GEOGRAPHIC STRUCTURE OF ADÉLIE PENGUIN POPULATIONS: OVERLAP IN COLONY-SPECIFIC FORAGING AREAS

David G. Ainley,[1,7] Christine A. Ribic,[2] Grant Ballard,[3] Sacha Heath,[3] Ian Gaffney,[4] Brian J. Karl,[5] Kerry J. Barton,[5] Peter R. Wilson,[5] and Sophie Webb[6]

[1]*H. T. Harvey and Associates, 3150 Almaden Expressway, Suite 145, San Jose, California 95118 USA*
[2]*USGS Wisconsin Cooperative Wildlife Research Unit, Department of Wildlife Ecology, University of Wisconsin, Madison, Wisconsin 53706 USA*
[3]*Point Reyes Bird Observatory, Stinson Beach, California 94970 USA*
[4]*1021 Greenwich Street, San Francisco, California 94904 USA*
[5]*LandCare Research New Zealand, Ltd., Private Bag 6, Nelson, New Zealand*
[6]*P.O. Box 683, Bolinas, California 94924 USA*

Abstract. In an investigation of the factors leading to geographic structuring among Adélie Penguin (*Pygoscelis adeliae*) populations, we studied the size and overlap of colony-specific foraging areas within an isolated cluster of colonies. The study area, in the southwestern Ross Sea, included one large and three smaller colonies, ranging in size from 3900 to 135 000 nesting pairs, clustered on Ross and Beaufort Islands. We used triangulation of radio signals from transmitters attached to breeding penguins to determine foraging locations and to define colony-specific foraging areas during the chick-provisioning period of four breeding seasons, 1997–2000. Colony populations (nesting pairs) were determined using aerial photography just after egg-laying; reproductive success was estimated by comparing ground counts of chicks fledged to the number of breeding pairs apparent in aerial photos. Foraging-trip duration, meal size, and adult body mass were estimated using RFID (radio frequency identification) tags and an automated reader and weighbridge. Chick growth was assessed by weekly weighing. We related the following variables to colony size: foraging distance, area, and duration; reproductive success; chick meal size and growth rate; and seasonal variation in adult body mass. We found that penguins foraged closest to their respective colonies, particularly at the smaller colonies. However, as the season progressed, foraging distance, duration, and area increased noticeably, especially at the largest colony. The foraging areas of the smaller colonies overlapped broadly, but very little foraging area overlap existed between the large colony and the smaller colonies, even though the foraging area of the large colony was well within range of the smaller colonies. Instead, the foraging areas of the smaller colonies shifted as that of the large colony grew. Colony size was not related to chick meal size, chick growth, or parental body mass. This differed from the year previous to the study, when foraging trips of the large colony were very long, parents lost mass, and chick meals were smaller. In light of existing data on prey abundance in neritic waters in Antarctica suggesting that krill are relatively evenly distributed and in high abundance in the Southern Ross Sea, we conclude that penguins depleted or changed the availability of their prey, that the degree of alteration was a function of colony size, and that the large colony affected the location (and perhaps ultimately the size) of foraging areas for the smaller colonies. It appears, therefore, that foraging dynamics play a role in the geographic structuring of colonies in this species.

Key words: Adélie Penguin; Antarctica; colonial breeding; foraging area; foraging distance; foraging theory; geographic colony structuring; metapopulation; Pygoscelis adeliae; telemetry.

INTRODUCTION

According to theory, if there are enough individuals actively foraging and their food supplies are not renewed, colonial bird species should reduce the availability of prey close to the breeding colony, thus requiring an ever-broadening search for new food sources (see reviews addressing the costs and benefits of coloniality in Wittenberger and Hunt [1985], Siegel-Cau-

sey and Karitonov [1990], Brown and Brown [2001]). Moreover, this effect should be intensified by the degree of breeding synchrony, which is usually very high among colonial species. Therefore, in the absence of nesting-space limitations, the amount and quality of foraging habitat available should eventually limit the size to which a colony can grow (Storer 1952, Ashmole 1963, Diamond 1978).

The idea of relating colony size to extent of foraging habitat lay fallow until, using indirect evidence, Furness and Birkhead (1984), followed by Cairns (1989), proposed that colonies in a region could become geo-

graphically structured through intraspecific competition for food. In other words, by occupying available foraging habitat at high density, a large colony could inhibit the presence or growth of other colonies within foraging range. In turn, the structuring that results could arise either through overlapping (Furness and Birkhead 1984) or abutting (Cairns 1989) foraging areas. These authors assumed explicitly that food availability was homogeneous throughout the region in question, and implied that a limit in density of foraging birds must be reached within the area used by adjacent colonies. When that limit is reached, additional individuals must search for food elsewhere to increase chances of success. Eventually, these individuals colonize locations closer to the less contested food source (Gibbs et al. 1987).

To better understand how populations of seabirds and other colonial species could become geographically structured, researchers have investigated whether a colony could deplete food in such a way that competition could ensue, either through interference or exploitative means (see Charnov et al. 1976, Ydenberg et al. 1986). The evidence has been largely indirect. Gaston et al. (1983) and Hunt et al. (1986) noted that the reproductive output of kittiwakes (*Rissa*) and murres (*Uria*) in large colonies was lower than in small colonies, implying a greater reduction in prey availability where larger numbers of breeders were foraging. Among colonial landbirds (e.g., swallows *Hirundo*), foraging trips are much shorter than in seabirds, and are directed toward highly ephemeral swarms of insects, lasting on the order of minutes. Because of information transfer among foragers, a phenomenon not known to exist among seabirds, larger colonies often fare better than smaller ones.

Other research has provided more direct evidence for prey depletion, demonstrating that foraging trip distance and duration and/or the extent of adjacent foraging habitat are positively correlated with colony size (e.g., gannets *Morus*, Lewis et al. [2001]; herons *Ardea*, Farhina and Leitao [1996], Gibbs et al. [1987], Gibbs and Kinkel [1997]; swallows *Hirundo*, Brown and Brown [1996]; rooks *Corvus*, Griffin and Thomas [2000]; and kittiwakes *Rissa*, Ainley et al. [2003*b*]). These results all rely on the assumption that, in the absence of predators, prey is homogeneously available. Also, in the case of the gannet, the growth rate of colonies is inversely related to size, thus further arguing for density-related processes of intraspecific competition for food (Lewis et al. 2001). Attempting to explain longer foraging trips of gannets from larger colonies, Lewis et al. (2001) offered a model in which seabirds, through their foraging activity, harry potential prey to the point at which they were no longer easily caught (interference competition), as opposed to actually depleting the prey resource.

Direct evidence for the depletion of food or feeding opportunities is sparse, owing to the extraordinary effort required in collecting the data. Birt et al. (1987) found depleted abundance of (likely territorial and, therefore, not quickly replaced) benthic fish within the flight range of a single cormorant (*Phalacrocorax*) colony (exploitative competition). Ainley et al. (2003*b*) showed that the frequency at which prey schools were encountered at the surface decreased with increased colony size among surface-foraging kittiwakes (interference competition); and the quality of prey taken was reduced at large compared to small colonies of Magellanic Penguins (*Spehiscus magellanicus*; Forero et al. 2002). Prey depletion has also been documented near colonies of swallows (Bryant 1975, Møller 1987, Earle and Underhill 1991) and nests of kestrels (*Falco naumanni*; Bustamante 1997). Only the studies by Forero et al. (2002) and Ainley et al. (2003*b*) attempted to quantify prey availability and depletion simultaneously at more than one colony. Brown and Brown (2001) discussed difficulties inherent to this task.

In a study of the geographic structure and colony growth rates of Adélie Penguin (*Pygoscelis adeliae*) populations, we have addressed two main questions. First, what factors maintain a three-order-of-magnitude range in size within the cluster of colonies that we are investigating? Second, why have colony growth rates over recent decades correlated negatively with colony size? Ainley et al. (1995) showed that populations are geographically structured in this species, with only small colonies existing near large ones throughout their circumpolar range. In addition, we have observed that colony growth rate, as in the gannet (Lewis et al. 2001), is related to colony size (obvious, although not stated, in Taylor and Wilson [1990] and Wilson et al. [2001]). We have also previously found that, in years of low food availability, both chick and adult mass can be negatively correlated with foraging trip duration and colony size (Ainley et al. 1998, cf. Gaston et al. 1983, Hunt et al. 1986).

Here we report annual and intra-annual variation in foraging distance, duration, and area, overlap of foraging areas, food load size, adult mass, reproductive success, and chick growth of Adélie Penguins at a cluster of four colonies in the southern Ross Sea, 1997–2000. We evaluate the relationship of these factors to colony size and density of foraging birds within range of a colony. We also test whether the expression of any of these relationships is most clear (1) later in the nesting season, theoretically after food is depleted close to colonies; and (2) at the largest colony, where we expected competition for food to be highest.

METHODS

Our study covered all of the guard stage and three-fifths of the crèche stage of the Adélie Penguins, 21 December to 12–15 January, for four austral summers, 1997–1998 to 2000–2001. During the guard stage, one parent remains with the chick(s) while the other forages, and nest reliefs are every 1–3 days. At this stage,
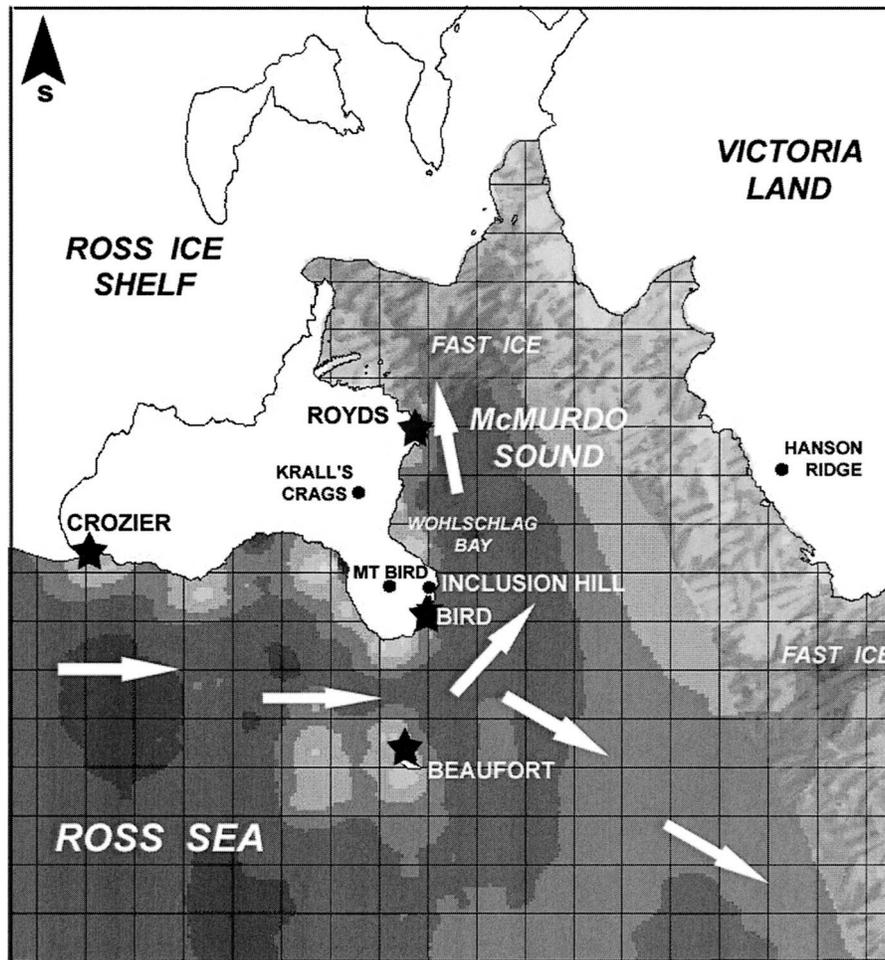
FIG. 1. The study area showing colonies (stars) and other locations where telemetry was conducted on Adélie Penguins, 1997–2000, as well as the 10-km grid used to plot locations. Sea-bottom relief is shown in gray scale. Data for the sea-bottom relief came from NOAA National Geophysical Data Center (1988). Arrows show the direction of the coastal current around Ross Island.

chicks are fed relatively small meals by the attending parent. During crèche, chick demands become too great for one parent at a time to provide, so chicks are left on their own while both parents forage simultaneously. The chick phase of the annual cycle has been identified as the most important in the question of geographic structuring of seabird populations, because it is during this phase that seabirds purportedly exert their greatest pressure on food resources (Furness and Birkhead 1984). Provisioning in the latter parts of chick development has the greatest influence on fledging mass (Salihoglu et al. 2001). Hereafter, we refer to austral summers as seasons, using the initial year (e.g., 1997 refers to the nesting season that began in October 1997 and ended in February 1998).

