

FACTORS AFFECTING THE DISTRIBUTION AND SIZE OF PYGOSCELID PENGUIN COLONIES IN THE ANTARCTIC

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ABSTRACT.—Using census data on three species of pygoscelid penguins, we tested the hypothesis that competition for food during the chick-provisioning stage of reproduction limits the number of conspecific seabirds in a region. This prey-depletion hypothesis predicts that a negative correlation should exist between colony population size and the total number of breeding pairs from other colonies within parental foraging range. We also tested whether or not a negative correlation exists between colony size and the population size of, or distance to, the nearest neighboring colony. Suitable data were available for Adélie, Chinstrap, and Gentoo penguins (*Pygoscelis adeliae*, *P. antarctica*, *P. papua*) along the coasts of Victoria Land and the Antarctic Peninsula, where major portions of these species' world populations nest. Results indicated that colonies were highly clustered, with small colonies grouped around one or two large ones, in turn spaced widely. Depending on species, two different patterns of geographic structuring were observed. For the Adélie and Gentoo penguins, no significant negative correlation existed between colony size and the total number of pairs breeding within parental foraging range of the reference colony; however, a significant negative correlation occurred at 150 and 200 km, well beyond foraging range. We found no relationship between colony size and size of or distance to the nearest neighboring colony. In contrast, for the Chinstrap Penguin, a significant positive correlation existed between colony size and total breeding population within the foraging range (50 km) but, as with the other two species, the correlations became more negative at greater distances. Moreover, a significant positive correlation existed between colony size and size of, but not distance to, the nearest colony in this species. We confirmed the hypothesis previously put forward that prey depletion by parents feeding chicks cannot explain size structuring of seabird colonies where breeding-season food supply is superabundant, as in polar regions. However, we also showed that prey depletion is not a necessary condition for negative size structuring. We suggest that if prey depletion occurs (by exploitative or interference competition), any manifestation in terms of colony distribution is overridden near to the colony by aggregating factors that originally led penguins to be colonial and philopatric, for example, social facilitation or predator avoidance. We further propose that geographic structuring is better explained by factors affecting the metapopulation (all breeders and nonbreeders associated with the colony cluster), especially during the prebreeding period, than by factors affecting chick-provisioning parents alone. Received 18 October 1993, accepted 11 January 1994.

AMONG FACTORS THAT regulate the number of seabirds breeding in a region, the most important appear to be prey availability (e.g. Ashmole 1963, 1971, Furness and Birkhead 1984, Cairns 1989) and/or nesting space (e.g. Duffy 1983, Ainley and Boekelheide 1990). Populations also may be regulated by density-dependent mortality during the nonbreeding season (a function of food availability) or by social factors

related to breeding (reviewed in Birkhead and Furness 1985, Cairns 1992). Regulating factors may be dependent upon physical and biological settings. Thus, where biological productivity is high but nesting sites are scarce, such as the case in eastern boundary currents, nesting space is the limiting factor (Duffy 1983, Ainley and Boekelheide 1990). Conversely, if nesting sites are numerous and prey availability is limited, such as in the British Isles, food supply appears to be the critical factor (Furness and Birkhead 1984, Cairns 1989).

Furness and Birkhead (1984) maintained that in an area where nesting space is not limiting and food abundance does not vary spatially, prey depletion (exploitative competition) with-

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in the foraging range of parents should affect the distribution of nesting colonies of conspecifics. These authors predicted a negative correlation between the population size of a given colony and the number of nesting birds in all other colonies within the foraging range of individuals of the reference colony. Foraging range is determined by food availability, the energetic needs of chicks, and species-specific flight ability (see Pennycuik et al. 1984). The Furness and Birkhead (1984) prediction was based on a theory of population regulation, first proposed by Ashmole (1963, 1971) for tropical seabirds, which states that breeding numbers are limited by density-dependent prey depletion that, in turn, leads to reduced chick provisioning rates and, ultimately, to reduced reproductive output. They found proof for their prediction among four species of seabirds nesting in Britain, although they could not distinguish between exploitative or interference competition as the factor that limited prey availability. They went on to propose that the prey-depletion hypothesis would not apply in areas where prey are seasonally "superabundant" (compared to the tropics), as for example, in polar regions.

