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Conflict or co-existence? Foraging distribution and competition for prey between Adélie and chinstrap penguins

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Abstract Adélie (*Pygoscelis adeliae*) and chinstrap penguins (*P. antarctica*) are morphologically and ecologically very similar, have very similar diet and breed sympatrically in the Scotia Arc from the South Sandwich Islands to the Antarctic Peninsula. To investigate how these two species co-exist, their foraging distribution and diet were studied during the chick-rearing period at Signy Island, South Orkney Islands, during the breeding seasons of 2000 and 2001. Satellite tracking data from of 19 Adélie penguins and 24 chinstrap penguins were used to compare foraging distributions. In both years the diet of both species was exclusively Antarctic krill (*Euphausia superba*) of the same size range. In a year of low prey availability (2000), there was a statistically significant segregation of foraging areas between the two species, however, in a year of normal resource availability (2001) there was no such segregation. There was a significant difference in the foraging areas used by Adélie penguins between years but not for chinstrap penguins. Adélie penguins foraged significantly farther (mean 100 km) from the colony than chinstrap penguins (mean 58 km) in 2000 but not in 2001 (mean 58 km and 35 km respectively). In 2000, the breeding success of Adélie penguins was 51% lower than the long-term mean compared to 15% lower in chinstrap penguins. Both species achieved above average breeding success in 2001. The changes in foraging distribution and breeding success suggest that in years of low resource availability, chinstrap penguins may be able to competitively exclude Adélie penguins from potential inshore foraging areas. Current trends in climatic change and possible effects on ice distribution and krill abundance suggest that conditions could become less favourable for Adélie penguins than chinstrap penguins in areas where both species occur.

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Introduction

Analysis of niche overlap in sympatric congeneric species is one of the main ways of investigating the nature and likelihood of interspecies competition (Pianka 1976; Connell 1983). In terrestrial systems, such studies are sometimes, and desirably, accompanied by experiments to test the inferences gained from niche overlap examination. However, in marine ecosystems such studies are rarely practicable; indeed determining the effective foraging range of individuals of known status (a pre-requisite for understanding the potential for interspecies interaction) has only been possible for a number of species relatively recently with the advent of sufficiently small satellite telemetry devices (Waugh et al. 1999; Wood et al. 2000; Barlow et al. 2002). The ability to define the area in which foraging occurs – and potentially to identify within this the main areas used for feeding – makes reappraisal of earlier ideas on interspecific competition in marine systems both feasible and timely.

In this study we investigate the foraging ranges and potential feeding areas of two congeneric penguin species (Adélie *Pygoscelis adeliae* and chinstrap *P. antarctica*). Adélie and chinstrap penguins are not only closely related taxonomically, but are morphologically and ecologically very similar (similar size, feeding mainly on Antarctic krill (*Euphausia superba*) and breeding during the austral summer) and breed sympatrically throughout the Scotia Arc from the southern South Sandwich Islands (at 59°S) south to the Antarctic Peninsula (at 64°S).

Previous studies investigating the circumstances of their coexistence inferred that differences in breeding timetable and diet might assist in reducing competition (Sladen 1955; Volkman et al. 1980; Lishman 1985a, b;

Trivelpiece et al. 1987). The difference in timing of breeding, with Adélie penguins starting 3–4 weeks earlier than chinstraps, is broadly consistent across all sites where they co-occur. Dietary differences, however, are mainly confined to small differences in the size of krill (often inconsistent between sites) and a suggestion that chinstrap penguins have a greater propensity to take fish, particularly during periods of low krill availability and when engaged in overnight foraging (Jansen et al. 1998). Most comparative studies of diet, however, took place in 1 year (occasionally 2) and few were linked directly to any data on foraging. Earlier studies also inferred, based on differences in the duration of foraging trips, that Adélie penguins might have larger foraging ranges than chinstrap penguins and/or feed in areas more distant from the breeding colony (White and Conroy 1975; Lishman 1985b; Trivelpiece et al. 1987; Wilson et al. 1989).

The aims of our study, of Adélie and chinstrap penguins at Signy Island, South Orkney Islands, were to use data on breeding season foraging ranges, derived from satellite tracking of at-sea distribution, in conjunction with data on diet and breeding success, to examine:

1. the extent to which diet and foraging range either separately or in combination might have the potential to reduce interspecies competition.
2. whether given the overlap in breeding timetable, changes in diet and foraging range occur particularly during the period of maximum potential competition.
3. whether variation in either of the 2 years of the study could be related to prey availability and/or breeding success.

Materials and methods

Study site and species

The study was conducted at Gourlay Peninsula on Signy Island, South Orkney Islands (60.72°S 45.57 W) (Fig. 1). Approximately 30,000 pairs of Adélie penguins and 50,000 pairs of chinstrap penguins breed on Signy Island of which 18,000 and 13,000 pairs, respectively, breed on Gourlay Peninsula (1994, British Antarctic Survey, unpublished data). Full details of their breeding biology at this site are given by Sladen (1955) and Lishman (1985a). Their breeding timetable is shown in Fig. 2.