Study area and colony growth

Study colonies were on Ross and Beaufort Islands in the Ross Sea (Fig. 1). Colony breeding population size estimates were derived from aerial photos taken on or about 1 December each year. On that date, essentially only one member of each pair is present in the colony while the other is foraging at sea, all breeders are incubating eggs, and very few nonbreeders are present (Taylor et al. 1990, Taylor and Wilson 1990; see Ainley [2002] for a comparison of seasonal population dynamics among these and other colonies). On 1 December, the number of active nests (nests containing eggs or chicks) is at maximum. By about 7 January, the beginning of the crèche stage, the number has been reduced by ~12% (Taylor 1962).

Although aerial photos of each colony have been taken annually to the present, financial resources have been available only to count penguins in the subcolonies used to assess annual reproductive success for some colonies in some years. Therefore, the sizes of colonies on Ross Island reported herein (Table 1) were extrapolated from the 1997 total counts using the same

TABLE 1.　Numbers of breeding pairs of Adélie Penguins and number of chicks near fledging, by colony and year.

Year and colony	No. pairs†	No. chicks/pair‡		Chicks provisioned§
		Mean	1 SE	
1997				
Crozier	**134 892**	1.36	0.05	183 453
Beaufort‖	42 005			
Bird	**47 508**	1.51	0.04	71 737
Royds	**3 933**	1.20	0.03	4 720
1998				
Crozier	*90 638*	0.80	0.04	69 360
Beaufort‖	32 797			
Bird	**38 252**	0.55	0.03	21 582
Royds	**3 411**	1.02	0.10	3 479
1999				
Crozier	*137 135*	1.39	0.11	182 335
Beaufort‖	40 517			
Bird	*45 449*	1.75	0.08	83 732
Royds	**3 620**	1.38	0.09	4 996
2000				
Crozier	*118 772*	0.96	0.06	109 067
Beaufort‖	31 033			
Bird	34 632¶	ND		ND
Royds	*2 387*	0.92	0.08	2 196

　† Pair numbers shown in boldface are based on direct (aerial) counts; those shown in italic are based on projection from counts of selected subcolonies (within 2–5% of true; see *Methods*).

　‡ The number of chicks per pair is an overestimate of actual breeding success because it does not consider early loss of eggs (see *Methods*).

　§ ''Chicks provisioned'' is the product of the number of nests (pairs) and the number of chicks/pair being raised during the study period each year.

　‖ The estimate of the Beaufort colony size in 1997 (no direct count) is based on the size ratio with the Bird colony (1.131:1) during 1983–1991, a period when both colonies were censused directly each year (K. J. Barton and P. R. Wilson, *unpublished data*). For each subsequent year, size is based on the average change in size from the previous year among the Crozier, Bird, and Royds colonies.

　¶ This estimate for 2000, when no aerial photos were available for Cape Bird, is based on the average change in colony size (0.762) for Royds and Crozier, 1999–2000; ND indicates that no chick data were available.

''productivity subcolonies'' ($n = 13–21$ depending on colony) as an index of total colony size. Subcolonies are the discrete groups of contiguous nests that, when considered together, comprise an Adélie Penguin colony (definitions are fully discussed in Ainley [2002]). Using the years shown, the indexed population was within the following percentage points of the actual population: Royds 1996–1999, 2.0%; Bird 1996–1998, 5.3%; and Crozier 1996–1997, 4.3%. The Royds index was almost the same as a full colony count; all but 2–3 sprawling subcolonies were included. At Crozier and Bird, the productivity subcolonies represented 5–10% of the total colonies. For Beaufort Island, we used the ratio in size between Bird and Beaufort during the years when both were directly censused to project Beaufort population size during the present study; thus, interannual variation in its size follows the same pattern as for Bird (Table 1).

　The estimates of colony size, corrected for population age structure and percentage of breeders to nonbreeders by age class, were combined with estimates of foraging area sizes in order to estimate the density of foraging birds at sea for each colony (number of foragers per square kilometer). We used this information to assess the consequences of foraging area overlaps. We derived a rough estimate, the only one possible without direct measurement, of the density of birds at sea in each colony's foraging area at any given time during the late chick-provisioning period (telemetry periods 3 and 4). Estimates of breeding population size (Table 1) were combined with estimates of population age structure and the percentage of each age class expected to be breeding (Ainley 2002). We assumed that 75% of birds feeding chicks (breeders) would be at sea, and we used age-specific estimates for nonbreeders as follows: 85% of 2- and 3-yr-olds, 25% of 4-yr-olds, and 15% of older birds. Finally, we used two approaches to estimate foraging density in cases where foraging areas overlapped. First we determined a total common foraging area and divided by the sum of the at-sea populations of the colonies involved. Second, we summed the respective foraging densities for each colony within the area of overlap. Figures for foraging area were taken from Table 6 (total area, all time periods).

TABLE 2. Mean mass (predicted on the basis of a regression model) of 34-day-old Adélie Penguin chicks (at 75% of the period to fledging and at the peak of the growth curve) by colony and year.

	Crozier		Royds		Bird	
Year	Chick mass (kg)	n†	Chick mass (kg)	n	Chick mass (kg)	n
1997	3.73	50	3.69	48	3.58	50
1998	3.86	48	3.82	48	3.70	50
1999	3.36	46	3.32	50	3.21	23
2000	3.75	49	3.71	50	3.59	48

† Sample size n is the number of chicks weighed to develop the model.

Reproductive performance

We assessed chick production by counting the number of chicks present on or about 20 January (7–10 days before fledging) in the subcolonies that had been photographed from the air on 1 December. Therefore, if the 1 December photos provided an estimate of the numbers of nesting pairs, then the result of chick counts was the number of chicks raised near-to-fledging per breeding pair. This is a high estimate of production because, by 1 December, pairs that had laid eggs but lost them early would not have been present. On the basis of data on the timing of peak hatching, peak laying would have occurred ~8–10 November at Capes Crozier and Bird, and 15–18 November at Cape Royds during the years of this study. Therefore, 1 December is about two-thirds of the way through incubation. Laying dates at Beaufort appeared to be similar to those at Crozier and Bird. The large majority of eggs that eventually will be lost disappear within a few days of laying, and most chick loss occurs within a few days of hatching (Young 1994, Ainley 2002). Therefore, given that the aerial photos were taken between these two periods, the estimate of productivity at Royds should be only slightly overstated relative to the other colonies using this method of productivity estimation.

We also assessed chick growth rates by weighing 50 chicks, selected randomly, at Capes Crozier, Bird, and Royds at weekly intervals. We then compared the mean mass of chicks 30–34 days old (75% of the time to fledging and point of heaviest mass) to gauge the relative growth of chicks among the colonies.

Foraging area and effort

Telemetry.—At Capes Bird, Crozier, and Royds, radio transmitters (model PN7, Advanced Telemetry Systems, Isanti, Minnesota, USA) were placed on the lower backs of 15 penguins using Tesa tape (Tesa, Charlotte, North Carolina, USA) within 1–2 days of 20 December during each season (for the method of attachment, see Wilson and Wilson [1989], Wilson et al. [1997]). Many chicks had hatched by that date, and all penguins given radios had chicks at the time. Radios were attached to eight penguins at Beaufort Island, depending on the availability of a ship to get us there, usually about 28 December. Radios were attached to different birds in each season; sex ratios were equal or close to equal. Sexes of individuals were determined using a combination of attributes (relative size of partners and behavior). Beginning in 1998, we attached radios to both members of pairs as they changed between foraging and brooding duty (i.e., at nest reliefs); see Ballard et al. (2001) for further details of sexing and radio attachment. Foraging trip durations and breeding success of penguins with radios did not differ, on average, from those of unencumbered penguins (Ballard et al. 2001). We removed radios on about 10–15 January each season.

Throughout the period of radio attachment, we attempted to triangulate positions of foraging birds. Here we report results only for penguins that were actively foraging, as judged from a signal characterized by long periods of radio silence (~120 s; bird diving) interspersed with short periods of constant signaling (10–45 s, mean 42 s; aerobic recovery). Radios on penguins standing on ice floes emitted a continuous signal, whereas those on swimming penguins gave infrequent single signals whenever the bird broke the surface to breathe. See Trivelpiece et al. (1986) for characterizations of foraging and swimming behavior as revealed by radiotelemetry signals.

Listening stations included positions above respective colonies or other sites, much higher than colony

TABLE 3. Overall foraging distance of penguins (n = number of individuals) by colony and year.

	Penguin foraging distance (km)											
	Crozier			Beaufort			Bird			Royds		
Year	Mean	1 SE	n	Mean	1 SE	n	Mean	1 SE	n	Mean	1 SE	n
1997	19.43[a]	2.24	16	24.30[b]	2.98	7	18.04[b]	1.04	14	10.33[a]	0.52	19
1998	24.18[a,b]	2.16	16	24.65[b]	1.38	6	15.38[a,b]	0.93	15	10.66[a,b]	0.34	15
1999	27.62[b]	1.42	15	19.52[a,b]	1.37	7	13.43[a]	0.90	15	9.70[a]	0.42	19
2000	19.20[a]	0.54	15	16.43[a]	0.74	7	14.01[a,b]	1.50	15	12.09[b]	0.81	15

Notes: Within a column, colony means with the same superscript letter do not differ significantly between years. Underlined groups within a row (year) indicate no statistical difference between colonies, based on Tukey's hsd.

TABLE 4. Foraging distances of penguins (n = number of individuals) during telemetry periods 1 and 4, with differences between these periods shown by colony and year.

| | Penguin foraging distance (km) | | | | | | | | | | | |
| | Crozier | | | Beaufort | | | Bird | | | Royds | | |
Year	Mean	1 SE	n	Mean	1 SE	n	Mean	1 SE	n	Mean	1 SE	n
Telemetry period 1 (20–25 December)												
1997	6.82[a]	0.45	7				15.78[a]	1.60	11	11.62[a]	0.81	14
1998	12.40[a]	2.02	12				14.71[a]	1.52	16	11.68[a]	0.73	14
1999	25.71[c]	1.60	13				12.53[a]	2.29	12	9.35[b]	0.49	16
2000	19.43[b]	0.72	13									
Telemetry period 4 (5–11 January)												
1997	23.49[a,b]	1.87	13	23.87[a,b]	1.62	5	17.58[a]	1.88	11	8.80[a]	1.12	9
1998	37.05[c]	3.71	12	25.82[b]	1.94	5	14.25[a]	1.61	13	11.98[a,b]	1.06	11
1999	29.41[b]	1.82	11	17.57[a,b]	2.38	7	15.02[a]	1.91	11	13.21[b]	2.01	6
2000	19.50[a]	1.42	14	16.43[a]	0.74	7	16.44[a]	2.12	15	12.77[b]	0.65	14
Difference between telemetry periods 1 and 4												
1997	−13.72[a,b]	3.08	8	0.82[a]	6.05	3	−3.47[a]	1.97	8	3.96[b]	0.91	6
1998	−25.86[a]	4.80	10				0.66[a]	2.30	13	0.46[a,b]	1.37	10
1999	−3.68[b,c]	2.19	10	2.92[a]	1.98	6	−2.02[a]	3.98	10	−4.49[a]	2.83	5
2000	−0.24[c]	1.50	12	−4.25[a]	3.13	6						

Notes: Within a column (colony), means superscripted with the same letter do not differ significantly between years (based on Tukey's hsd). Negative differences between the telemetry periods indicate that the foraging trip distance was greater for period 4. Colonies grouped by underlines within rows (years) do not differ significantly in foraging distance. In 1997 and 1998, Crozier penguins fed farther away in period 4; in 1999, the colonies were similar.

