table 4). Also, we recorded more Chinstrap locations on the slope and offshore at night than during the day. These differences were all statistically significant (paired *t*-tests: average distance from shore: $t_{31} = -5.9$, $P < 0.001$; maximum distance from shore: $t_{31} = -4.4$, $P < 0.001$; percent time on shelf: $t_{31} = 5.7$, $P < 0.001$). At Admiralty Bay, however, foraging locations did not differ between day and night (Table 4).

INTER-ANNUAL EFFECTS

Both the diet and foraging areas of Chinstrap and Gentoo Penguins varied by year (Fig. 3). However, the patterns were not consistent by species or by site; there were no significant correlations of multi-year trends within a site or within a species for any of the measures of diet or foraging location.

DISCUSSION

Ecological theory predicts that two species cannot successfully occupy the same niche over time; competition should ultimately force species to adapt behaviorally or evolutionarily in order to occupy different niches (Lack 1945, MacArthur

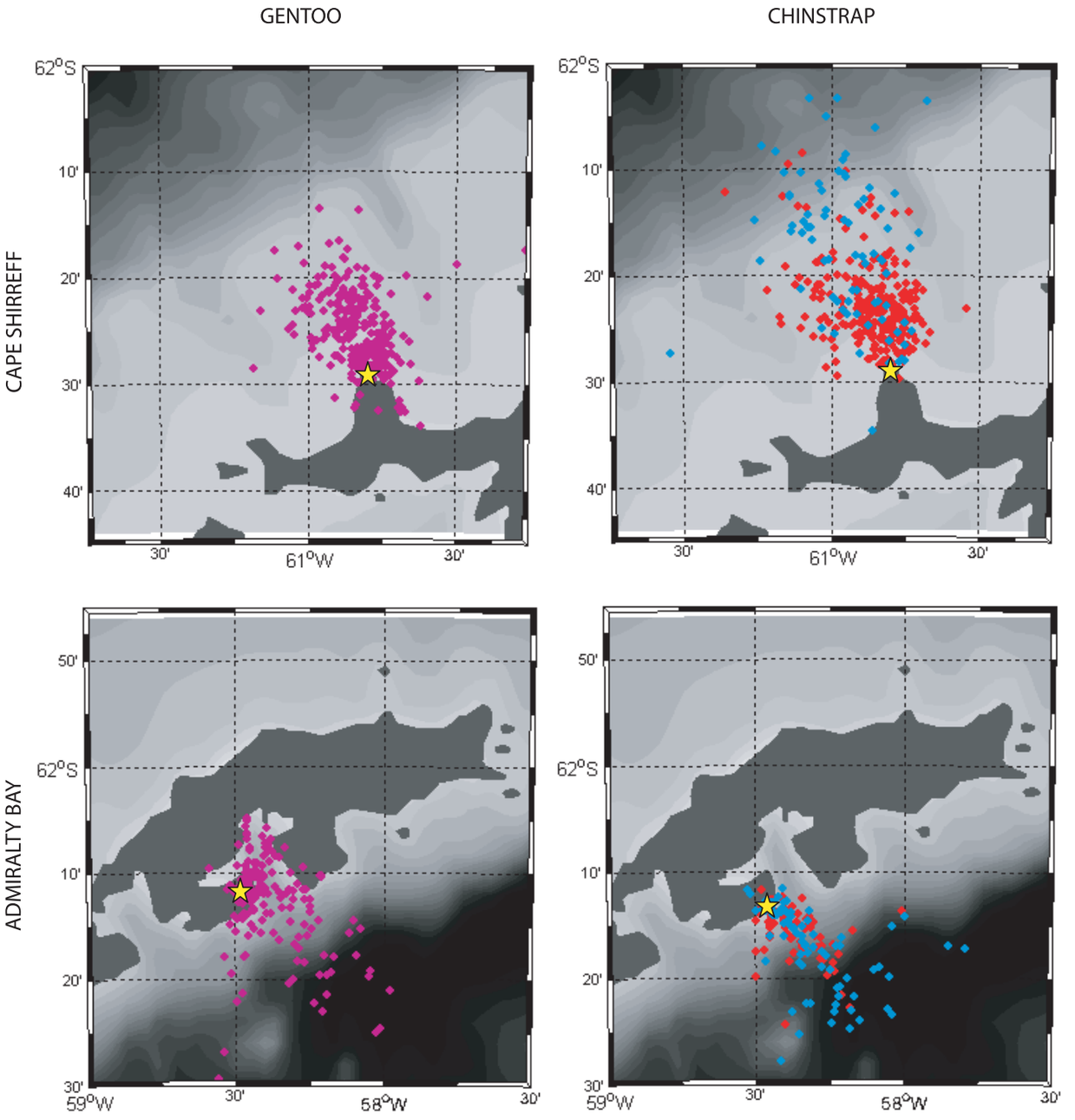

FIGURE 2. Foraging locations of Gentoo Penguins (purple) and Chinstrap Penguins (red and blue) at Cape Shirreff and Admiralty Bay, South Shetland Islands, Antarctica, from 2004–2005 to 2007–2008. Red locations for Chinstrap Penguins represent daytime foraging locations; blue locations represent nighttime foraging locations. Gentoo Penguins rarely foraged at night. Colony locations are indicated with a star.

1958, Hardin 1960). Since the Gentoo and Chinstrap Penguins breed sympatrically, we expected to see resource partitioning in their foraging and dietary habits. Furthermore, in recent decades the two species' population trajectories have differed remarkably, suggesting their realized niches are being affected by changes in the environment differently. However, we also expected that the way these species separate their niches would vary between the sites and over time. Some measures of the two species' foraging were consistent at the two sites and over time in our study, and furthermore they were consistent with previously published studies, suggesting that they are fundamental to the species' niches. Other character-