Data on reproductive performance and diet samples were collected during both years of the study as part of the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) Ecosystem Monitoring Programme (CEMP, CCAMLR 1995). The total length of the krill from diet samples was calculated using the equations in Hill (1990) for specific maturity stage and sex (Makarov and Denys 1981).

Deployment of satellite tracking instruments

Breeding adult penguins were captured at the nest during the chick-rearing period in December and January (Adélie penguin) and January and February (chinstrap penguin). Birds were chosen for

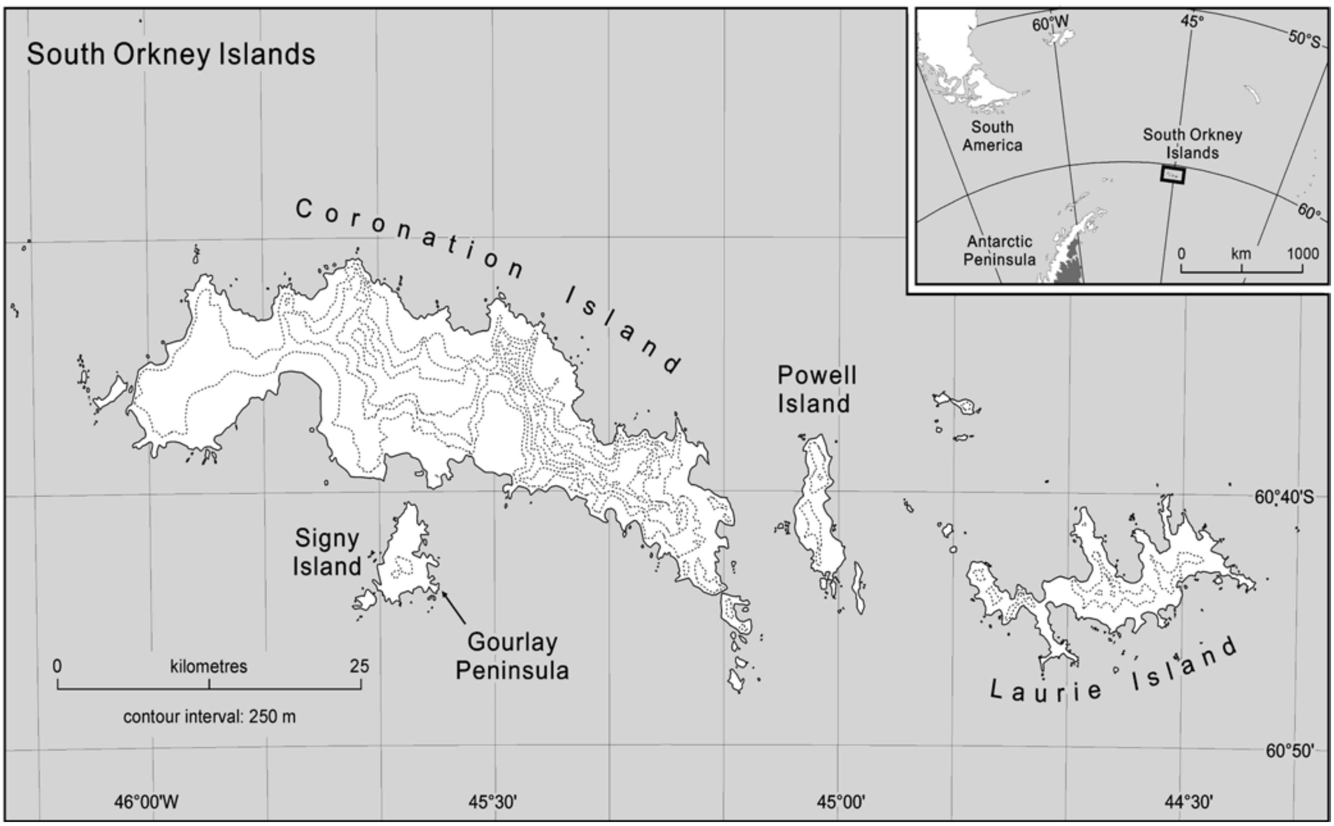

Fig. 1 Breeding timetable of Adélie (*Pygoscelis adeliae*) and chinstrap (*P. antarctica*) penguins at Signy Island, South Orkney Islands based on data from the breeding seasons of 2000, 2001 and Lishman (1985a)