TABLE 5. Mean duration of foraging trips by parents provisioning chicks as a function of colony, year, and telemetry period (TP) within a year; n is the number of trips.

| | Crozier | | Bird | | Royds | |
TP†	Trip length (h)	n	Trip length (h)	n	Trip length (h)	n
1997						
1	24.1	61			17.3	87
2	24.9	103			15.9	148
3	27.3	99			15.3	148
4	41.0	104			14.8	188
1998						
1	32.0	53			33.3	57
2	30.5	63			25.4	97
3	33.7	60			28.9	84
4	33.8	83			22.4	137
1999						
1	31.3	61	29.2	114	31.9	71
2	31.9	76	28.4	129	22.3	94
3	29.0	90	30.1	118	23.0	142
4	37.4	88	38.5	149	20.0	192
2000						
1	24.7	76	26.8	114	24.6	59
2	19.9	136	23.0	127	20.7	70
3	17.6	130	20.2	140	16.5	106
4	18.7	181	23.1	182	18.2	100

Notes: Data were derived from the reading of radio frequency identification (RFID) tags by the weighbridge at each colony. No data are available for Cape Bird during 1997 and 1998 due to a faulty weighbridge.

† Telemetry periods: (1) 20–25 December; (2) 26–30 December; (3) 31 December–4 January; (4) 5–11 January.

locations, and chosen for reasons of access, camping safety, and triangulation value. Stations were as follows (east to west, Fig. 1): Cape Crozier (Pat's Peak: 77°27.6′ S, 169°12.1′ E), elevation 400 m, all years; Mt. Bird, north slope of summit (77°15.4′ S, 166°51.5′ E), 1766 m, all years; Beaufort Island summit (76°57.1′ S, 166°58.4′ E) 841 m, 1997 only; Cape Bird (New College Hill, 77°13.2′ S, 166°26.7′ E), 85 m, all years; Inclusion Hill (lower, southwest slope of Mt. Bird: 77°15.1′ S, 166°25.3′ E), 400 m, all years; Krall's Crags (77°27.3′ S, 166°48.7′ E), 1460 m, only in 2000; Cape Royds (78°32.8′ S, 166°9.6′ E), 30 m, all years; and Hanson Ridge (77°17.6′ S, 163°15.9′ E), 611 m, only in 1997. Inclusion Hill and Hanson Ridge were used by Sadleir and Lay (1990) in a previous telemetry study of the Cape Bird colony's foraging area; one of us (B. J. Karl) participated in that study.

Listening/tracking occurred three times daily at each site at 0700, 1400, and 2100 hours, using Telonics TR4 receivers (Telonics, Mesa, Arizona, USA), earphones, a four-element yagi antenna (affixed atop a 2-m pole, the lower end of which had a pointer), and a compass rosette. When the signal was strongest, the bearing of the pointer was noted (as in Sadleir and Lay 1990). We also recorded the relative strength of each signal: very weak, weak, medium, strong, or very strong. Although such categories were relative (quantitative verification follows), our perceptions of the categories did not vary: little turnover existed among listeners from year to

TABLE 6. Summary of foraging area of colonies as a function of telemetry period (TP 1–4) within each year, and the percentage of a colony's foraging area that overlapped the foraging area of adjacent colonies.

TP† by year	Crozier Area (km²)	Overlap (%)	Beaufort Area (km²)	Overlap (%)‡	Bird Area (km²)	Overlap (%)‡	Royds Area (km²)	Overlap (%)‡
1997								
All	2461.6	0.0	2488.2	73.4	3652.6	85.9	2167.5	60.6
1	500.0	ND	ND		1226.5	34.5§	563.7	75.1
2	1545.4	0.0	1538.3	5.7	1316.8	26.4	432.2	60.2
3	1125.0	0.0	1850.0	57.6	2600.3	62.9	1250.0	45.6
4	1524.8	0.0	940.2	71.8	1669.2	44.2	296.3	20.9
1998								
All	3459.9	22.2	2192.0	45.6	1235.8	55.6	674.9	67.6
1	450.0	ND	ND		666.4	30.8§	474.9	43.2
2	1545.5	ND	ND		898.7	9.0§	233.2	34.7
3	1945.7	0.0	1592.0	2.1	500.0	37.0	283.4	53.4
4	3693.4	6.4	1349.6	23.1	600.0	41.6	383.4	45.5
1999								
All	2275.0	7.3	2991.8	54.2	3208.4	65.2	917.4	69.3
1	1350.0	ND	ND		2037.2	10.4§	527.3	40.3
2	700.0	0.0	1163.2	4.3	950.0	5.3	161.3	0.0
3	1550.0	0.0	1388.3	18.2	1674.9	39.3	617.2	65.6
4	1775.0	4.5	2791.3	8.9	700.0	59.3	727.2	33.9
2000								
All	1075.0	0.0	1764.6	29.2	2214.8	44.0	1162.9	39.5
1	925.0	ND	ND		ND		ND	ND
2	450.0	0.0	1012.4	14.6	550.0	26.9	862.6	0.0
3	600.0	0.0	938.3	4.0	600.0	6.3	283.2	0.0
4	675.0	0.0	1639.5	15.5	2066.1	36.8	1068.1	47.3

Notes: Area represents the minimum convex polygons calculated in GIS using telemetry fixes; sizes and overlaps of areas were then calculated. ND indicates no data, resulting when foraging area for that colony was not investigated or the area of the adjacent colony was not investigated.

† Telemetry periods are: (1) 20–25 December, (2) 26–30 December, (3) 31 December–4 January, and (4) 5–11 January.

‡ Overlap of foraging area with that of adjacent colonies.

§ Overlap with Royds only, because the foraging area of the Beaufort Colony was unknown in this telemetry period.

year, all receivers were serviced and standardized by the manufacturer after each season; and during sessions within a season, batteries were changed frequently to ensure sensitive reception. We began listening sessions from multiple locations at the same time and listened to channels in the same order. If no signal was detected from a given radio at a given listening location, observers recorded "no signal." The approximate range of radio reception was 65 km at Mt. Bird and Krall's Crags; 50 km at Hanson Ridge; 40 km at Inclusion Hill and Pat's Peak; and 15 km at Cape Royds and New College Hill. Maximum reception distances were slightly longer than those summarized by Wanless and Harris (1992) and Wilson et al. (2002), probably because we did not have any extraneous electronic interference, given the isolation of our study area. We determined our ranges by comparing signals being emitted from known locations. First, we had reference transmitters at all colonies, which at each respective colony provided an indication of a "very strong" signal, and which, in many cases, could be heard from listening stations at varying distances. For example, from Mt. Bird (1800 m elevation) we could hear "very weak" signals from radios on penguins known to be just leaving Cape Crozier (65 km), heard as "very strong" from the Crozier listening site (distance ~5

km) or seen leaving the colony <1 hour from listening time; from Krall's Crags (1500 m) we heard "strong" signals from birds in the Royds colony (20 km); from Inclusion Hill (400 m), "medium" signals from just off the Royds beach (30 km); and from Mt. Bird, "medium" signals from birds on the colony at Beaufort (30 km). Beaufort birds that were immediately below Mt. Bird summit (the strongest signal being obtained with the antenna angled 30° downward), i.e., ~15 km away, came in as "very strong."

On the basis of signal strength and range, we feel that almost all birds from Royds, Bird, or Beaufort were detectable if in line-of-sight. Penguins that moved to the inshore side of Wohlschlag Bay, located between Capes Royds and Bird (Fig. 1) were not in line-of-sight because of intervening topographic features, although they were well within range of Inclusion Hill (5–10 km). Individuals from both colonies fed in that vicinity, with Royds penguins going northeast and Bird penguins going southeast to reach it. The result is that we under–estimated the degree of overlap between Royds and Bird foraging areas (however, this only strengthened our conclusions). Any birds traveling west from either Royds or Bird, two-thirds of the way across Mc-Murdo Sound (~20 km) would meet nutrient- and plankton-depleted water, much of which was also cov-

ered by fast ice, and there they would not find food (Barry 1988). Our tracking conducted from Hanson Ridge, on the west side of the Sound, confirmed that penguins did not frequent those waters. Therefore, we believe that all Royds and Bird penguins foraged within range of our listening posts. This was confirmed in 2001 and 2002 when use of satellite tags revealed that the foraging locations were all within the foraging areas described in the present study.

Our efforts resulted in under–estimates of average foraging distance and foraging area for Cape Crozier. However, minimum estimates for the maximum values of these attributes for Crozier would only serve to strengthen our conclusions (see *Results*). Although we detected any penguins that went west to north from the colony (combination of detections from Mt. Bird and Crozier), any that went northeast would be out of range of Mt. Bird and could be tracked only out to the radio limit of the Pat's Peak listening post at Cape Crozier (40 km). In fact, the northeastern boundary of the estimated foraging area for Crozier usually followed the ~65-km radius from Mt. Bird in periods when that foraging area was extensive (see Fig. 2). We were alerted to this in 2000, when we attached satellite transmitters (SPOT2, Wildlife Computers, Redmond, Washington, USA) to nine individuals for 1–2 foraging trips each. A comparison of the VHF detections with the satellite detections revealed that penguins were going beyond the VHF range by another ~10 km to the north and northeast (they could not go farther southeast due to the Ross Ice Shelf; Fig. 2D). In subsequent years, satellite fixes indicated that Crozier birds traveled even farther (D. Ainley and G. Ballard, *unpublished data*). Also, it appeared from the satellite fixes in 2000 that the penguins traveled west as far as a huge grounded iceberg would allow, that iceberg then blocking their line-of-sight detection from the Mt. Bird summit. This iceberg, known as C-16, moved into the study area in December 1999 and grounded against Beaufort Island in January (Fig. 2D). Simultaneously, an even larger iceberg, B-15A, positioned itself against the Ross Ice Shelf to the east of Crozier (Fig. 2D). It remained there until after the telemetry effort ended, but has since moved into much of the previous Crozier foraging area, thus ending use of radiotelemetry in this study.

Weighbridge.—We determined trip duration by recording the departure and arrival of individuals implanted with a passively interrogated transponder (PIT, also known as RFID, or radio frequency identification tag). Data were recorded automatically as the birds passed through a reader; a set of photocells switched the reader on and off, and logged direction of movement across the scale (Kerry et al. 1993, Ainley et al. 1998, Ballard et al. 2001). A reader-scale (weighbridge, WB) was set up at one subcolony at each study colony, except Beaufort Island. WB data were collected successfully at Capes Crozier and Royds for all four seasons, but only for the last two at Cape Bird. Plastic

fencing that encircled each WB subcolony channeled parents through the reader. Trip durations determined from WB data were statistically similar to those determined by recording the presence of radio-tagged birds using a scanning receiver and data logger, but were far more accurate because the receiver scanned only once every 90 minutes (Ballard et al. 2001). Therefore, we report here trip durations as determined by the WB.

Meal sizes fed to chicks as a function of trip duration during the telemetry periods were determined using the same WB. We subtracted the body mass of parents upon departure from their mass at their previous arrival in the WB subcolony. This was taken to be the amount of food fed to chicks, and is quite different from ''meal sizes'' reported by other researchers and determined by stomach flushing; parents usually do not feed their entire stomach load to their chicks (cf. Lishman 1985, Ainley et al. 1998). For each subcolony and season, we used a unique algorithm to estimate the mass of a given penguin upon each WB crossing, because each WB and WB installation varied slightly in physical characteristics. In all cases, the scale measured mass 12 times per second and the bird had to be on the scale for at least 0.8 s for a valid estimate to be made. About 80% of crossings resulted in a valid mass estimation. Most invalid estimates occurred when more than one individual was on the scale. For analysis, we used estimated meal sizes that were >0 g and <1300 g, a range encompassed by directly measured stomach loads at Cape Crozier (cf. Emison 1968).

To determine whether adult mass varied among seasons and colonies, we used WB data to calculate the mean mass of each adult departing for foraging trips to provision chicks that were >25 days old in each year, 1997–2000 (see also Ainley et al. 1998). Having chicks of that age was assurance that they were in crèche. Data were not available for Cape Bird in 1997 or 1998, due to WB technical difficulties.