Subsequently, at temperate latitudes equivalent to Britain, Hunt et al. (1986) detected reduced reproductive output as a function of colony size among Thick-billed Murres (*Uria lomvia*) nesting on the Pribilof Islands, and surmised that reduced prey availability was affected by interference competition. Birt et al. (1987) found depleted prey within the foraging range of Double-crested Cormorants (*Phalacrocorax auritus*) breeding in southeastern Canada, a study that is the only demonstration of exploitative competition for food among seabirds. At polar latitudes, Gaston et al. (1983) detected a negative correlation between chick growth rates and colony size in the Thick-billed Murre on Hudson Bay, Canada, although chick growth rates do not necessarily determine breeding success and/or population regulation. Wittenberger and Hunt (1985) provided other examples of reproductive performance correlated inversely to colony size among birds.

Cairns (1989) proposed that the prey-depletion model would be more robust if it addressed the question of why certain seabirds live in large colonies in the first place. Following Diamond (1978), who noted that species foraging offshore have a greater extent of foraging area and cor-

respondingly larger populations compared to inshore species, Cairns estimated the foraging area available (i.e. area of continental shelf within foraging range) for each of the colonies in the Furness and Birkhead (1984) study, and found a positive correlation between colony size and foraging area for some of the species. In a departure from Furness and Birkhead, Cairns assumed that the foraging zone around neighboring islands did not overlap; Furness and Birkhead assumed the opposite (see also Wittenberger and Hunt 1985). Although he showed a positive relationship between colony size and size of the presumed foraging habitat for some species, Cairns' analysis was not able to provide statistical evidence that would favor his hypothesis over that of Furness and Birkhead (1984).

Neither Furness and Birkhead (1984) nor Cairns (1989) discussed why seabirds formed dense colonies (other than suggesting that a paucity of nesting sites encourages coloniality), nor did they address what role, if any, the factors promoting coloniality played in modifying the results of their analyses. The existence of large colonies (when nesting space is available at other colonies) would seem to contradict the prey-depletion hypothesis, because for such colonies prey would be even more easily depleted (a conclusion supported by Gaston et al. 1983, Hunt et al. 1986). The benefits of coloniality include information transfer, social facilitation, antipredator strategies, and access to mates (Wittenberger and Hunt 1985, Burger and Gochfeld 1990), and may or may not lead to natal philopatry. As stated by Wittenberger and Hunt (1985:2), "A one-factor or single-variable model is simply not a very useful way to understand a phenomenon as complex as avian coloniality."

We believe that a model of seabird colony distribution should incorporate both aggregating and dispersive factors, because: (1) dense colonies are characteristic of seabirds (not explicable by prey exploitation alone); (2) seabirds tend to initiate breeding in a highly synchronous fashion, which would exacerbate prey depletion if prey were limiting; and (3) many seabirds show high natal philopatry, and the negative aspects of crowding do not dissuade them breeding where they were born.

We tested Furness and Birkhead's (1984) corollary hypothesis that prey depletion should not influence seabird colony size and distri-

bution in polar regions. We know of no other tests of this hypothesis. We used those authors' approach to analyze colony distribution for the Adélie, Chinstrap and Gentoo penguin (*Pygoscelis adeliae*, *P. antarctica*, and *P. papua*) in two regions of Antarctica: Victoria Land, and the western Antarctic Peninsula. Within these areas, 66, 18, and 18%, respectively, of these species' world populations breed (Woehler 1992). If polar seabird populations are not structured by prey depletion, then we reasoned that, all else being equal, polar seabirds should not show the negative size relationship displayed by temperate (and tropical) populations, as observed (or surmised) by Furness and Birkhead (1984). If prey depletion does not structure polar seabird populations, predictions derived from the prey-depletion hypothesis should not be upheld. If, instead, these predictions are upheld, then we would conclude that either: (1) polar seabird populations can show size structuring similar to that observed in temperate areas in the absence of prey depletion (i.e. prey depletion is not a necessary condition for size structuring); or (2) polar regions do in fact manifest the effects of prey depletion.