TABLE 3. Characteristics of locations (means ±SD) of Gentoo and Chinstrap Penguins foraging at Cape Shirreff and Admiralty Bay, South Shetland Islands, Antarctica, from 2004–2005 to 2007–2008.

	Gentoo		Chinstrap	
	Cape Shirreff ($n = 47$)	Admiralty Bay ($n = 36$)	Cape Shirreff ($n = 54$)	Admiralty Bay ($n = 29$)
Maximum distance from shore (km)	14.4 (±6.6)	15.1 (±9.5)	26.2 (±11.5)	13.5 (±8.6)
Mean distance from shore (km)	6.1 (±2.9)	6.2 (±3.3)	13.2 (±5.2)	6.1 (±3.8)
Locations on shelf (%)	98% (±2%)	53% (±38%)	82% (±14%)	46% (±35%)

TABLE 4. Characteristics of locations of day and night foraging (means ±SD) of Chinstrap Penguins at Cape Shirreff and Admiralty Bay, South Shetland Islands, Antarctica from 2004–2005 to 2007–2008.

	Cape Shirreff		Admiralty Bay	
	Day	Night	Day	Night
n	35	35	22	22
Maximum distance from shore (km)	19.2 (±6.1)	29.2 (±11.6)	10.2 (±6.1)	13.6 (±9.5)
Mean distance from shore (km)	11.5 (±3.2)	23.2 (±10.5)	5.8 (±3.5)	7.1 (±4.8)
Locations on shelf (%)	91% (±13%)	46% (±43%)	38% (±36%)	49% (±36%)

istics of foraging behavior and diet were variable, indicating that these aspects of the species' behavior are plastic and influenced by local environmental characteristics.

CHINSTRAP PENGUIN FORAGING PATTERNS

At both Cape Shirreff and Admiralty Bay, Chinstrap Penguins fed their chicks krill almost exclusively. We found evidence of fish in diet samples at both sites, though only in trace amounts by weight. Meal sizes at the two sites were similar, and both female and male Chinstrap Penguins carried meal masses equal to roughly 14% of their body weight (Volkman et al. 1980). The absolute size of meals was smaller for the Chinstrap than for the Gentoo Penguin, but it represented a larger proportion of their body weight. At both sites Chinstrap Penguins fed in open water and typically traveled to the shelf-slope region or beyond into deeper waters. At Cape Shirreff, however, Chinstrap Penguins foraged farther from the colony than did their conspecifics at Admiralty Bay. Furthermore, at Cape Shirreff the Chinstrap Penguin's foraging locations varied through the diel cycle: at night the birds foraged farther offshore, on average. In contrast, at Admiralty Bay Chinstrap Penguins foraged relatively close to shore both by day and at night.