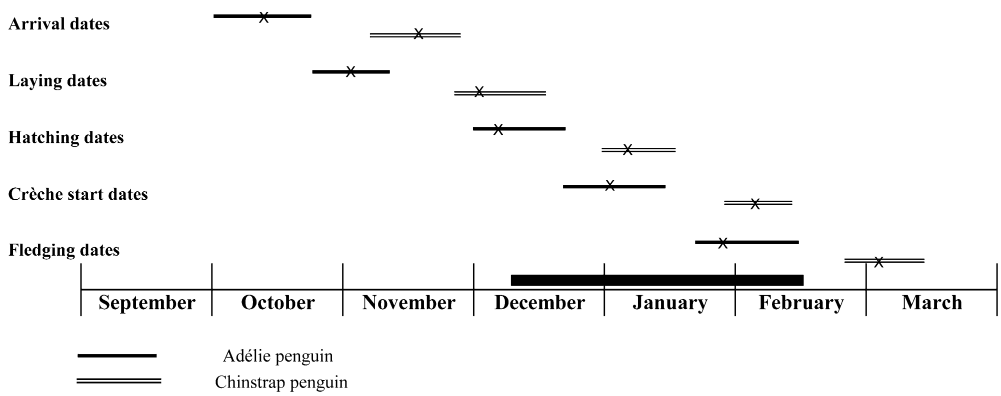

Fig. 2 Location of South Orkney Islands and of the study site at Gourlay Peninsula, Signy Island

the study from medium-sized (100–1500 pairs) colonies that were easily accessible; individuals breeding in the centre of colonies were not used in order to minimise disturbance. None were selected from nests within 1 m of the periphery to reduce the risk of choosing poorer quality, inexperienced birds (Williams 1995).

During the brood guard phase, outgoing birds were captured at the nests when both adults were present; during the crèche period, birds were captured after they had fed their chicks and left the colony. Upon capture the sex of each bird was determined by measurement of bill length, bill depth and flipper width for Adélie penguins (Kerry et al. 1992) and bill length and depth for chinstrap penguins (Amat et al. 1993).

A platform terminal transmitter (either ST-10 PTT, mass 94 g or ST-18 PTT, mass 97 g, dimensions of both 115×44×15 mm, antenna at 90°; Telonics, USA, packaged by Sirtrack, New Zealand) was attached to the lower medial portion of the back of the penguin just above the uropygial gland using Tesa Tape and a two-part quick set epoxy resin following the methods described by Wilson et al. (1997). The front of each device were streamlined to reduce hydrodynamic drag (Culik et al. 1994). Devices were deployed on each individual for between 2 and 12 days in order to record more than one foraging trip. Deployments were carried out during chick-rearing from mid-December 1999 until mid-February 2000, referred to as the 2000 season and mid-December 2000 until-mid February 2001, referred to as the 2001 season (Table 1). In both years, the sea-ice edge was outside the foraging range of the penguins during the deployment period (National Ice Center data, www.natice.noaa.gov).

Location data and analysis

Locations of penguins carrying devices were provided by the ARGOS system and assigned to one of six accuracy classes (3, 2, 1, 0, A, B). Following the approach of Barlow et al. (2002) only classes 1–3, which gave positions accurate to within 1–2 km, and class 0, which gave positions accurate to 4 km, were used in the analysis. Location data were used to estimate foraging distributions within 0.1° squares for individual penguins and the sum of the proportions for all individuals within each 0.1° square were used to produce overall foraging density distributions. The frequency with which 0.1° squares were utilised by either one or both species was compared to the expected frequencies based on a binomial probability distribution. Maps of the foraging density distributions were produced using a linear spline interpolation in Matlab (www.mathworks.co.uk).

The distribution of foraging intensity both within and between species was compared using the product-moment correlation coefficient of the overall foraging density distributions following Barlow et al. (2002) and Barlow and Croxall (2002). However, since the locations are serially auto-correlated (i.e. the probability of a location in a given 0.1° square is not independent of the previous location), a bootstrapping procedure was used that does not rely on assumptions about the parameters used in the correlation. In order to compare two foraging distributions, the product-moment correlation coefficient was calculated from the overall foraging density distributions. The individual foraging densities were then randomly re-sampled with replacement to create two new overall distributions in which the number of individuals in each group was the same as in the original samples and the product-moment correlation coefficient re-calculated. In comparing the two correlation coefficients, if there is a greater degree of overlap the r value between the simulated distributions is higher; conversely a greater degree of spatial segregation produces a lower value of r. The re-sampling procedure was repeated 1,000 times and the frequency distribution of the r values was used to determine the probability that the level of differences in the initial foraging distribution arose by chance. Where less than 5% of the bootstrapped correlation coefficients did not exceed the r value from the comparison of overlap using the original data, this was taken to indicate a statistically significant spatial segregation between the two foraging distributions.

The maximum distance travelled from the colony for each individual penguin was estimated using the Haversine formulation (Sinnott 1984). The duration of foraging trips to the nearest hour was estimated from a combination of direct observations and satellite location data where these indicated that individuals were arriving or departing the colony.