On the basis of the prey-depletion hypothesis we tested several predictions. First, we evaluated whether penguin colony size is inversely related to the total number of breeding conspecifics foraging within range of the reference colony (Furness and Birkhead 1984). Second, we predicted that the effects of prey depletion should be most obvious when nearest neighboring colonies are considered, assuming (like Cairns 1989) that, for energetic reasons, seabirds forage as closely as possible to their respective colonies. Third, we predicted that, all else being equal, size of a colony is inversely related to the number of colonies within foraging range. In this regard, it is instructive to consider that the total number of conspecifics (the variable analyzed by Furness and Birkhead 1984) is itself the product of two components, mean colony size and number of colonies within a specified range; hence, we looked at how all three variables are related to the size of a reference colony. Fourth, we predicted that the total number of birds within foraging range is more tightly correlated with size of a colony than is the mean size of other colonies within that range. If this prediction is not upheld, this would favor the view that social factors, more than prey depletion, affect the observed pattern. Finally, we

predicted that the above correlations would be maximized within the foraging range of parents provisioning chicks.

We were unable to test Cairns' (1989) ideas relating to the prey-depletion hypothesis. Unlike the species examined in Britain, Adélie and Chinstrap penguins forage over both shelf and deep waters, the continental shelf in Antarctica being much deeper than elsewhere. This makes it difficult to estimate available nesting habitat solely on the basis of the extent of the continental shelf offshore a given colony. Similarly, we did not simultaneously analyze patterns of all three penguin species together, because their distribution in our study area overlapped too little and because prey depletion should be felt most strongly within a single species (Furness and Birkhead 1984).

METHODS

Data analysis.—Seabird colony sizes and locations are sufficiently well known and unaffected by local anthropogenic factors to permit an analysis such as this one in only a few regions. We selected two regions of the Antarctic for our study: the coast of Victoria Land in the Ross Sea (Taylor et al. 1990); and the western coast of the Antarctic Peninsula (Poncet and Poncet 1987, Shuford and Spear 1988). In both regions, thorough regional surveys of penguins have been undertaken recently by only a few researchers and within a short time span, thus enhancing comparability of data among sites. Our selection of study areas insured that all colonies within the basic data set had been censused since 1985. These and other censuses for Adélie, Chinstrap, and Gentoo penguins are summarized in Woehler (1992).

Data also were restricted to colonies in a limited diversity of oceanographic conditions in order to satisfy Furness and Birkhead's (1984) and Cairns' (1989) stipulation that, for prey depletion to be apparent overall, food abundance should be similar throughout the area under study. While this is difficult to measure and was only inferred to be so in their study, the criterion could be met at a minimum level, according to Furness and Birkhead (1984), if study colonies occurred within a limited number of oceanographic regimes. In the Ross Sea region, we included all colonies along the Victoria Land coast and offshore islands, from Cape Barne, Ross Island (77°35'S, 166°14'E), north to the Aviation Islands, Pennel Coast (69°16'S, 158°47'E; Fig. 1); the next-closest colonies to this region are well beyond 200 km. All penguins, except those in the northernmost 11 colonies, forage over the continental shelf in Ross Sea Surface Water (RSSW); individuals in the remaining colonies are more likely to forage in the shelf-break front, a mix-

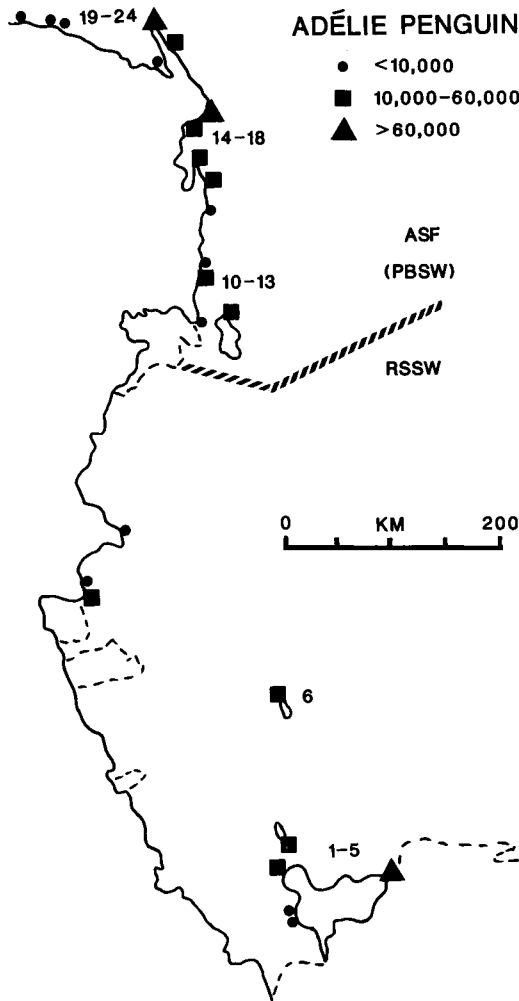


Fig. 1. Distribution and size of Adélie Penguin colonies along coast of Victoria Land. Colonies numbered consecutively south to north; clusters comprise colonies 1-5, 6, 7-9, 10-13, 14-18 and 19-24. Boundary of water masses indicated by hatched line: Ross Sea Surface Water (RSSW) and Antarctic Slope Front (ASF), which is composed of RSSW and Pacific Basin Surface Water (PBSW).