Data analysis

We divided each season into four roughly five-day segments: 20–25 and 26–30 December, 31 December–4 January, and 5–11 January. Hereafter these will be referred to as telemetry periods (TP) 1–4, respectively. Using ArcView 3.2 (ESRI 2000), we overlaid the entire southwestern Ross Sea and McMurdo Sound with a 10–km x,y-grid (Fig. 1). Fast ice, where the penguins normally do not forage unless cracks are present, and large tabular icebergs, which also covered potential foraging habitat, were drawn from satellite images taken within each TP-year (Fig. 2). Fast ice or iceberg-related boundaries changed between and within seasons, and were used in the GIS analysis as limits to respective foraging areas. In cases in which we knew that penguins were foraging in tide cracks, we included that portion of fast ice in the foraging range. Among birds judged to be diving for food, position fixes oc-

curred when at least two bearings from different listening posts intersected within 1.5 h of each other for Mt. Bird-Crozier, or within 1 h in other cases. The wider time period for Mt. Bird-Crozier was necessary because sessions were slightly less coordinated, owing to the extreme conditions sometimes present at the Mt. Bird summit and difficult radio communications among observers. Results from time-depth-recorders placed on penguins indicate that these penguins, when acquiring food, usually dive continuously for a few hours nonstop and, therefore, in the same location (D. Ainley and G. Ballard, *unpublished data*; see Chappel et al. 1993). In cases in which only one bearing was available (i.e., the penguin was within range of just one listening post), we estimated the straight-line distance away (the appropriate 10-km cell) on the basis of signal strength. Pairs of bearings that did not cross in a cell but were consistent (both pointing to the same cell) were treated in the same way. The strongest bearing from the pair was used in the allocation. The frequency of cases in which only one listening post heard a radio was minimal, except for Beaufort, as follows: Beaufort, 15 of 28 birds, radios otherwise heard from Mt. Bird, Cape Bird, and Inclusion Hill; Cape Bird, nine of 61 birds, heard from Cape Bird, Mt. Bird, Hanson Ridge, and Inclusion Hill; Crozier, 11 of 65 birds, heard from Mt. Bird and Cape Crozier; and Royds, eight of 69 birds heard from Cape Royds, Inclusion Hill, and Krall's Crags (2000 only). We conducted simulations to assess how the number of radios deployed would affect the estimated foraging area size, given that we deployed only half the number of radios each season at Beaufort compared to the other colonies.

One location was used to classify a cell as occupied by a feeding bird. On average, Beaufort had 38% of grid cells as single foraging locations, with Bird having 36%, Crozier 23%, and Royds 24%. Most of these cells were on the edges of the areas. Therefore, results are comparable among colonies, and tightest for the smallest and largest colony. On average, we obtained 1.5 feeding locations per day per individual. We filtered the locations for errors: if two listening posts disagreed about the trajectory (e.g., pointed in opposite directions), then the location was not used even as a bearing.
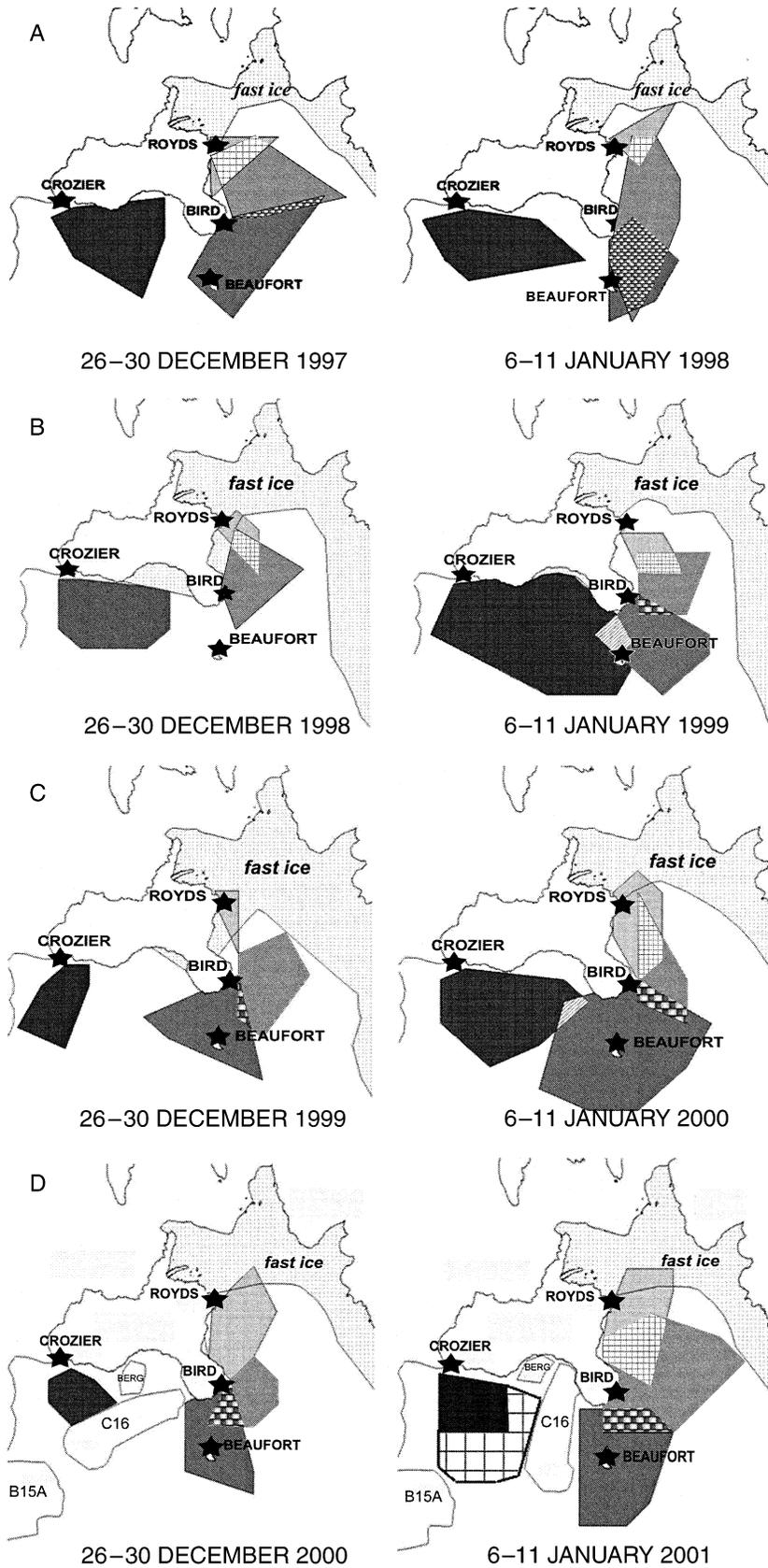
Once all useful records were allocated to grid cells, we used minimum convex polygons (MCPs) to describe foraging areas for each colony. A data point was the midpoint of each cell in which that penguin was heard (by true fix or allocation of bearing). Size of the MCP in square kilometers, along with extent of overlap with adjacent colony-specific foraging areas, was determined for each five-day TP. Foraging distance from the colony was estimated for each individual by averaging all of its (feeding) data points for each TP.

To investigate variation in chick mass, we used a three-way linear model to test the effects of colony, year, and chick age on the cube-root of chick mass at Capes Crozier, Royds, and Bird, 1997–2000. Only near-to-fledging chicks (aged 30–34 days, 75% of the age to fledging and at peak mass), were included. We excluded the lightest 4% ($<$2000 g) because doing so normalized model residuals, and these most likely represented chicks that hatched significantly later than the generally synchronous peak hatch days used for age determination. The interaction of year and colony was also evaluated.

In regard to trip durations (WB data), we used four-way ANOVA on log(foraging trip duration) to determine variation by year, TP within a year, or colony, all while controlling for individual penguins. Only individuals for which two or more trips (or meals) were recorded in a TP were included, and the four interactions (year $\times$ colony, year $\times$ TP, colony $\times$ TP, and year $\times$ colony $\times$ TP) were also evaluated. We further limited the data to include only individuals known to have young at the time of the trip, and who made trips of $\geq$6 h duration (following Ballard et al. 2001). We calculated meal sizes by subtracting the mass of parents upon departure from their mass upon arrival if they had young at the time of arrival, and if their calculated food loads were between 0 and 1300 g. Again, we used four-way ANOVA to evaluate the impact of colony, season, and TP on untransformed food load, while controlling for individual penguins. The same four interactions were also included. Residuals from both models were normally distributed, and we used Tukey's hsd (pairwise comparison of means) for postregression comparison of predicted values of the dependent variable [log(trip duration or meal size)] when ANOVA indicated significant variation. In regard to the mass of adults having crèche-age chicks, we compared the cube-roots of these masses among colonies and seasons using a two-way linear model, including the colony $\times$ season interaction.

For the telemetry data, we used two-way ANOVA to determine whether foraging distances (overall or by TP) changed between years and colonies, including the year $\times$ colony interaction. The unit of measure was, for each individual, mean distance from the breeding colony (overall and by TP) and differences between TP 1 and 4 (TP 2 and 4 for Beaufort). By the Central Limit Theorem, the means should be normally distributed. In addition, residual analysis did not reveal any patterns indicating a violation of assumptions. Tukey's hsd (all pairwise comparisons of means) was used for multiple comparisons. To be consistent with the analysis of the WB data, we used any individual for which we had at least two distances overall or by TP. To determine whether the areas of the minimum convex polygons for TP 1 and 4 changed by colony or year, we used a three-way repeated-measures ANOVA with interactions; TP was considered the repeated measure. When interactions were significant, data were analyzed by colony and then by year within a colony. We calculated minimum convex polygons for individuals with

A

26–30 DECEMBER 1997

6–11 JANUARY 1998

B

26–30 DECEMBER 1998

6–11 JANUARY 1999

C

26–30 DECEMBER 1999

6–11 JANUARY 2000

D

26–30 DECEMBER 2000

6–11 JANUARY 2001

three or more locations in TP 1 and 4 (TP 2 and 4 for Beaufort, as TP 1 data were not available).

To investigate the relationship between foraging trip distance and colony size, we used correlation and calculated Spearman's rho (nonparametric equivalent of Spearman's *r*). For each year, we used an average distance for each colony (overall and for TP 4) by averaging over all individuals. Colony size was represented by both population size and provisioned population (breeding pairs × chicks/pair) by year. To assess significance, we used a randomization approach (Manly 1997). The three years (1997–1999) were used as replicates. For each year, a correlation was calculated and then averaged to summarize the correlations. Assuming that there is no relationship between foraging distance and colony size, we randomly assigned the foraging distances to a colony/year. We then calculated correlations by year and averaged over the three years, as we did for the data values. If the average correlation from the data values proved to be extreme compared to the average correlations from the randomly assigned data, then we would conclude that the relationship between foraging distance and colony size is significantly different from random assignment. We calculated 1000 average correlations based on random assignment to assess significance at $\alpha = 0.05$ (Manly 1997). Because we were expecting a positive relationship, we used a one-tailed test; the *P* value was calculated as (number of average correlations equal to the data value or greater)/1000. We did this for all four combinations of foraging distance and colony size.

RESULTS

Variation in colony size

The largest colony was Cape Crozier (1997 count, the last available: 135 000 pairs, including both east and west sections); the smaller colonies were Cape Bird (1997 count, 45 000 pairs, including north, middle, and south sections), Beaufort Island (1991 count, 38 000 pairs), and especially Cape Royds (1997 count, 3900 pairs). All have grown in population size since 1970 (the earliest census common to all, except Beaufort; Taylor et al. 1990, Wilson et al. 2001). Overall differences in size were as follows (1997 vs. 1970): Royds, 260% larger; Bird, 60% larger; and Crozier, 14% larger. Within that span of years, the colonies grew to reach a maximum in 1987, followed by a sharp three-year decline and then renewal of growth (Wilson et al. 2001). Average annual percentage growth rates (expressed as mean ± 1 SE) at the three colonies, respec-

tively, until the abrupt decline (1980–1987), were as follows: 13.4 ± 6.8%, 7.5 ± 4.9%, and −0.25 ± 2.8% (only the last three years were available for Crozier). During 1986–1997 (without the three-year period of decline; annual censuses available for all colonies), the average annual percentage growth rates, respectively, were: 7.5 ± 4.0%, 6.4 ± 5.7%, and −2.3 ± 1.8%.