Table 1 Details of timing and number of Platform Terminal Transmitters deployed on Adélie (*Pygoscelis adeliae*) and chinstrap (*P. antarctica*) penguins at Signy Island, South Orkney Islands, during the 2000 and 2001 seasons

	Adélie penguin		Chinstrap penguin	
	2000	2001	2000	2001
Period of deployment	13 Dec 1999–5 Jan 2000	8 Dec 2000–2 Jan 2001	13 Jan 2000–7 Feb 2001	6 Jan 2001–9 Feb 2001
Total deployment time (days)	52	73	54	91
Total number of trips recorded	16	37	30	72
Total number of birds instrumented (female:male)	9 (6:3)	10 (3:7)	10 (7:3)	14 (8:6)

Results

Diet

In both 2000 and 2001, Antarctic krill was the dominant prey of both species, consistent with results from previous years (Table 2). In 2000, the modal size of krill in the diet of both species was 54 mm and >80% of krill were within 4 mm of the mode. In 2001, the modal size was 52 mm and, while there was a relatively greater proportion of krill of <40 mm compared to 2000, more than 60% of krill in the diet of both species was within 4 mm of the mode (Fig. 3).

Breeding success

The number of breeding pairs of both species in 2000 was the lowest ever recorded at this site; numbers of both species increased in 2001 (Table 2). Breeding success in 2000 was lower than the long-term mean in both species; however, whereas Adélie penguin breeding success was the lowest on record at this site, chinstrap penguin breeding success was only slightly lower than long-term mean (Table 2). By contrast, in 2001 there was much less difference between the breeding success of Adélie and chinstrap penguins, values for both of which were above the respective long-term means (Table 2).

Spatial distribution

In both 2000 and 2001, the areas of highest foraging density of Adélie penguins were on the continental shelf south and west of Signy Island with some birds visiting the shelf-break. Chinstrap penguins also foraged south of Signy Island, although they were confined to the inner shelf region (Fig. 4). In 2000, a total of 139 0.1° squares was utilised by both species and of these 108 (78%) were

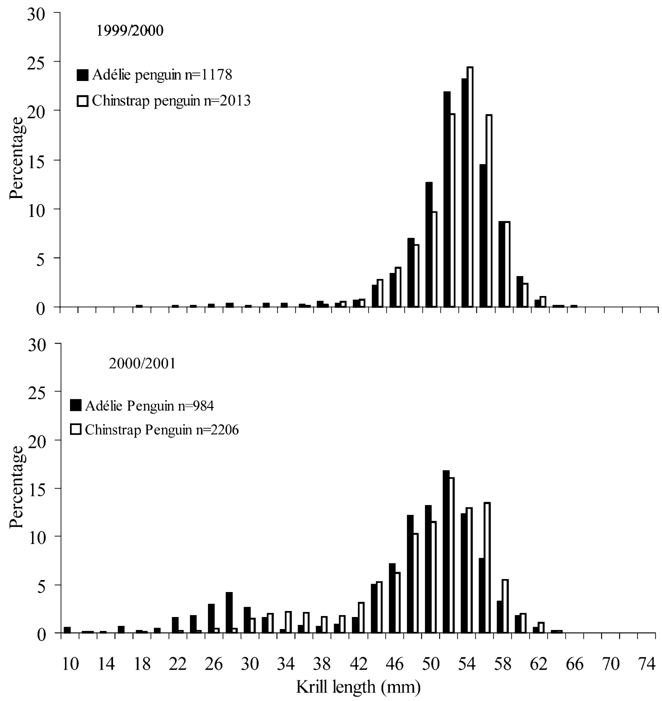

Fig. 3 Length frequency distribution of Antarctic krill (*Euphausia superba*) in the diet of Adélie and chinstrap penguins at Signy Island, South Orkney Islands

used by Adélies, 58 (30%) by chinstraps and only 27 (19%) were visited by both species. In 2001, a total of 105 0.1° squares was utilised by both species and of these 94 (90%) were used by Adélies, 36 (34%) by chinstraps and only 25 (24%) were visited by both species. In both years Adélie penguins occurred in a greater proportion of squares than expected (see methods) and the two species co–occurred in fewer than squares than expected (2000 $\chi^2_2=53.9$, $P<0.001$; 2001 $\chi^2_2=42.1$, $P<0.001$).

The foraging density distribution of Adélie penguins differed significantly between years ($r=0.281$, $P=0.017$), whereas there was no such difference in the density

Table 2 Number of breeding pairs, breeding success, mean krill size and the mean percentage (%) of krill per stomach sample brought back to Adélie and chinstrap chicks during 2000 and 2001 at Gourlay Peninsula study colonies, Signy Island, South Orkney Islands. Data are compared with the mean and range values for 1980–2001 (population size) and 1997–2001 (diet)