ture of RSSW, Circumpolar Deep Water and Pacific Basin Surface Water (PBSW; cf. Ainley et al. 1984, Jacobs 1991). Also, the shelf-break front likely plays an important role in nutrient transfer to upper trophic levels in the Antarctic Peninsula region but, unlike the Ross Sea, the front off the Antarctic Peninsula has not been studied extensively (Jacobs pers. comm.). In the eastern Bellingshausen Sea, we included as reference colonies only those colonies along the Antarctic Peninsula from Marguerite Bay (69°45'S, 68°30'W) north to Trinity Island (63°45'S, 61°W), as

well as colonies offshore of the South Shetland Islands, south of Nelson Island. This insured that penguins in the reference colonies likely would be foraging within only two water masses, Bellingshausen Sea Surface Water (BSSW) or Pacific Basin Surface Water (PBSW); farther to the east and north, additional water masses exist (Hunt et al. 1990). In summary, the oceanography in the study areas we chose is no more complex than that around Britain, the area for which Furness and Birkhead (1984) and Cairns (1989) completed their analyses. The geographic scale of those and our analyses also are similar.

We analyzed, within species, the relationship between colony population size and the size of, and distance to, the next nearest colony, as well as the total number of pairs breeding among all colonies within radii of 50, 100, 150, and 200 km from each colony. These radii represent increments of potential foraging range (see below) and reflect shortest over-water distance. We defined "colony" to conform with usage in other seabirds (thus, replacing the term "rookery" as used by Penney [1968] and many subsequent authors writing about penguins), as a contiguous group of breeding subcolonies (i.e. groups of contiguous territories) serviced by the same landing beach(es). Following Woehler (1992), we modified the definition slightly to include all penguin breeding areas within 1 km of one another as a single colony. The term "colony size" refers to the number of breeding pairs and not the areal extent of the breeding aggregation. We analyzed these data using linear regression (Computing Resource Center 1989), as did Furness and Birkhead (1984).

Foraging ranges.—Adélie Penguins have the greatest foraging range among pygoscelid penguins. At King George Island, South Shetland Islands (Antarctic Peninsula), Trivelpiece et al. (1987) used radio telemetry to estimate the TMFR of chick-provisioning Adélie, Chinstrap, and Gentoo penguins: 50, 27, and 17 km, respectively. In the Ross Sea, Ainley et al. (1983) surmised that Adélie Penguins regularly foraged as far as 125 km on the basis of: (1) chick feeding intervals much longer than the 20 h in the South Shetlands (once every 36 h among parents having young chicks and once every 48-72 h among those having creche chicks; cf. Taylor 1962, Trivelpiece et al. 1987); and (2) the distance to colonies of foraging concentrations of Adélie Penguins as observed on at-sea surveys (Ainley et al. 1984). This estimation of range in the western Ross Sea has since been supported by the radio-telemetric data of Sadleir and Lay (1990), who lost radio contact with most chick-provisioning Adélie Penguins at about 40 km, but detected some up to 179 km away (reliability of their estimates declined with distance beyond 40 km). Clarke and Kerry (1992), using satellite telemetry, detected foraging ranges typically out to 110 km for chick-provisioning parents. We used 125 km as the estimate of TMFR of Adélie Penguins.

In the case of Chinstrap Penguins, few direct data on foraging range are available to compare with results of Trivelpiece et al. (1987). Foraging-trip duration among parents feeding chicks in the South Orkney Islands was much longer (mean 20 h) than at the South Shetland Islands (6 h; cf. Croxall and Davis 1990, Trivelpiece et al. 1987). This suggests a TMFR of about 90 km (an increase of the Trivelpiece et al. estimate by a factor of 3.3). As for Gentoo Penguins, mean nest-relief intervals vary among several widely spaced study sites, mean 8 to 45 h (summarized by Bost and Jouventin 1990), compared to 12 h at South Shetland Islands (Trivelpiece et al. 1987). Increasing the range determined by Trivelpiece et al. (1987) 3.5-fold (45-h compared to 12-h trip time), estimates a TMFR of 60 km.