The first census of Beaufort was in 1983. In 1991, the last year in which a census was made there, the population was 4% larger than the Cape Bird colony and, to a limited degree, probably grew in subsequent years (as did the other colonies; Wilson et al. 2001). However, of all the study colonies, only Beaufort has limited nesting space. Currently (2002, no census data available), after additional growth, it probably has reached its limit: penguins nest on all dry terrain and have even scaled steep slopes where subcolonies cover gravel benches 30 m above the main colony (D. Ainley and G. Ballard, *personal observations*). There is no room for in-filling of nesting areas and, in some areas, peripheral nests are subject to flooding (by both ocean waves and snow melt) and snow drifting. The Beaufort Island population reached a peak of 53 000 pairs in 1986–1987, with high counts at the other colonies in those years as follows: Crozier 177 000; Bird 60 000, and Royds 4000 pairs. Therefore, its growth rate appears to have slowed severely compared to adjacent Cape Bird, and 53 000 pairs is likely its limit.

During this study, the Ross Island study colonies ranged in size over three orders of magnitude, except in 1998 (Table 1). The colony at Beaufort was at least the same size, perhaps larger, than that at Cape Bird (Taylor and Wilson 1990), but we had no census data with which to directly assess yearly fluctuation in size at Beaufort. The respective numbers of pairs and provisioned population (includes parents and their chicks) were lowest at Crozier and Bird in 1998, followed by 2000; greater numbers in 1997 and 1999 were equivalent. At Royds, colony size was lowest in 2000, followed by 1998. We used the ratio in size between Bird and Beaufort during the years when both were directly censused to project Beaufort population size during the present study. Accordingly, interannual variation in its size follows the same pattern as for Bird (Table 1).

No colony other than Beaufort was even close to being space limited. If ice-free terrain with plenty of gravel for nests was the only factor that constrained colony size, Crozier could grow at least three times and Royds probably 100 or more times in size. Cape Bird could probably grow at least five times larger. All

←

FIG. 2. Minimum convex polygons representing colony-specific penguin foraging areas constructed from telemetry fixes during periods 2 and 4 in (A) the 1997 season, (B) the 1998 season, (C) the 1999 season, and (D) the 2000 season. These two periods are common to all colonies in all years. In (D), the heavy line around the Crozier MCP shows the outer bounds of positions of Cape Crozier penguins detected using satellite transmitters, indicating that penguins fed in the VHF radio shadow of C16 (from Mt. Bird) and also went a bit out of radio range of Cape Crozier and Mt. Bird.

colonies were within foraging range of one another, particularly if the longer foraging ranges measured elsewhere are allowed to apply in the Ross Sea (see the summary of foraging ranges in Ainley [2002]). Moreover, based on our more recent satellite telemetry (D. Ainley and G. Ballard, *unpublished data*), the Crozier birds have demonstrated an ability to effectively forage >100 km away, a distance that would take them past Beaufort to the beach at Cape Bird.

Breeding performance

No obvious relationship was apparent between colony size and the number of chicks produced per pair (Table 1). Cape Bird exhibited the most variability in productivity (0.55–1.75 chicks per pair), and Cape Royds (the smallest colony) showed the least (0.92–1.38 chicks per pair).

Chick mass varied with year ($F_{3, 548} = 10.4$, $P < 0.001$, $r^2 = 0.05$) and chick age ($F_{1, 548} = 19.6$, $P < 0.001$, $r^2 = 0.03$), but not consistently with colony ($F_{2, 548} = 0.81$, $P < 0.44$, $r^2 = 0.002$) (Table 2). Chicks at Royds showed the least amount of between-year variation in mass. The effect of year was variable, depending on colony (year × colony interaction, $F_{5, 548} = 2.3$, $P < 0.04$, $r^2 = 0.02$). Mass was lowest at two of the three colonies in 1999. The combined model explained ~20% of variation in the cube-root of chick mass ($F_{11, 548} = 13.7$, $P < 0.001$, adjusted $r^2 = 0.20$).

Foraging trip distance and duration

Average foraging trip distance, and ultimately the expanse of foraging areas (cf. Fig. 2), differed between years depending on colony (year × colony interaction, $F_{9, 200} = 5.4$, $P < 0.001$). Specifically, for Crozier, Beaufort, and Bird, foraging distance was shortest or near shortest in 2000, but for Royds, it was longest in that year (Table 3). Foraging distance was longest at Crozier in 1999, at Beaufort in 1998, and at Bird in 1997 (Table 3). Looking between colonies by year, foraging distance at Royds was the shortest in all years compared to that at Crozier. Bird and Beaufort foraging distances were on a continuum between the other two colonies; the foraging distance at Bird typically overlapped with that at Royds, and the distance at Beaufort typically overlapped with Crozier. However, we believe that the average trip distance for Crozier is greater than what we measured; any birds that foraged >45 km to the northeast of Crozier would not be detected (see *Methods*). Therefore, distance could well have been longest at Crozier in most years.

Foraging trip distance changed between TP 1 and 4, with differences between years depending on colony (year × colony interaction, $F_{4, 71} = 6.9$, $P < 0.001$). Specifically, penguins from Crozier fed farther from the colony in TP 4 than in TP 1 in all years except for 2000; in particular, they fed farthest from the colony in 1998 TP 4 (Table 4). This difference between 2000 and the other years may be due to the presence of

icebergs that blocked the foraging area of the Crozier colony (Fig. 2). However, as previously noted (including *Methods*), the longest trip distances for Crozier penguins were underestimated if they went to the northeast; this was a greater problem in 2000 (especially TP 4), when iceberg C16 forced the Crozier penguins to forage more to the northeast than usual. Bird and Beaufort penguins did not change foraging trip distance between TP for any year, although this was difficult to assess for Beaufort penguins, where we lacked TP 1 data (Beaufort TP 2 vs. 4, for year, $F_{1, 13} = 0.90$, $P = 0.36$). The relationship at Royds was not consistent; the penguins fed farther from the colony in TP 4 than TP 1 in 1999, but closer to the colony during TP 4 in 1997 (Table 4). Within a year, penguins from Cape Crozier fed farther from the colony in TP 4 than in TP 1 compared to the other colonies in two of three years (Table 4).

The duration of foraging trips was longer at Cape Crozier than at Cape Royds, and varied by season, colony, TP, and individual (combined model, $F_{301, 2372} = 10.21$, $P < 0.001$; see Table 5; for a three-way season × colony × TP interaction, $F_{9, 2372} = 6.86$, $P < 0.001$). For both colonies, trip durations were longest in 1998. Durations were shortest for Crozier in 2000 and for Royds in 1997. Overall, the differences in trip duration were most pronounced during TP 4, when Crozier trips were longest and Royds trips were shortest. Differences between Royds and Crozier during TP 1 were smallest, although they were still significant ($P < 0.05$). During TP 1, before the fast ice blew out, Royds penguins usually had to walk several kilometers to reach open water and this added disproportionately to the time (whereas penguins from Crozier could swim the whole way). From limited data, it appeared that foraging trips at Bird were equivalent in duration to those at Crozier. Within a given year, durations increased at Crozier in all years except 2000, when they decreased after TP 1 to then remain at the same level. At Royds, durations decreased over time in all years. Thus, these data for Cape Crozier are generally consistent with the distance data provided by radiotelemetry: foraging trips increased in distance and duration within seasons.

Foraging trip distance and colony size

Foraging distances in all years ranked according to colony size: Crozier > Beaufort > Bird > Royds (with some ties in a few cases; Table 3). To test this relationship more formally, we examined 11 colony-year estimates of the number of breeding pairs and size of the provisioned population (number of chicks; Table 1). We looked at overall average distance and distance during TP 4 (when distance tended to be longest). In all cases, there was a strong positive linear relationship between foraging distance and number of pairs or chicks (P values <0.01 in all cases; Fig. 3). Again, as previously noted, foraging trips at Crozier were

FIG. 3. The linear relationship between average foraging distance over all periods (upper panels) or period 4 only (lower panels) and colony size for pairs and for the provisioned population (pairs × no. chicks/pair × 10^5). Rho values are also given (all $P < 0.05$).

probably even farther than what we measured (see *Variation in colony size* and *Methods*).

Foraging area size and overlap

Several general patterns were evident in regard to foraging area size and whether or not foraging areas overlapped among adjacent colonies. Changes in foraging area size differed by colony and year (colony × year × TP, $F_{6,82} = 8.3$, $P < 0.001$). Therefore, changes in foraging area were examined by colony. For Crozier, the changes in foraging area differed by year (TP × year, $F_{3,27} = 8.8$, $P < 0.001$); colony-specific foraging area increased in size as the summer progressed in three of four years (paired *t* for each year, $P < 0.05$ for 1997–1999, $P = 0.6$ for 2000; Table 6). For Beaufort, foraging area size increased in TP 4 compared to TP 2, regardless of year (for TP, $F_{1,9} = 1.3$, $P = 0.008$; for TP × year, $F_{2,9} = 1.0$, $P = 0.4$). For Bird, the changes in foraging area differed by year (for TP × year, $F_{3,27} = 3.9$, $P = 0.02$); however, colony-specific foraging area increased in size as the summer progressed in only one of the four years (paired *t* for each year, $P > 0.15$ for 1997, 1998, 1999; $P = 0.003$ for 2000). This same pattern held for Royds; the changes in foraging area differed by year (for TP × year, $F_{3,28} = 3.3$, $P = 0.03$), but colony-specific foraging area increased in size in only one of the four years (paired *t* for each year, $P > 0.15$ for 1997, 1998, 1999; $P = 0.02$ for 2000; Table 6).

This derivation of foraging area for Beaufort resulted from only half of the number of radios deployed com-

pared to the other colonies (7–8 vs. 15 radios). We used Cape Bird data to simulate the potential reduction in foraging area resulting from this difference in study design. Cape Bird penguins went both north and south of the colony, which is also the case for Beaufort Island birds. We randomly sampled seven of 15 Cape Bird radios for each simulation. We did 20 simulations for each year (a total of 80 simulations). On average, the Cape Bird areas were 74 ± 1.8% as large as the original area (based on 15 birds). In other words, the area was reduced (on average) by 26%. However, such a result would not change any of the conclusions in this paper.

The total area used in a season by a given colony was greater, often dramatically so, than the area used in a particular week, because boundaries of foraging areas shifted from week to week (Fig. 2). Thus, the area estimate for ''all'' weeks integrated these shifting boundaries. Using the area estimate for ''all'' weeks (Table 6), Royds, the smallest colony, had the smallest or near-to-smallest foraging area in all years. The exception was 2000, when the Crozier colony was probably affected by the icebergs, resulting in less available foraging area and fewer breeding adults competing for food. The larger colonies competed for the distinction of having the largest foraging area. Cape Bird had the largest area in most years, except that the Crozier foraging area was underestimated. Therefore, the estimate of the Cape Crozier foraging area was always smaller than its actual size and, therefore, was probably always larger than that for Cape Bird. In 2000, the Crozier foraging area was ~30–40% larger than what we es-

TABLE 7. Estimated numbers and at-sea densities of penguins foraging in the foraging areas of each colony and in the combined areas of the Beaufort Island, Cape Bird, and Cape Royds colonies (Beau-Brd-Ryd).

| Colony, by year | No. foraging penguins | | | | Density of foraging penguins (no./km²) |
	Breeding pairs	Breeders at sea	Nonbreeders at sea	Total at sea	
1997					
Crozier	134 892	202 338	29 448	231 786	94.2
Beaufort	42 005	63 008	9 170	72 177	29.0
Bird	47 508	71 262	10 371	81 633	22.4
Royds	3 933	5 900	859	6 758	3.1
Beau-Brd-Ryd					31.1
1998					
Crozier	90 638	135 552	19 728	155 280	44.9
Beaufort	32 797	49 196	7 160	56 356	27.5
Bird	38 252	57 378	8 351	65 729	53.2
Royds	3 411	5 117	745	5 861	8.7
Beau-Brd-Ryd					48.3
1999					
Crozier	137 135	205 703	29 937	235 640	103.6
Beaufort	40 517	60 775	8 845	69 620	23.3
Bird	45 449	68 174	9 922	78 095	24.3
Royds	3 620	5 430	790	6 220	6.8
Beau-Brd-Ryd					31.7
2000					
Crozier	118 772	178 158	25 928	24 086	189.8
Beaufort	31 033	46 550	6 775	53 324	30.2
Bird	34 632	51 948	7 560	59 508	26.9
Royds	2 387	3 581	521	4 102	3.5
Beau-Brd-Ryd					28.1

Notes: Values for breeders, nonbreeders, and total penguins represent birds foraging at any given time during the mid-to-late chick-provisioning period. Data on the number of breeding pairs are from Table 1; area measurements used to calculate density are from Table 6 (''All'').

timated using radio transmitters (see *Methods* and *Results: Variation in colony size*; Fig. 2D).