Season	2000		2001		Across all years n = no. of years			
Species	Adélie penguin	Chinstrap penguin	Adélie penguin	Chinstrap penguin	Adélie penguin		Chinstrap penguin	
					Mean ± SE	Range	Mean ± SE	Range
Number of breeding pairs	1,313	1,440	1,939	1,579	2,522 ± 145.5 $n=14$	1,313–3,395	1,997 ± 62.2 $n=21$	1,440–2,405
Breeding success (chicks crèched per pair)	0.40	0.72	0.93	0.98	0.82 ± 0.1 $n=21$	0.40–1.24	0.85 ± 0.1 $n=21$	0.24–1.22
Mean percentage krill in diet by mass	98.9	99.8	99.7	99.8	99.5 ± 0.1 $n=5$	78.8–100 $n=5$	99.4 ± 0.4 $n=5$	22.5–100 $n=5$
Mean krill size (mm) ± SE	51.5 ± 0.1	52.0 ± 0.1	45.6 ± 0.3	48.4 ± 0.2	46.4 ± 0.1	8.2–64.8 $n=5$	49.5 ± 0.1	9.2–71.3 $n=5$

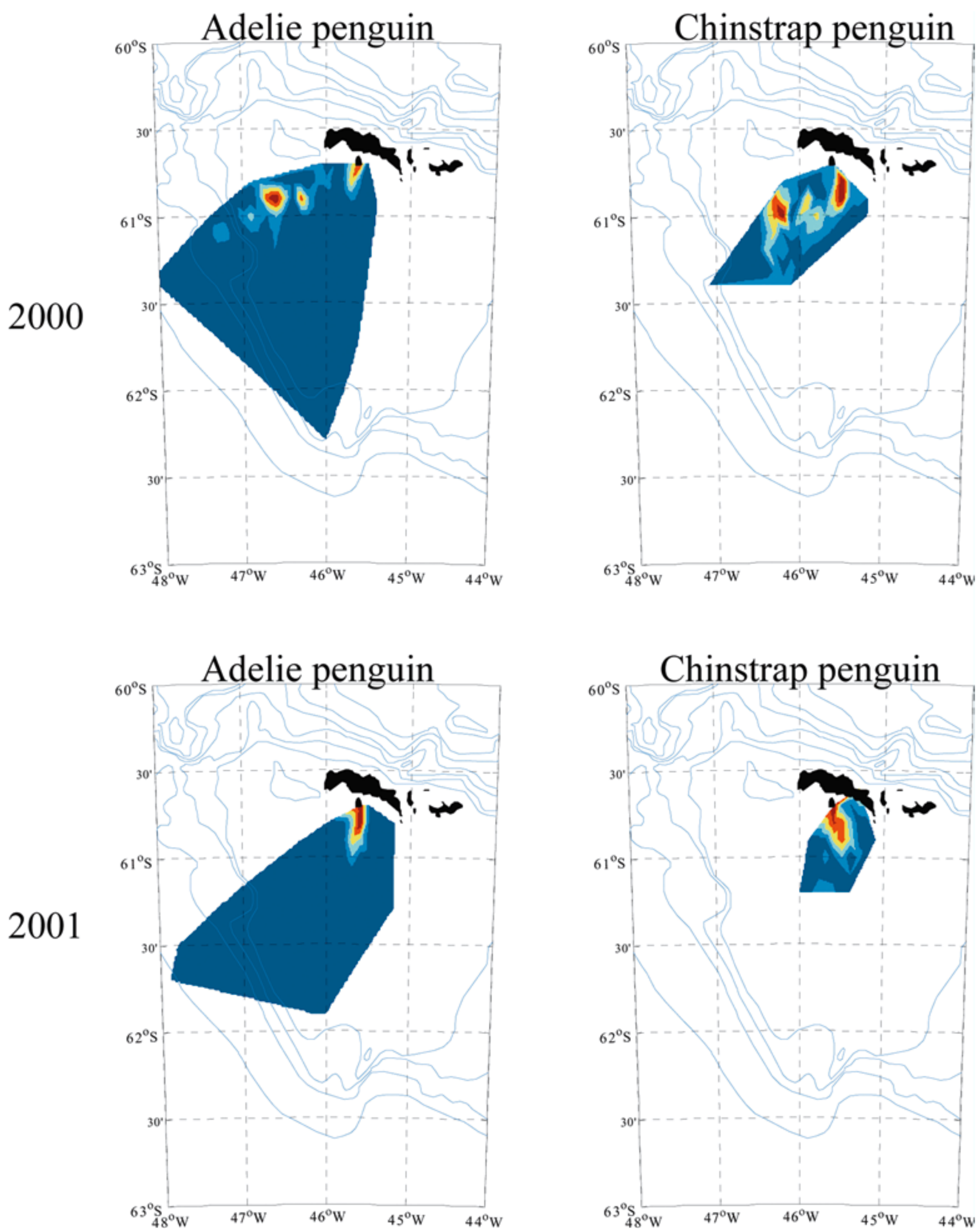

Fig. 4 Foraging density distribution of Adélie and chinstrap penguins (red shows highest and blue lowest) at Signy Island, South Orkney Islands in 2000 and 2001. *Scale units* are the proportion of the total number of locations for each species in each year

distribution of chinstraps between years ($r = 0.239$, $P = 0.125$). There was a significant difference in the foraging density distribution of Adélie and chinstrap penguins in 2000 ($r = 0.012$, $P = 0.005$); however, the foraging density distribution of the two species was not significantly different in 2001 ($r = 0.624$, $P = 0.22$).