Chinstrap Penguins breed primarily around the Scotia Sea and throughout their range feed their chicks krill almost exclusively (Lynnes et al. 2002, Rombolá et al. 2006, Volkman et al. 1980, Jansen et al. 1998, Ichii et al. 2007), just as we observed at Cape Shirreff and Admiralty Bay. However, some fish may be found in the diet of birds that have foraged overnight (Jansen et al. 1998). At Cape Shirreff and around the South Shetland Islands Chinstrap Penguins generally forage in the pelagic zone, where they dive to average depths of 15–30 m (Croll et al. 2006, Miller and Trivelpiece 2008, Wilson and Peters 1999, Kokubun et al. 2010). Wilson (2010) found that the dives of Chinstrap Penguins are most efficient at these mid-water depths. Around the South Orkney Islands Chinstrap Penguins dive somewhat deeper and may reach the benthos (Takahashi et al. 2003), and they also generally forage farther from shore than around the South Shetland Islands (Wilson and Peters 1999, Ichii et al. 2007, this study, Lynnes et al. 2002).

Durations of the Chinstrap Penguin's foraging trips are fairly consistent from site to site: 6- to 8-hr trips during the day and >14-hr trips at night (Jansen et al. 1998, Takahashi et al. 2003, Ichii et al. 2007; AMLR, unpubl. data). Those studies that did not separate trips by time of day found average trip durations of 10–12 hr (Croll et al. 2006, Wilson and Peters 1999, Kokubun et al. 2010). Jansen et al. (1998) demonstrated that overnight foragers consumed a higher proportion of fish (4–35% by weight) and suggested that these birds were making long trips at night to the shelf break, where more fish are found (Ichii et al. 2007), and remained inshore feeding on krill during the day. As we found at Cape Shirreff, Ichii et al. (2007) also found at Seal Island that Chinstrap Penguins tend to be farther from shore at night. This evidence suggests that an alternation of short daytime trips close to shore and long overnight trips to the shelf break and slope region may be a common strategy of the Chinstrap Penguin even though we did not observe this pattern at Admiralty Bay.

GENTOO PENGUIN FORAGING PATTERNS

The Gentoo Penguin's diet at Cape Shirreff differed from that at Admiralty Bay. Krill was the dominant food at both