The most striking pattern in Table 6 was that the percentage overlap of a given colony-specific foraging area increased within a year, with two exceptions. First, the foraging area of Cape Crozier, the largest colony, almost never overlapped other areas; Beaufort or Bird penguins foraged on the Crozier side of Beaufort Island only early in the summer, but then switched more to the other side of Beaufort when Crozier birds began to forage farther toward Beaufort (Fig. 2). The exceptions were 1999 TP 4, when, for unknown reasons, the Crozier penguins did not forage very far west (toward Beaufort; Fig. 2C); and 2000 TP 4, when iceberg C16 blocked Crozier penguins from doing so (Fig. 2D). In a way, the iceberg provided a ''natural experiment'' by preventing westward excursions of Crozier birds; this is most obvious in a visual comparison of the panels of Fig. 2. The other exception involved Royds, where the overlap with Bird, usually extensive (33–75%), did not change consistently as the seasons progressed (it possibly decreased a bit). The foraging areas of Royds, Bird and Beaufort overlapped extensively, on the order of 30–75%. As noted in Methods, the overlap between the Royds and Bird foraging areas could have been underestimated owing to birds shadowed from detec-

tion in Wohlschlag Bay. Crozier's foraging area exhibited the least overlap, ranging from zero to 6.4%.

Foraging density

We assume that, initially, prey patches are evenly distributed throughout the study area, and thus the presumed clumps of foraging penguins are also spread evenly (see *Discussion*). In that context, at the meso-scale, the average density of foraging birds in the areas of Royds, Bird, and Beaufort combined was 31–33% of that for Crozier in 1997 and 1999, and 15% in 2000 (Table 7). Only estimates for 1998 diverged radically from this pattern. Due to an extremely high foraging density for the Cape Bird colony in that year, the total density for the three smaller colonies was equivalent to that of Crozier. Even if the respective foraging density of colonies are additive within the areas of overlap (Royds density + Bird density + Beaufort density), the pattern would be about the same. On the other hand, if we underestimated the size of the Crozier foraging area, especially in 2000, then combined or additive foraging density of the smaller colonies would have approximated that of Crozier in all years.

Meal sizes fed to chicks

The mass of meals fed to chicks at Capes Crozier and Royds varied by TP and among individuals de-

TABLE 8. The average mass of meals fed to chicks at the three study colonies on Ross Island.

TP by year	Crozier Meal (kg)	n	Bird Meal (kg)	n	Royds Meal (kg)	n
1997						
1	0.433	13			0.293	7
2	0.467	22			0.586	46
3	0.452	23			0.512	23
4	0.424	36			0.649	81
1998						
1	0.508	16			0.567	35
2	0.560	16			0.632	41
3	0.591	12			0.606	26
4	0.611	40			0.700	81
1999						
1	0.473	18	0.450	46	0.611	35
2	0.539	18	0.572	44	0.447	47
3	0.703	18	0.668	41	0.539	49
4	0.607	34	0.628	91	0.573	113
2000						
1	0.575	25	0.533	41	0.398	19
2	0.652	29	0.645	38	0.572	14
3	0.696	36	0.759	38	0.612	25
4	0.779	48	0.696	80	0.568	25

Notes: Data were limited to 21 December–15 January and included only breeders for which two or more meals in a telemetry period (TP) were obtained. Sample size (n) is number of meals per TP. TPs are: (1) 20–25 December, (2) 26–30 December, (3) 31 December–4 January, and (4) 5–11 January.

pending on season and colony ($F_{281, 1245} = 2.32$, P < 0.001; Table 8). Treated individually, the effect of colony and season were both nonsignificant (P > 0.3), but the three-way interaction colony × season × TP was significant (P = 0.017). Combining seasons and colonies, meals in TP 4 were significantly larger than those in TP 1 or 2 (P = 0.02; this was also true when colonies were analyzed separately). This may be the result of the greater needs and more persistent begging by older chicks (see Salihoglu et al. 2001), demanding more of the parent's stomach load. In that regard, Emison (1968) found that the mass of a parent's entire stomach contents increased soon after its eggs hatched, but not thereafter. In 2000, significantly larger meals were fed at Crozier and smaller ones at Royds (P < 0.04 in all comparisons) compared with other years at the same colonies. Average meal sizes at Crozier in 1997 were

particularly small, averaging only 0.479 kg compared with meals >0.514 kg in other years for both colonies. Average chick meal size in the present study was equal to or larger than the average adult prey loads measured by stomach pumping by Clarke et al. (1998) in 1994 and 1995 at Terra Nova Bay, which is ~200 km north of Ross Island, but was equivalent to meal sizes measured by a weighbridge at Béchervaise Island, East Antarctica, in 1991–1998 (Clarke et al. 2002).

Body mass of provisioning adults

The mass of adults provisioning chicks that were >25 days old varied by colony and season ($F_{9, 486} = 7.6$, P < 0.001, adjusted $r^2 = 0.11$), with Crozier adults being heavier than Royds adults in 1997 and 1999. Adults were lightest in 1997 at both Crozier and Royds. Crozier adults were heavier than Bird adults in both 1999 and 2000. The colony × season interaction term was nonsignificant (P = 0.08). Therefore, no consistent pattern was evident relative to colony size (Table 9).

DISCUSSION

The Ross Sea is the most productive stretch of water of comparable size in the Antarctic region (Arrigo et al. 1998, 2002) and populations of penguins, other birds, seals, and whales are immense (reviewed in Ainley 2003), including the smaller region where this study took place (see also Ainley 1985, Saino and Guglielmo 2000). Little is known about the distribution of the prey taken by neritic-foraging Adélie Penguins, owing to the difficulties of study in areas of extensive sea ice (Ainley 2003). However, the spatial spread of schools of Antarctic krill (*Euphausia superba*; the best known of all krill and a major food of Adélie Penguins in *pelagic* waters), within areas of high concentration, can extend hundreds of kilometers. At smaller scales, areas of high krill concentration often exceed the size of our study area by many times (Murphy et al. 1988). In the only published krill survey in Antarctic neritic waters, Azzali and Kalinowski (2000) found that high biomass of krill in the southwestern Ross Sea was continuous when viewed at the large scale and mesoscale. Only toward the center of the Ross Sea, away from our study area, did any discontinuities become apparent. In this case, the krill species was *Euphausia crystallorophias*, a major prey item in our study area (Ainley et al. 2003*a*). Within the region of high concentration, in-

TABLE 9. Body mass of adult penguins that were provisioning chicks ≥25 days old, 1997–2000; n is the number of adults weighed.

Year	Adult penguin body mass (kg)								
	Crozier Mean	1 SE	n	Royds Mean	1 SE	n	Bird Mean	1 SE	n
1997	3.42	0.045	43	3.3	0.032	65			
1998	3.59	0.056	26	3.61	0.060	31			
1999	3.67	0.047	37	3.46	0.036	63	3.55	0.052	28
2000	3.62	0.038	73	3.59	0.052	57	3.5	0.030	73

dividual krill schools were equally dispersed and averaged several hundred square meters in area. Therefore, we assumed that normal variation in spatial distribution of food did not explain the observed patterns in Adélie foraging areas, and, further, that within the southwest Ross Sea, its mesoscale distribution was equal for all colonies. More recent satellite telemetry results (D. Ainley and G. Ballard, *unpublished data*) indicate that, as the season passes, Crozier males continue to feed close to the colony, whereas females feed farther away (a similar result was reported by Clarke et al. 1998). The fact that this pattern is evident at Crozier, the largest colony, but not at the smaller colonies, further suggests that a bottom-up forced redistribution of prey does not explain our results.

Although colony size increased by successive orders of magnitude from Royds to Bird/Beaufort to Crozier, sizes of the respective colonies' foraging areas did not. Although Cape Royds consistently had the smallest foraging area, Cape Crozier did not seem to have the largest area (only in 1998). However, it is almost assured that we underestimated the Crozier foraging area and, therefore, it was highly likely to have been the largest in all years. Overlap of the foraging areas of the other colonies with Crozier was minimal, and occurred late in the season, but foraging areas among the smaller Royds, Bird, and Beaufort colonies overlapped extensively. The density of foraging birds was usually much higher in the Crozier area than in the other colonies combined. Judging from the extent of the Cape Crozier foraging area in 1998 TP 4 and, to a lesser extent, in 1997 TP 4 (as a gauge to how far these penguins would go in search of food), as well as the even longer foraging trips measured by Clarke et al. (1998), foraging within the Crozier area was well within the capabilities of penguins from Bird and Beaufort in any season or time period, had they so chosen. Therefore, the patterns exhibited by Bird and Beaufort penguins were not due to the Crozier foraging area being too far away.

Colony size and resource availability

Only the colony at Beaufort Island can grow no larger, having reached a limit determined by the availability of nesting space. The other colonies have grown from 1970 at least through 1997, and possess a huge amount of suitable habitat for additional expansion. The high population growth rate for Cape Royds, especially, indicates that immigration is probably involved, because the typical 0.9 chicks fledged per pair (cf. Ainley 2002) alone could not sustain such growth.

There are a number of reasons why recruits would be more attracted to one colony than another (Danchin and Wagner 1997, Reed et al. 1999, Brown and Brown 2001), but here we are concentrating only on aspects of foraging effort. During our study, we lacked the opportunity to directly quantify prey availability, not unlike all other studies in which the relationship between colony size and foraging behavior has been studied (except Ainley et al. 2003b). We do know, however, that diet composition and quality are the same for all colonies involved (Ainley et al. 2003a), and we suspect that prey patches or schools, initially at least, are distributed at similar density in the waters bordering the study colonies, judging by the continuity of foraging areas and data presented by Azzali and Kalinowski (2000). Moreover, the various colony-specific foraging areas do not differ appreciably or consistently in habitat heterogeneity, which could affect prey availability (Brown et al. 2002). Bathymetry is essentially similar throughout the foraging areas: the ocean is deeper than the maximum foraging depth for penguins at all colonies, except within a kilometer of shore (and a small bank immediately east of Beaufort), and the same ocean current flows through all foraging areas (cf. Ainley et al. 2003a; Fig. 1). The only possible difference in habitat quality is the seasonal reduction of sea ice at Crozier, and (to a lesser extent) at Beaufort and Bird. The short-term impacts of this ice reduction on diet quality have been discussed elsewhere (Ainley et al. 1998, 2003a). Unlike Forero et al. (2002), we detected no reduction in prey quality within the foraging area of the larger colony (Crozier) (Ainley et al. 2003a).