Maximum distance travelled and foraging trip duration

The maximum distance travelled by Adélie penguins did not differ between years ($F_{1,18} = 3.69$, $P = 0.07$). The maximum distance travelled by chinstrap penguins was significantly greater in 2000 compared to 2001 ($F_{1,23} = 8.24$, $P = 0.009$) (Table 3). Whereas the maximum distance travelled by Adélie penguins in 2000 was greater than for chinstraps ($F_{1,18} = 7.76$, $P = 0.013$), there was no such difference in 2001 ($F_{1,23} = 2.34$, $P = 0.14$) (Table 3).

The foraging trip duration of Adélie penguins was significantly positively correlated with maximum distance in both 2000 ($r = 0.876$, $P = 0.001$) and 2001 ($r = 0.514$, $P = 0.017$); however, there was no relationship between the trip duration and maximum distance in chinstrap penguins in either year (2000: $r = 0.404$, $P = 0.171$; 2001: $r = -0.098$, $P = 0.739$). In both years the maximum distance travelled by Adélie penguins increased during the course of the chick rearing period (2000: $F_{1,8} = 23.78$, $P = 0.002$; 2001: $F_{1,9} = 27.83$, $P = 0.001$), whereas there was no change in the maximum distance travelled by chinstrap penguins (2000: $F_{1,9} = 0.17$, $P = 0.65$; 2001: $F_{1,13} = 1.1$, $P = 0.31$)

Table 3 Mean, minimum and maximum distances (km) of Adélie and chinstrap penguins foraging from Signy Island, South Orkney Islands, 2000 and 2001

	2000				2001			
	n	Mean ± SE	Minimum distance	Maximum distance	*n*	Mean ± SE	Minimum distance	Maximum distance
Adélie penguin	9	99.9 ± 13.1	56.1	177.1	10	57.8 ± 17.1	2.8	163.8
Chinstrap penguin	10	57.8 ± 8.2	18.5	112.0	14	35.1 ± 3.4	19.1	55.6

(Fig. 5). There was no difference in the maximum distance travelled by male and female Adélie penguins in either 2000 ($F_{1,8}=0.39$ $P=0.55$) or 2001 ($F_{1,9}=0.00$, $P=0.97$). Similarly there was no inter-sex difference in the maximum distances traveled by chinstrap penguins (2000: $F_{1,9}=0.53$, $P=0.48$; 2001: $F_{1,13}=0.23$, $P=0.64$).

Discussion

This is the first study to examine simultaneously the foraging distribution of Adélie and chinstrap penguins breeding sympatrically. Although the two species foraged in the same general directions from the colony and had similar diets, there were consistent differences in the foraging areas used. In addition to the inter-specific differences there were inter-annual differences; the foraging areas of Adélie and chinstrap penguins were significantly different in 2000 but not 2001.

It is therefore important to consider collateral information, such as reproductive success, which might indicate differences in the level of resource availability to both species. By analogy with the situation at South Georgia, where low numbers of adults returning to breed and low reproductive success of krill-dependent predators has been shown to reflect low krill abundance (Croxall et al. 1999), it seems likely that the reduced population size and reproductive success of both species in 2000 at Signy Island reflected a low availability of krill within their foraging areas. Consistent with this, there was an order of magnitude increase in the abundance of krill in the Elephant Island region of the South Shetland Islands between 2000 and 2001 (Loeb, unpublished data). It therefore follows that the improvement in reproductive success in 2001 at Signy Island likely reflects an increase in the availability of krill in that year. Thus in a year of good food availability (2001) there was overlap in foraging areas and both species achieved above average reproductive success. In contrast when conditions were poor (2000) there was a pronounced separation of foraging areas and both species, especially Adélie penguins, suffered reduced reproductive success (i.e. 57% lower in Adélie penguins in 2000 compared with 27% lower in chinstrap penguins, Table 2). Since the foraging distribution of Adélie penguins differed between years, unlike that of chinstrap penguins, this suggests that Adélie penguins had to make a greater change to their foraging areas in response to changes in resource avail-