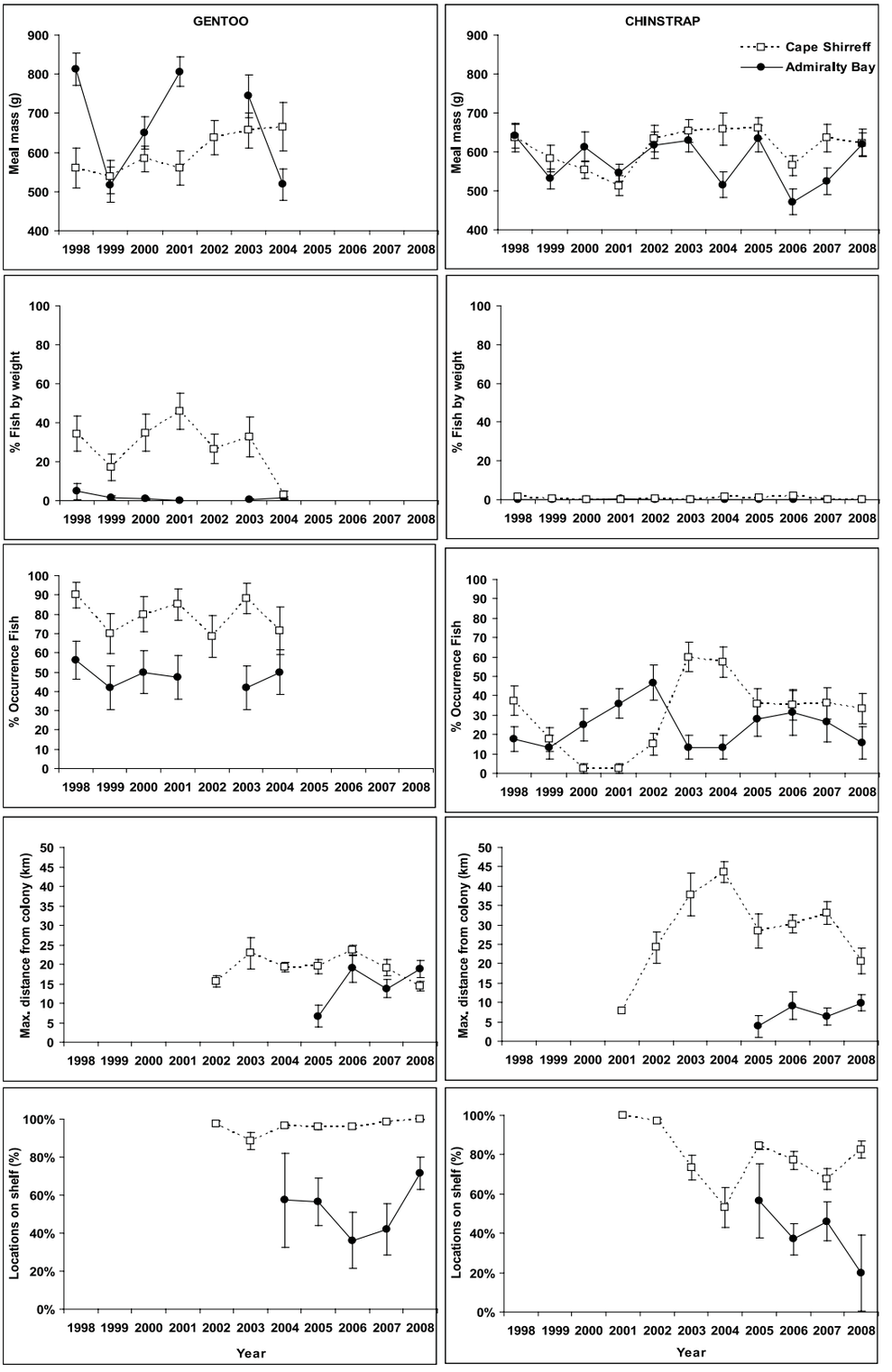

FIGURE 3. Characteristics of diet and foraging locations by year for Gentoo and Chinstrap Penguins at Cape Shirreff and Admiralty Bay, South Shetland Islands, Antarctica. Error bars represent means ± SE.

colonies, but at Admiralty Bay Gentoo Penguins ate krill almost exclusively, while at Cape Shirreff they consumed on average 71% krill and 29% fish. At Cape Shirreff Gentoo Penguins also carried smaller meal masses, on average, than did their conspecifics at Admiralty Bay. Although their diet at the two sites differed, Gentoo Penguins traveled similar distances from shore at both sites and were more likely to spend time in the shelf regions than were Chinstap Penguins.

Variability in diet and foraging strategy is characteristic of the Gentoo Penguin, even among colonies in close proximity (Bost and Jouventin 1990, Lescroël and Bost 2005). The species has a circumpolar breeding distribution in the subantarctic (Woehler et al. 1993), but its population that breeds sympatrically with the Chinstrap in the Scotia Sea and Antarctic Peninsula regions is relatively small. In the Scotia Sea region Gentoo Penguins tend to have a diet of mixed krill and fish, although at particular sites and in particular years the diet may be exclusively krill or, less commonly, exclusively fish (Croxall and Prince 1980, Croxall et al. 1999). In the South Shetland Islands, krill typically represents 70–100% of the diet (Volkman et al. 1980, Kokubun et al. 2010, present study).

Gentoo Penguins forage both pelagically and benthically, diving to average depths of 30–50 m (Williams et al. 1992, Miller et al. 2009, Kokubun et al. 2010). They dive more efficiently (stay longer at the bottom in relation to the dive and post-dive interval) at deeper depths than do Chinstrap Penguins. Gentoo Penguin dives may also be more efficient when they are benthic (Kokubun et al. 2010). Gentoo Penguins are larger (Williams 1995), and this larger size likely contributes to their efficiency at deeper depths.

Gentoo Penguins generally forage only during the day (Wilson et al. 1996), and mean trip durations range from 7 to 12 hr (Williams et al. 1992, Croxall et al. 1988, Miller et al. 2009). The Gentoo Penguin's foraging range is generally within 25 km or less of the breeding colonies, and the species tends to forage closer to shore than other *Pygoscelis* penguins (Trivelpiece et al. 1987, Wilson et al. 1998, Kokubun et al. 2010, Wilson 2010). These estimates are comparable to our observations in this study: the maximum distance traveled by any individual averaged 19 km at both Cape Shirreff and Admiralty Bay.