Forced reduction in availability of prey or actual prey depletion can occur if the density of foragers reaches a level beyond which the colony's prey capture rate exceeds the rate at which prey or feeding opportunities are renewed (Charnov et al. 1976, Lewis et al. 2001). Wittenburger and Hunt (1985) viewed food resource competition and depletion as a negative consequence of coloniality, and we concur. There is strong, indirect evidence for such intraspecific competition in our study, because the penguins foraged successively farther from their colonies (and also deeper; D. Ainley and G. Ballard, *unpublished data*) as the chick-provisioning period progressed. This was especially true for the largest colony, Cape Crozier. Penguins began the chick-provisioning task by foraging as close to the colony as possible, a new finding among studies directed at elucidating colony-related patterns of foraging in birds. It appears that foraging trip durations increased slightly within the season at Béchervaise Island, East Antarctica, as well, although Clarke et al. (2002) did not comment on this pattern in their data. This was true in spite of the fact that, in the guard stage (TPs 1 and 2), the single foraging parent has the time to feed even farther away than it would later when the needs of chicks force both parents (at least at Crozier) to forage almost continuously. Moreover, foraging distance and area increased with colony size, also indirectly indicating prey depletion (especially at Crozier). Simultaneously, as time passed, the parents themselves probably required more prey, assuming that they at least maintained their own food intake, because meal size to chicks increased over time. In fact, when trips during crèche regularly exceeded 2 days, which occurred at

Crozier in 1996 (and also at Béchervaise Island in 1994), but not in the present study, parents lost body mass (Ainley et al. 1998, Clarke et al. 2002). Clarke et al. (1998, 2002), who investigated the foraging of penguins at colonies even smaller than Cape Royds, found no seasonal change in foraging trip distance but a slight increase in duration, results similar to those of our study.

The reason that Crozier birds took longer trips is evident in the context of foraging density. In most years, the density of foraging birds in the Crozier foraging area was far greater than for the area of the other colonies combined. Even if we underestimated the size of the Crozier foraging area, the error would not have been sufficient to change this pattern. For instance, instead of foraging birds being three times more dense off Crozier, they might have been twice as dense.

Overlap in foraging areas

For kittiwakes and other seabirds around Britain, Furness and Birkhead (1984) argued that foraging areas among adjacent colonies overlapped broadly (but did not specify the degree of overlap), whereas Cairns (1989) argued that they abutted. Cairns gave much more attention to this particular aspect of colony dynamics. He based his idea on the points that individuals would (or should) feed as close as possible to their colony (see also Horn 1968, Andersson 1978) and that they would not go farther unless food became more difficult to obtain (the ''hungry horde,'' as he termed it). Therefore, it would not be beneficial for individuals from one colony to forage in the area of another, especially if they met a high density of foragers from the other colony. These points had not been tested prior to completion of the present study (and that of Ainley et al. [2003b]).

In their study of kittiwakes, Ainley et al. (2003b) found that individuals from a small colony did not feed within the foraging area of an adjacent larger colony. In the present study, we found evidence for both the model of Furness and Birkhead (1984) and that of Cairns (1989; see *Introduction*). Which model applied in our study depended on colony size and, therefore, on foraging density. In fact, the degree of overlap between Royds (the smallest colony) and Bird (an adjacent, medium-sized colony) was almost always greater than the degree of overlap between the two medium-sized colonies, Bird and Beaufort (even if we underestimated the Beaufort area by 20%). As time passed, the foraging areas of the small- and medium-sized colonies overlapped more and more, but little appreciable overlap occurred between these colonies and the foraging area of the large colony (Crozier). It appeared, therefore, that the foraging areas of the small colonies could accommodate additional foragers. This was not true, apparently, for the Crozier colony. Early in the chick-provisioning period, when Crozier birds were feeding near the colony, penguins from Beaufort Island foraged much more to the east, in the direction of Crozier, than they did later, once the Crozier birds expanded toward Beaufort. This was most apparent in 1997 and 1999. Moreover, in 2000, when an immense grounded iceberg blocked Crozier birds from foraging toward Beaufort, individuals from Beaufort foraged more extensively toward Crozier than they had late in the season in previous years.

Other factors (prior to the chick period) reduced the size of the Crozier breeding population in 2000; therefore, the foraging area eventually used by Crozier penguins was even smaller than it would have been later in the season, had breeders been more abundant. One such factor could be interannual variation in food availability in the study area. For example, in 1998 when the Crozier breeding population was smallest, the foraging area was largest. This seems likely to be a function of low food availability in that season, which may have also caused the relatively low breeding population size that season. Conversely, food load sizes were larger for Crozier birds in 2000, when the breeding population was small (compared with 1997 and 1999), possibly indicating more availability (or less depletion) of prey relative to the density of foraging individuals.

Consequences of colony size

This study adds one more species to the growing list in which foraging trip distance and duration are related positively to colony size: gannets (Lewis et al. 2001), herons (Gibbs et al. 1987), kittiwakes (Ainley et al. 2003b), corvids (Griffin and Thomas 2000), and swallows (Brown and Brown 1996). Similar to the kittiwake study, the relationships are more evident on an interannual basis for the larger colonies, where individuals have to deal not only with the vagaries of prey availability, but also with the presence of large numbers of conspecific competitors (see also Forero et al. 2002). These results should raise a cautionary flag for future researchers who study colonies of birds: the range in size and proximity of colonies investigated may affect whether or not these relationships become evident. At the least, the full range in colony size for a given species should be compared. Another flag should be raised in relation to the time of investigation. We found these relationships to hold true for a majority of years, but not all, and we found that these relationships increased in strength as the chick-provisioning season progressed (consistent with the increasing pressure on prey resources; cf. Salihoglu et al. [2001]).

We did not find an effect of colony size on reproductive success (cf. Hunt et al. 1986, Brown and Brown 1996), chick growth, size of food loads, adult body mass, or quality of diet (Ainley et al. 2003a). It appears that greater foraging effort is required of Adélie Penguins in larger colonies (longer trips), but also that these penguins did not approach their behavioral and energetic limits during the four years of the present study. Only when foraging trips were very long, as in

1996 (Ainley et al. 1998; Clarke et al. 2002), were repercussions expressed (loss of parental body mass, smaller food loads). Unfortunately, we did not have information on foraging areas during that interesting year (1996). Moreover, we have not been able to continue our study in the form described herein, hoping for another year like 1996, because the arrival and grounding of mega-icebergs has changed the scene radically (e.g., Cape Royds ceased as a viable colony and most of the Crozier foraging area of 1996–2000 became occupied by a second iceberg).

Colony size and geographic structure

Only five other Adélie colonies are greater than or equal in size to Cape Crozier (Woehler 1993, Ainley 2002). We have identified an important cost for living in such a large colony: greater foraging effort apparently is required and is expressed by foraging trips that are longer in distance and duration. Clarke et al. (2002) found a reduction in Adélie breeding success when very long foraging trips were needed. Although fledging success was not compromised in the present study, chicks fledged at lower mass and adults were leaner as well when very long foraging trips were needed (as in 1996; Ainley et al. 1998; D. Ainley and G. Ballard, *unpublished data*). Whether or not lower mass affected the subsequent survival of juveniles and adults is a question that will be answered eventually (as we search for marked birds from the 1996 and subsequent cohorts). Also awaiting future analysis are data on the direction of emigration among recruits, which could explain the high growth rate of the Royds colony (see Reed et al. [1999] for factors affecting recruitment in colonial birds).

Although food resource depression (or, at the least, loss of opportunities through interference competition) apparently is a factor within the foraging range (~70 km) of Adélie Penguin parents (Ainley et al. 1998) in the southwestern Ross Sea, Ainley et al. (1995) found that negative geographic structuring (i.e., only small colonies exist adjacent to large ones) is expressed among colonies viewed at spatial scales of 200 km, which is greater than the observed foraging range of breeding Adélies. To account for this, they hypothesized that the addition of nonbreeders, which do not come and go frequently and, therefore, can forage slightly farther away, could expand colony foraging areas (Ashmole's ''halo''; Diamond 1978, Birt et al. 1987). Perhaps a more reasonable explanation of the structure, however, is that factors operating outside of the chick-provisioning period determine colony size and proximity in Adélie Penguins, which is true for the Rook (Griffin and Thomas 2000) and the Cliff Swallow (Brown and Brown 2002). This is explained more fully as follows.

Almost all Adélie Penguin colonies, and particularly the larger ones (with the exception of those at the northern periphery of their distributional range), occur ad-

jacent to polynyas, which are areas of persistent open water within areas of extensive sea ice (Fraser and Trivelpiece 1996, Ainley 2002). The dispersed or open pack ice characteristic of polynyas allows for quicker travel, i.e., the penguins can swim (8–9 km/h) rather than having to walk (1–3 km/h). Adélie Penguins have a well-developed capacity to accumulate subcutaneous fat, which allows them to fast and, therefore, to deal to some extent with extensive sea ice and slower travel. They do have limits, however. Among high-latitude colonies (>70° S, the majority of colonies for this species), the percentage of a colony population that actually breeds in a given year is related positively to the degree of polynya development (Ainley 2002). Conversely, for low-latitude colonies near the periphery of the sea-ice zone, a greater percentage of individuals of this sea-ice-obligate species breed when any sea ice is present during early spring than when no ice is present (Fraser et al. 1992, Ainley and Divoky 2001, Ainley 2002). In accord, the foraging range during the early incubation period is much greater than during chick provisioning. For the Ross Island colonies, this means ≥100 km (Davis et al. 1988, Sadleir and Lay 1990). It may be that greater range is needed during early spring, because the extensive and concentrated sea-ice cover that usually occurs at that time can significantly reduce the amount of available foraging habitat. That is, all waters would not be within breath-holding limits of the swimming penguins, and there would be a limit to foraging density within the leads between ice floes. Therefore, the population would be spread over an even wider area than later, when the sea ice has broken into smaller, more widely spaced floes.

It seems reasonable, therefore, that the clusters of colonies characteristic of the Adélie Penguin are the products of opposing pressures of philopatry, which maintains the cluster and perhaps helps to keep large colonies large (see Ainley et al. 1995), and competition for food, which may force population dispersion (the founding of more colonies). With Cape Crozier being closest to the Ross Sea Polynya and, therefore, more persistently enjoying divergent pack ice in early spring, philopatry is encouraged. Further work on the demographics of the individual colonies, including interannual variation in the extent of philopatry under different conditions, is underway (D. Ainley, G. Ballard, K. Barton, K. Dugger, and P. Wilson, *unpublished data*).

Literature Cited

Ainley, D. G. 1985. The biomass of birds and mammals in the Ross Sea, Antarctica. Pages 498–515 *in* W. R. Siegfried, P. R. Condy, and R. M. Laws, editors. Antarctic nutrient cycles and food webs. Springer-Verlag, Berlin, Germany.

Ainley, D. G. 2002. The Adélie Penguin: bellwether of climate change. Columbia University Press, New York, New York, USA.

Ainley, D. G. 2003. The Ross Sea, Antarctica, where all ecosystem processes still remain for study, but maybe not for long. Marine Ornithology **30**:55–62.

Ainley, D. G., G. Ballard, K. R. Barton, B. J. Karl, G. H. Rau, C. A. Ribic, and P. R. Wilson. 2003*a*. Spatial and temporal variation of diet within a presumed metapopulation of Adélie Penguins. Condor **105**:95–106.

Ainley, D. G., and G. J. Divoky. 2001. Seabirds: effects of climate change. Pages 54–65 *in* J. Steele, S. Thorpe, and K. Tarekian, editors. Encyclopedia of Ocean Sciences. Academic Press, London, UK.

Ainley, D. G., R. G. Ford, E. D. Brown, R. M. Suryan, and D. B. Irons. 2003*b*. Prey availability, interference competition, and the geographic structure of seabird colonies: a study of Black-legged Kittiwakes and forage fish in Prince William Sound, Alaska. Ecology **84**:709–723.

Ainley, D. G., N. Nur, and E. Woehler. 1995. Factors affecting the distribution and size of pygoscelid penguin colonies in the Antarctic. Auk **112**:171–182.

Ainley, D. G., P. R. Wilson, K. R. Barton, G. Ballard, N. Nur, and B. Karl. 1998. Diet and foraging effort of Adélie Penguins in relation to pack-ice conditions in the southern Ross Sea. Polar Biology **20**:311–319.

Andersson, M. 1978. Optimal foraging area: size and allocation of search effort. Theoretical Population Biology **13**: 397–409.

Arrigo, K. R., G. L. Van Dijken, D. G. Ainley, M. A. Fahnestock, and T. Markus. 2002. The impact of the B-15 iceberg on productivity and penguin breeding success in the Ross Sea, Antarctica. Geophysical Research Letters **29**(7) [DOI: 10.1029/2001GLO14160].

Arrigo, K. R., A. M. Weiss, and W. O Smith, Jr. 1998. Physical forcing of phytoplankton dynamics in the western Ross Sea. Journal of Geophysical Research **103**:1007–1022.

Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic seabirds. Ibis **103b**:458–473.