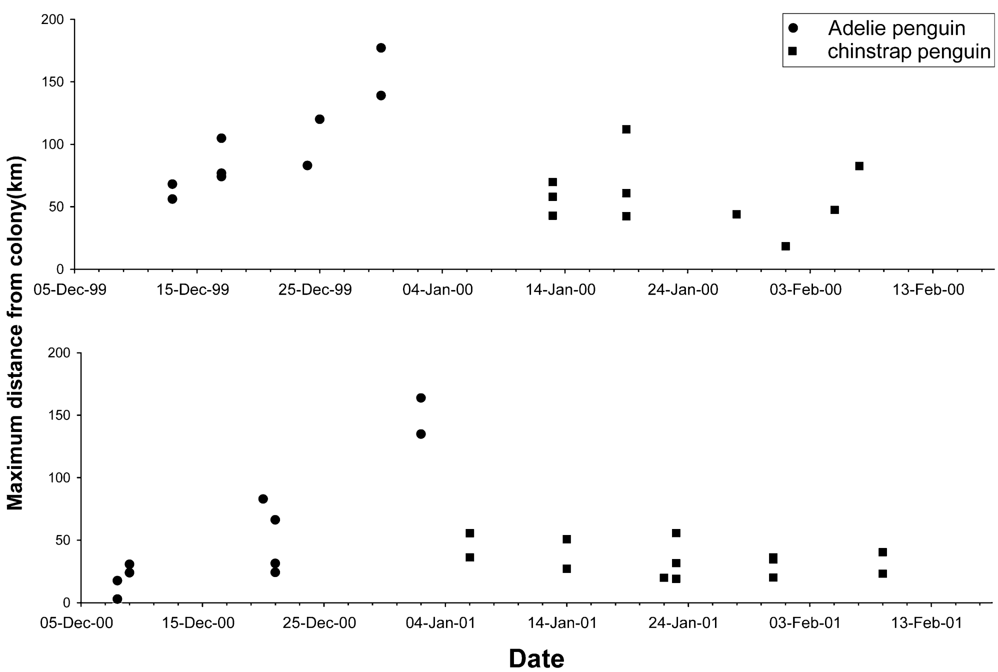

Fig. 5 Maximum distance travelled by breeding Adélie and chinstrap penguins at Signy Island, South Orkney Islands in 2000 and 2001

ability and as a result suffered a comparatively greater reduction in breeding success.

In general, the results of this study are consistent with data and inferences from previous work at Signy Island (Lishman 1985b) and other locations (Trivelpiece et al. 1987; Wilson et al. 1989) that Adélie penguins forage farther from the colony than chinstrap penguins. The maximum distance travelled by Adélie penguins in this study was greater than earlier estimates (Table 4). However, the tendency of Adélie penguins to forage further afield than chinstrap penguins did not result in two discrete foraging areas because the maximum distance of Adélie penguin foraging trips during the course of the study period increased in both years, whereas there was no such systematic change in the foraging distance of chinstrap penguins (Fig. 5). Indeed the mean distance travelled by Adélie penguins at the beginning of their chick-rearing period was similar to the mean foraging distances of chinstrap penguins at the beginning of their chick-rearing period, one month later. However, during the period of overlap when both species are engaged in chick-rearing, Adélie penguins foraged much further from the colony (Fig. 5). Although data are limited, this increase in foraging distance has rarely been reported at other sites. In a single season study, (Wienecke et al. 2000) reported an increase in foraging distance during chick rearing at Shirley Island (East Antarctica) but not at Petrel Island (South-East Antarctica); and there was no evidence of an increase in foraging distance during the chick rearing period at Béchervaise Island (Kerry et al. 1995).

This poses the question of why Adélie penguins forage further from the colony as the chick-rearing period progresses. Such a pattern could reflect local prey depletion, forcing penguins to forage further from the colony as time progresses. However, since chinstrap penguins forage in the areas formerly used by Adélie penguins, this seems very unlikely. The change in Adélie penguins from initially foraging at similar distances from the colony to chinstrap penguins, to foraging significantly further afield, appears to coincide with the onset of chick-rearing in chinstrap penguins. This might indicate that local competition for resources could cause the change in Adélie penguin foraging range. This change in foraging location occurred in a season when Adélie penguins achieved above average breeding success (Fig. 5), indicating that it does not necessarily have a negative effect on reproductive performance per se. However, when prey availability is reduced this effective exclusion of Adélie penguins by chinstrap penguins from potential inshore foraging areas may be a factor contributing to the much lower reproductive success of Adélie penguins compared to chinstrap penguins. That such competitive exclusion of Adélie penguins by chinstrap penguins might exist is supported by observations of aggressive dominance in the breeding colonies where, despite arriving later, chinstrap penguins are observed to evict Adélie penguins from nest sites in order to begin their own breeding attempt (Trivelpiece and Volkman 1979).