SPATIAL AND TEMPORAL EFFECTS ON NICHE PARTITIONING

In general, niche separation appeared to be stronger at Cape Shirreff than at Admiralty Bay. At Cape Shirreff, Gentoo Penguins consumed more fish than did Chinstrap Penguins, while Chinstrap Penguins traveled farther from shore than did Gentoo Penguins and had diel variability in foraging. At Admiralty Bay, Chinstrap and Gentoo Penguins both consumed only krill and foraged relatively close to their colony. Kokubun et al. (2010) and Wilson (2010) also compared the foraging niches of sympatrically breeding Chinstrap and Gentoo Penguins. Both studies showed a segregation of foraging habitat in which Chinstrap Penguins traveled farther from shore but dove to shallower depths. While we did not investigate the patterns of the penguins' diving at Admiralty Bay, at Cape Shirreff the niches are separated in similar ways, with the Gentoo diving deeper than the Chinstrap (Miller et al. 2009) but foraging closer to shore (this study). However, Kokubun et al. (2010) found that both species ate krill almost exclusively, as we found at Admiralty Bay. Our result suggest that niche partitioning between the Chinstrap and Gentoo Penguins is most strongly correlated with differences in the adjacent marine habitat and, potentially, by the number of sympatrically breeding congeners at the two sites.

The marine habitat at Cape Shirreff is quite distinct from that at Admiralty Bay. Cape Shirreff faces north into the Drake Passage, making it a highly exposed site. Admiralty Bay is on the south side of King George Island, so it provides the protection of the bay and opens to the relatively protected Bransfield Strait. Cape Shirreff also has a wide shelf region, whereas Admiralty Bay is deep, and the shelf region outside of the bay is quite narrow. The most obvious effect of these habitat differences is that both species of penguins spent more time foraging in deep (>200 m) water at Admiralty Bay than at Cape Shirreff. This difference would be almost unavoidable given the bathymetry. At Admiralty Bay Chinstrap Penguins may also have been able to forage closer to shore because of the bathymetry. They dive most efficiently in mid-water depths (Kokubun et al 2010, Wilson 2010) and tend to forage pelagically (Miller and Trivelpiece 2008). Since the shelf break is located closer to shore at Admiralty Bay, they may not have needed to travel as far to reach this optimal habitat. The difference in bathymetry could also explain why at Cape Shirreff Gentoo Penguins took more fish than at Admiralty Bay. When Gentoo Penguins consume fish, they are most often benthic fish (Karnovsky 1997). The Gentoo Penguin's foraging area at Cape Shirreff is generally in waters shallow enough that the benthos is within its diving range (Miller et al. 2009), while this is not the case at Admiralty Bay.

Differences in the sizes of the penguins' populations at the two sites could also explain site-specific differences in niche separation. At Admiralty Bay, the Chinstrap Penguin population is relatively small and the Gentoo Penguin population relatively large, while the opposite is true at Cape Shirreff. Gentoo Penguins may be forced to eat a more varied diet including more fish at colonies supporting larger Chinstrap Penguin populations, but they may consume a higher proportion of krill at colonies where they face less interspecific competition, as at Admiralty Bay. Intraspecific competition might also explain site-specific foraging niches: at Admiralty Bay, where their population is smaller, Chinstrap Penguins might not need to travel as far.

The presence of other competitors also affects site-specific niche-separation patterns. At Admiralty Bay, the Adélie Penguin (*Pygoscelis adeliae*) breeds sympatrically with the Chinstrap

and Gentoo, and small colonies of all three species of *Pygoscelis* are found around the bay. At Cape Shirreff, there are fewer nearby colonies of *Pygoscelis*, but there is a large rookery of the Antarctic fur seal (*Arctocephalus gazella*) at this site. The role of these other competitors in driving niche partitioning is not clear from our study but should be considered as well in future research.

While niche separation reduces competition for resources, the mechanism leading to niche separation is not always competition. Trivelpiece et al. (1987) suggested that the Chinstrap and Gentoo Penguins evolved to occupy different niches because they have different population ranges, so different patterns of foraging are optimal for the two species as wholes, rather than being a result of competition in the Scotia Sea and Antarctic Peninsula, where their ranges overlap. The Chinstrap Penguin breeds almost exclusively around the Scotia Sea, where krill is abundant, so its optimal foraging strategies should be based around krill behavior. The Gentoo, in contrast, has a circumpolar distribution, and in much of its range its diet is dominated by fish, squid, or amphipods (Robinson and Hindell 1996, Pütz et al. 2001, Lescroël et al. 2004), so the flexibility to target variable prey, at greater depths, as well as in different habitats (benthic and pelagic) would be advantageous for this species as a whole. Even if niche separation is a product of evolution for different geographical ranges, a reduction in competition for food, based on a separation of foraging niches, would nonetheless improve the probability of stable co-existence of these species.