Azzali, M., and J. Kalinowski. 2000. Spatial and temporal distribution of krill (*Euphausia superba*) biomass in the Ross Sea (1989–1990 and 1994). Pages 433–456 *in* F. M. Faranda, L. Guglielmo, and A. Ianora, editors, Ross Sea ecology: Italiantaride Expeditions (1987–1995). Springer-Verlag, Berlin, Germany.

Ballard, G., D. G. Ainley, C. A. Ribic, and K. R. Barton. 2001. Effect of instrument attachment and other factors on foraging trip duration and nesting success of Adélie Penguins. Condor **103**:481–490.

Barry, J. 1988. Hydrographic patterns in McMurdo Sound, Antarctica and their relationship to local benthic communities. Polar Biology **8**:377–391.

Birt, V. L., T. P. Birt, D. Goulet, D. K. Cairns, and W. A. Montevecchi. 1987. Ashmole's halo: direct evidence for prey depletion by a seabird. Marine Ecology Progress Series **40**:205–208.

Brown, C. R., and M. B. Brown. 1996. Coloniality in the Cliff Swallow: the effect of group size on social behavior. University of Chicago Press, Chicago, Illinois, USA.

Brown, C. R., and M. B. Brown. 2001. Avian coloniality: progress and problems. Pages 1–81 *in* V. Nolan, Jr., and C. F. Thompson, editors. Current ornithology. Volume 16. Kluwer Academic/Plenum Publishers, New York, New York.

Brown, C. R., and M. B. Brown. 2002. Does intercolony competition for food affect colony choice in Cliff Swallows? Condor **104**:117–128.

Brown, C. R., C. M. Sas, and M. B. Brown. 2002. Colony choice in Cliff Swallows: effects of heterogeneity in foraging habitat. Auk **119**:446–460.

Bryant, D. M. 1975. Breeding biology of House Martins *Delichon urbica* in relation to aerial insect abundance. Ibis **117**:180–216.

Bustamante, J. 1997. Predictive models for lesser kestrel *Falco naumanni* distribution, abundance and extinction in southern Spain. Biological Conservation **80**:153–160.

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

Chappell, M. A., V. H. Shoemaker, D. N. Janes, T. L. Bucher, and S. K. Maloney. 1993. Diving behavior during foraging in breeding Adélie Penguins. Ecology **74**:1204–1215.

Charnov, E. L., G. H. Orions, and K. Hyatt. 1976. Ecological implications of resource depression. American Naturalist **110**:247–259.

Clarke, J., K. Kerry, L. Irvine, and B. Phillips. 2002. Chick provisioning and breeding success of Adélie penguins at Béchervaise Island over eight successive seasons. Polar Biology **25**:21–30.

Clarke, J., B. Manly, K. Kerry, H. Gardner, E. Franchi, S. Corsolini, and S. Focardi. 1998. Sex differences in Adélie penguin foraging strategies. Polar Biology **20**:248–258.

Danchin, E., and R. H. Wagner. 1997. The evolution of coloniality: the emergence of new perspectives. Trends in Ecology and Evolution **12**:342–347.

Davis, L. S., G. D. Ward, and R. M. F. S. Sadleir. 1988. Foraging by Adélie Penguins during the incubation period. Notornis **35**:15–23.

Diamond, A. W. 1978. Feeding strategies and population size in tropical seabirds. American Naturalist **112**:215–223.

Earle, R. A., and L. G. Underhill. 1991. The effects of brood size on growth of South African Cliff Swallow *Hirundo spilodera* chicks. Ostrich **62**:13–22.

Emison, W. B. 1968. Feeding preferences of the Adélie Penguin at Cape Crozier, Ross Island. American Geophysical Union, Antarctic Research Series **12**:191–212.

ESRI (Environmental Systems Research Institute). 2000. ArcView Geographic Information System. Version 3.2a. Environmental Systems Research Institute, Redlands, California, USA.

Farinha, J. C., and D. Leitao. 1996. The size of heron colonies in Portugal in relation to foraging habitat. Colonial Waterbirds **19**(Special Publication 1):108–114.

Forero, M. G., J. L. Tella, K. A. Hobson, M. Bertellotti, and G. Blanco. 2002. Conspecific food competition explains variability in colony size: a test in Magellanic Penguins. Ecology **83**:3466–3475.

Fraser, W. R., and W. Z. Trivelpiece. 1996. Factors controlling the distribution of seabirds: winter–summer heterogeneity in the distribution of Adélie Penguin populations. American Geophysical Union, Antarctic Research Series **70**:257–272.

Fraser, W. R., W. Z. Trivelpiece, D. G. Ainley, and S. G. Trivelpiece. 1992. Increases in Antarctic penguin populations: reduced competition with whales or a loss of sea ice due to environmental warming? Polar Biology **11**:525–531.

Furness, R. W., and T. R. Birkhead. 1984. Seabird colony distributions suggest competition for food supplies during the breeding season. Nature **311**:655–656.

Gaston, A. J., G. Chapdelaine, and D. G. Noble. 1983. The growth of Thick-billed Murre chicks at colonies in Hudson Strait: inter- and intra-colony variation. Canadian Journal of Zoology **61**:2465–2475.

Gibbs, J. P., and L. K. Kinkel. 1997. Determinants of the size and location of Great Blue Heron colonies. Colonial Waterbirds **20**:1–7.

Gibbs, J. P., S. Woodward, M. L. Hunter, and A. E. Hutchinson. 1987. Determinants of Great Blue Heron colony distribution in coastal Maine. Auk **104**:38–47.

Griffin, L. R., and C. J. Thomas. 2000. The spatial distribution and size of rook (*Corvus frugilegus*) breeding colonies is affected by both the distribution of foraging habitat and by intercolony competition. Proceedings of the Royal Society of London B **267**:1463–1467.

Horn, H. S. 1968. The adaptive significance of colonial nesting in Brewer's Blackbird (*Euphages cyanocephalus*). Ecology **49**:682–694.

Hunt, G. L., Z. A. Eppley, and D. C. Schneider. 1986. Reproductive performance of seabirds: the importance of population and colony size. Auk **103**:306–317.

Kerry, K. R., J. R. Clarke, and G. D. Else. 1993. The use of an automated weighing and recording system for the study of the biology of Adélie Penguins (*Pygoscelis adeliae*). Proceedings NIPR [National Institutes of Polar Research] Symposium on Polar Biology **6**:62–75.

Lewis, S. T. N. Sherratt, K. C. Hamer, and S. Wanless. 2001. Evidence of intra-specific competition for food in a pelagic seabird. Nature **412**:816–819.

Lishman, G. S. 1985. The food and feeding ecology of Adélie penguins (*Pygoscelis adeliae*) and Chinstrap penguins (*P. antarctica*) at Signy Island, South Orkney Islands. Journal of the Zoological Society of London (A) **205**:245–263.

Manly, B. F. J. 1997. Randomization, bootstrap, and Monte Carlo methods in biology. Second edition. Chapman and Hall, New York, New York, USA.

Møller, A. P. 1987. Advantages and disadvantages of coloniality in the Swallow, *Hirundo rustica*. Animal Behaviour **35**:818–832.

Murphy, E. J., D. J. Morris, J. L. Watkins, and J. Priddle. 1988. Scales of interaction between Antarctic krill and the environment. Pages 120–130 *in* D. Sahrhage, editor. Antarctic ocean and resources variability. Springer-Verlag, Berlin, Germany.

NOAA (National Oceanic and Atmospheric Administration) National Geophysical Data Center. 1988. Digital relief of the surface of the earth. NOAA National Geophysical Data Center Data Announcement 88-MGG-02. [Online, URL: ⟨http://www.ngdc.noaa.gov/mgg/global/etopo5.html⟩.]

Reed, J. M., T. Boulinier, E. Danchin, and L. W. Oring. 1999. Informed dispersal: prospecting by birds for breeding sites. Pages 189–259 *in* V. Nolan, Jr., E. D. Ketterson, and C. F. Thompson, editors. Current Ornithology. Volume 15. Kluwer Academic/Plenum Publishers, New York, New York.

Sadleir, R. M. F., and K. M. Lay. 1990. Foraging movements of Adélie Penguins (*Pygoscelis adeliae*) in McMurdo Sound. Pages 157–180 *in* L. S. Davis and J. Darby, editors. Penguin biology. Academic Press, New York, New York, USA.

Saino, N., and L. Guglielmo. 2000. ROSSMIZE Expedition: distribution and biomass of birds and mammals in the western Ross Sea. Pages 469–478 *in* F. M. Faranda, L. Guglielmo, and A. Ianora, editors. Ross Sea ecology: Italian-taride Expeditions (1987–1995). Springer-Verlag, Berlin, Germany.

Salihoglu, B., W. R. Fraser, and E. E. Hofmann. 2001. Factors affecting fledging weight of Adélie penguin (*Pygoscelis adeliae*) chicks: a modeling study. Polar Biology **24**:328–337.

Siegel-Causey, D., and S. P. Karitonov. 1990. The evolution of coloniality. Pages 285–330 *in* D. M. Power, editor. Current Ornithology. Volume 7. Plenum Press, New York, New York, USA.

Storer, R. W. 1952. A comparison of variation, behavior and evolution in the seabird genera *Uria* and *Cepphus*. University of California Publications in Zoology **52**:121–222.

Taylor, R. H. 1962. The Adélie Penguin *Pygoscelis adeliae* at Cape Royds. Ibis **104**:176–208.

Taylor, R. H., and P. R. Wilson. 1990. Recent increase and southern expansion of Adélie Penguin populations in the Ross Sea, Antarctica, related to climatic warming. New Zealand Journal of Ecology **14**:25–29.

Taylor, R. H., P. R. Wilson, and B. W. Thomas. 1990. Status and trends of Adelie Penguin populations in the Ross Sea region. Polar Record **26**(159):293–304.

Trivelpiece, W. Z., J. L. Bengtson, S. G. Trivelpiece, and N. J. Volkman. 1986. Foraging behavior of Gentoo and Chinstrap penguins as determined by new radiotelemetry techniques. Auk **103**:777–781.

Wanless, S., and M. P. Harris. 1992. At-sea activity budgets of a pursuit-diving seabird monitored by radio telemetry. Pages 591–598 *in* I. G. Pride and S. M. Swift, editors. Wildlife telemetry: remote monitoring and tracking of animals. E. Horward, Chichester, UK.

Wilson, P. R., D. G. Ainley, N. Nur, S. S. Jacobs, K. J. Barton, G. Ballard, and J. C. Comiso. 2001. Adélie Penguin population change in the Pacific sector of Antarctica: relation to sea-ice extent and the Antarctic Circumpolar Current. Marine Ecology Progress Series **213**:301–309.

Wilson, R. P., D. Grémillet, J. Snyder, M. A. M. Kierspel, S. Garthe, H. Weimirskirch, C. Schäfer-Nerth, J. A. Scolaro, C.-A. Bost, J. Plötz, and D. Nel. 2002. Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. Marine Ecology Progress Series **228**:241–261.

Wilson, R. P., K. Putz, G. Peters, B. Culik, J. A. Scolaro, J. B. Charrassin, and Y. Ropert-Coudert. 1997. Long-term attachment of transmitting and recording devices to penguins and other seabirds. Wildlife Society Bulletin **25**:101–106.

Wilson, R., and M.-P. Wilson. 1989. Tape: a package attachment technique for penguins. Wildlife Society Bulletin **17**:77–79.

Wittenberger, J. G., and G. L. Hunt. 1985. The adaptive significance of coloniality in birds. Pages 1–78 *in* D. S. Farner, J. R. King, and K. C. Parkes, editors. Avian Biology, Volume VIII. Academic Press, New York, New York, USA.

Woehler, E. J. 1993. The distribution and abundance of antarctic and subantarctic penguins. Scientific Committee for Antarctic Research, Scott Polar Research Institute, Cambridge, UK.

Ydenberg, R. C., L.-A. Giraldeau, and D. L. Kramer. 1986. Interference competition, payoff asymmetries, and the social relationships of central place foragers. Theoretical Population Biology **30**:26–44.

Young, E. C. 1994. Skua and penguin: predator and prey. Cambridge University Press, Cambridge, UK.