In this study we have considered only the role of foraging location, diet and prey availability in relation to breeding performance and interspecies interactions. However, the factor most often cited as a key determinant of breeding population size and reproductive success is the duration and extent of sea-ice adjacent to the colony (Lishman 1985a; Fraser et al. 1992). In assessing the circumstances and mechanisms whereby Adélie and chinstrap penguins achieve stable co-existence, it is important to recollect that, despite the existence of an extensive zone of overlap in and near the island groups associated with the Antarctic Peninsula, the two species have basically complementary distributions and habitat preferences. In general, the Adélie penguin is a circum-Antarctic species of high latitudes, where it inhabits ice-associated areas, including breeding sites surrounded by fast ice year-round. Except for an isolated colony at the South Sandwich Islands, its effective northern breeding limit is at 61°S. The chinstrap penguin is primarily a species of year-round open water habitats in the Atlantic sector of the Southern Ocean, breeding from 54°S at South Georgia to 65°S on the Antarctic Peninsula. Studies of the foraging behaviour of Adélie penguins at a range of sites indicate that this species exhibits considerable site-specific variability in foraging behaviour both within and between years (Table 4). These differences have largely been attributed to regional differences in sea-ice cover since the foraging areas of Adélie penguins range from being largely in open water (i.e. this study) to under semi-permanent fast-ice for the entire breeding season (Watanuki et al. 1993). Although data on the foraging behaviour of chinstrap penguins during chick-rearing are less extensive (Table 4), the distances travelled indicate that it is predominantly an inshore species and does not show the same range of foraging behaviour as Adélie penguins, perhaps reflecting its more northerly distribution with generally similar environmental conditions, i.e. open water, in the vicinity of breeding colonies.

In the zone where both species have similar distribution and abundance as breeding species, it appears that co-existence is achieved by differential abilities to cope with or take advantage of certain aspects of the biological and physical environment. Thus in years when extensive sea-ice cover persists into the chinstrap penguin breeding season, this has an adverse effect on both the numbers of birds returning to breed and their subsequent breeding success (Lishman 1985a; Trivelpiece et al. 1987; Trathan et al. 1996). Adélie penguins usually show little effect under these circumstances, unless the sea-ice is so extensive that they cannot reach breeding sites (or these are still snow-covered) in time for laying. In years when sea-ice is absent near colonies throughout the breeding season and when food availability is normal to high, both species appear to breed equally successfully, suggesting that the advantages and disadvantages of more inshore and more offshore feeding habitats are of little importance when food is abundant. In years of reduced food availability, however, chinstrap penguins may be able to derive com-

Table 4 Maximum foraging distances (km) of Adélie and chinstrap penguins

Species	Location	Ice conditions during chick rearing	Maximum foraging distance from colony (km)	Method	*n* (number of birds)	Source
Adélie penguin	Signy Island, South Orkney Islands	Open water	94.5	Time budgets and swim speed	–	Lishman (1985b)
			177.1 (2000)	Satellite telemetry	9	This study
			163.8 (2001)		10	
	King George Island, South Shetland Islands	Open water	50	Time budgets and swim speed	–	Trivelpiece et al. (1987)
	Hukuro Bay, Lützow-Holm Bay	Fast sea-ice throughout	2	Radio-telemetry	18	Watanuki et al. (1993)
	Béchervaise Island, E Antarctica	Fast ice during brood guard, open water during creche	135 (1992)	Satellite telemetry	17	Kerry et al. (1995)
			124 (1993)		10	
	Magnetic Island, E Antarctica	Fast sea-ice during brood-guard, pack ice during crèche	100	Satellite telemetry	3	Kerry et al. (1997)
	Shirley Island, E Antarctica	Open water and pack ice	144	Satellite telemetry	13	Wienecke et al. (2000)
	Petrel Island, SE Antarctica	Fast sea-ice during brood-guard, pack ice during crèche	79	Satellite telemetry	40	Wienecke et al. (2000)
Chinstrap penguin	Signy Island, South Orkney Islands	Open water	132	Time budgets and swim speed	–	Lishman (1985b)
			112 (2000)	Satellite telemetry	10	This study
			55.6 (2001)		14	
	King George Island, South Shetland Islands	Open water	33	Time budgets and swim speed	–	Trivelpiece et al. (1987)
	Seal Island, South Shetland Islands	Open water	26.4	Time budgets and swim speed	4	Bengtson et al. (1993)
	Ardley Island, South Shetland Islands	Open water	40	Vector analyses of swim speed, direction and dive depth as function of time	14	Wilson and Peters (1999)

petitive advantage (at least in terms of breeding success) by excluding Adélie penguins from at least part of the inshore habitats around breeding colonies.

Testing and refining this assessment, given the dynamic interactions between these two species and their physical and biological environments, will require extensive series of data on population size, breeding success, diet, prey availability and foraging range. The nature of interspecies interactions outside the breeding season may also need investigating, although present indications are that their wintering areas may be discrete (Fraser and Trivelpiece 1996). If our hypothesis is correct, the present trends, at least in the Antarctic Peninsula section of the Southern Ocean, to climate warming (Vaughan et al. 2001), reduced frequency of years of extensive sea-ice (Fraser et al. 1992; Jacobs and Comiso 1993; Murphy et al. 1995), and potentially increased frequency of years of low krill availability (Reid and Croxall 2001), suggest that conditions are likely to become increasingly less favourable to Adélie penguins than to chinstrap penguins in their main areas of co-occurrence.

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