RESULTS

Adélie Penguin in Victoria Land.—The breeding population consisted of about one million pairs in 24 colonies, or about 35,900 pairs per colony (Taylor et al. 1990); the mean distance between colonies was $19.0 \pm \text{SE of } 4.9$ km. Major clusters of colonies centered around the large ones at Cape Crozier (colony 1 in Fig. 1) and Cape Adare (colony 20). Three smaller clusters existed around Possession Island (18), Coulman Island (10) and Inexpressible Island (7). Each colony within the Crozier-centered cluster has ample room for expansion (pers. obs.). This is the case for most other colonies as well (P. Wilson, Landcare Research New Zealand, pers. comm.), but no formal analysis of the availability of nesting habitat has been conducted. On the basis of penguin aggregations observed at sea (Ainley et al. 1984), the feeding areas of respective clusters do not extend beyond one water type. Individuals in the Cape Adare and Possession Island clusters feed in waters of the Antarctic Slope Front and those from other clusters feed over the shelf in RSSW.

Total number, mean colony size, and number of colonies did not correlate significantly with reference colony size within any of the four foraging radii considered (Fig. 2). The results in Figure 2 also demonstrate that correlations to mean colony size tend to become more negative as radius increases from 100 to 200 km, whereas coefficients involving total number of pairs were consistently near zero. Results for correlations between colony size and nearest-neighbor colony size and distance indicated no relationship ($r = -0.034$, $P > 0.8$), or at best a

weak positive one ($r = 0.305$, $P = 0.15$), respectively.

Adélie Penguin along the Antarctic Peninsula.—The population in the study area comprised 123,840 pairs in 32 colonies, or 3,870 pairs per colony (Poncet and Poncet 1987, Woehler 1992; Fig. 3); closest-colony distance averaged 14.7 ± 2.1 km. One cluster of colonies centered around Avian Island (colony 5), another around Armstrong Island (17), and a third around the closely spaced islands in Arthur Harbor (29). Ample habitat exists for founding and expansion of colonies within the Arthur Harbor cluster (pers. obs.), but we have no knowledge of this aspect elsewhere in the study area. All clusters occur within one water type, BSSW. Although excluded from the study area because of the availability of recent and consistent population estimates, two other colony clusters were evident in the Antarctic Peninsula region, all within WSSW: one on King George Island, around the large colony at Stranger Point (in PBSW, and where ample room for expansion is available; pers. obs.); and the second on Joinville Island (northern tip of the Peninsula), around large colonies at Danger and Paulet islands (Woehler 1992; Fig. 3).

An inverse correlation existed between colony size and number of breeding pairs, but was significant only at 150 and 200 km; equally strong and similar in pattern was the negative correlation between colony size and the mean size of other colonies within specified range (Fig. 2). The overall pattern exhibited by the correlation coefficient between reference colony size and mean colony size within foraging radius was similar to the pattern observed among Ross Sea penguins: correlations near 0 at 50 km, increasing to a positive value at 100 km and then decreasing with greater distance (150 and 200 km). In regard to the number of pairs within a specified distance, however, results were dissimilar between Victoria Land and the Antarctic Peninsula: for the latter, correlations became more negative with increasing distance (cf. Fig. 2A,B). No significant correlations occurred between colony size and the total number of colonies, at any distance.

The significant negative correlation between colony size and number of pairs within 200 km was dependent upon a single colony, Avian Island (35,000 pairs), by far the largest Adélie colony in the Antarctic Peninsula study area. When this colony was removed from the anal-