Marine environments are highly dynamic, and the quantity, locations, and depth of prey are likely to vary over time. Antarctic krill is a patchy, variable resource whose population size varies significantly from year to year (Hewitt et al. 2003). This variability may lead predators to increase the time they spend foraging or the distances they travel in order to reach krill (Lea et al. 2006, Harding et al. 2007), or they may switch to alternative prey (Barrett 2002, Mills et al. 2007). We anticipated that measures of Gentoo and Chinstrap Penguin foraging would both vary over the years, but we expected that these responses would be consistent either within a species or within a site. Consistency within a species at multiple sites would suggest a strongly developed species-specific foraging niche, while consistency of multiple species within a site would indicate strong influences of local conditions.

Year-to-year changes in measures of foraging at these two colonies were not correlated for either the Chinstrap or Gentoo (except for the diet of the Chinstrap, which was consistently krill at both sites). During the chick-rearing period, penguins are spatially constrained by their obligation to return daily to their nests to feed their chicks, so the lack of consistency between sites suggests that penguin foraging is highly influenced by local conditions. Interestingly, the two penguin species breeding at the same site also did not respond in parallel over the years. That is, the size of meals may have increased for one species but decreased for the other in the same year at the same site. This finding suggests that the Chinstrap and Gentoo Penguins have patterns of foraging distinct enough that they do not respond in the same manner to changes in the marine environment and prey availability.

Earlier studies at Admiralty Bay showed a clearer separation between the foraging niches of the Gentoo and Chinstrap Penguins than we saw in our study: Gentoo Penguins ate more fish, foraged closer to shore, and dove to deeper depths than did Chinstrap Penguins (Trivelpiece et al. 1986, 1987, Volkman et al. 1980). These results are more comparable to what we saw at Cape Shirreff. These historic trends show that the degree of foraging-niche separation between species may shift over time. The shift of the Gentoo to a greater concentration on krill at Admiralty Bay is not likely to be the result of changes in the marine environment and the availability of prey; krill abundance in the region has decreased over several decades (Atkinson et al. 2004). However, the sizes of penguin populations at Admiralty Bay have also changed dramatically over the last several decades, and these trends may contribute to the apparent reduction of niche separation. The population of Chinstrap Penguins has declined by 46% since 1997–1998. Another formerly abundant congener at Admiralty Bay, the Adélie Penguin, has also had a precipitous population decline in the last two decades (Hinke et al. 2007). In contrast, the relatively small population of the Gentoo Penguin has increased by 95% since 1997–1998. These population changes raise the question of whether Gentoo Penguin foraging is changing as a result of competitive release.

CONCLUSIONS AND QUESTIONS FOR FUTURE RESEARCH

Our results, together with those of previous studies, demonstrate that species-specific potential niche ranges can be generalized over space and time. Gentoo Penguins tend to forage close to shore, forage during the day, and exploit both benthic and pelagic prey. Chinstrap Penguins generally feed on pelagic prey, primarily krill. They forage farther from shore than do Gentoo Penguins but dive to shallower depths and may forage both by day and by night.

However, it is clear that each species' realized niche is influenced by the specific characteristics of its breeding site, which may include both the habitat and the number of competitors. Furthermore, these penguins' realized foraging niches vary over time as a result of changes in the quantity and location of the prey, variability in the marine environment, or changes in competitor populations. When these penguin species are used as indicators of the local environment or their prey species, these local and temporal influences on their foraging behaviors will need to be accounted for.

On the basis of our results, and those of other studies in the Scotia Sea region, we suggest that Chinstrap Penguins will maintain a relatively uniform diet of krill for their chicks, but

vary their trip lengths and the distance they travel by site and over time. Gentoo Penguins, in contrast, will consistently forage within a limited range of their colonies but vary their diets.

Future research should consider more specifically how changes in penguin populations are connected to their foraging niches at different sites and over time. The separation of foraging niches between the Gentoo and Chinstrap Penguins may help explain why the population of the former is increasing and that of the latter is declining. Furthermore, changes in the sizes of penguin population may alter the amount of competition, both within and among species, and lead to changes in each species' realized foraging niche.

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