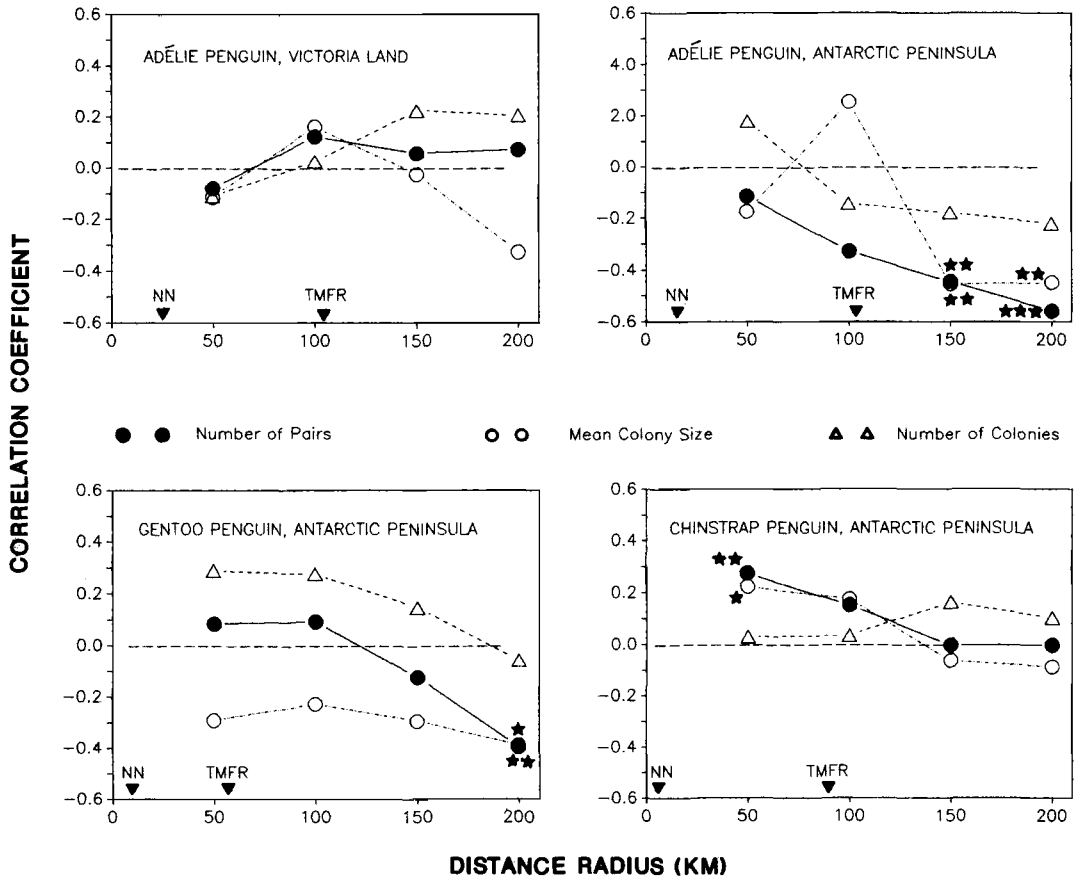


Fig. 2. Correlation coefficients, at incremental foraging radii, between size of reference colony and total number of breeding pairs, mean colony size, and number of other colonies: Adélie Penguin, Victoria Land ($n = 24$ colonies); and for the Antarctic Peninsula, Adélie Penguin ($n = 41$), Gentoo Penguin ($n = 42$), and Chinstrap Penguin ($n = 103$). NN indicates mean distance to nearest neighboring colony; TMFR indicates typical maximum foraging range of parents with chicks. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

ysis, no significant correlation was found. There is no reason to drop this colony from analysis, but doing so points out that the correlation observed, while very significant ($P < 0.001$), is not robust.

No significant correlations in any respect existed between colony size and nearest neighboring colony. The correlations between colony size and the size of and distance to nearest neighbor were 0.052 ($P > 0.7$) and -0.082 ($P > 0.6$), respectively.

Gentoo Penguin along the Antarctic Peninsula.—The population in the study area comprised 24,016 pairs in 42 colonies, or 571 pairs per colony (Poncet and Poncet 1987; Fig. 3); no Gentoo Penguin colonies occur in Victoria Land (Woehler 1992). Nearest-colony distance averaged 8.8 ± 1.6 km. Clusters of colonies were evident,

but not as clearly as in the Adélie Penguin. Clusters were centered around large colonies at Doumer Island and Port Lockroy (colonies 9, 10), Gerlache Island (13), and Cuverville Island (25), all within BSSW; and Hannah Point and Robbery Beaches on opposite sides of Livingston Island (34, 41), within PBSW. Much available habitat exists for new colonies in the Port Lockroy/Gerlache Island region (pers. obs.)

The correlations of colony size with total number of pairs, as well as with mean colony size, became increasingly negative beyond 100 km. Correlations with mean colony size were more negative than with total pairs until 200 km, where they became similar and statistically significant (-0.396 and -0.375 , respectively; Fig. 2). Correlations with mean colony size approached significance at 50 and 150 km ($P <$

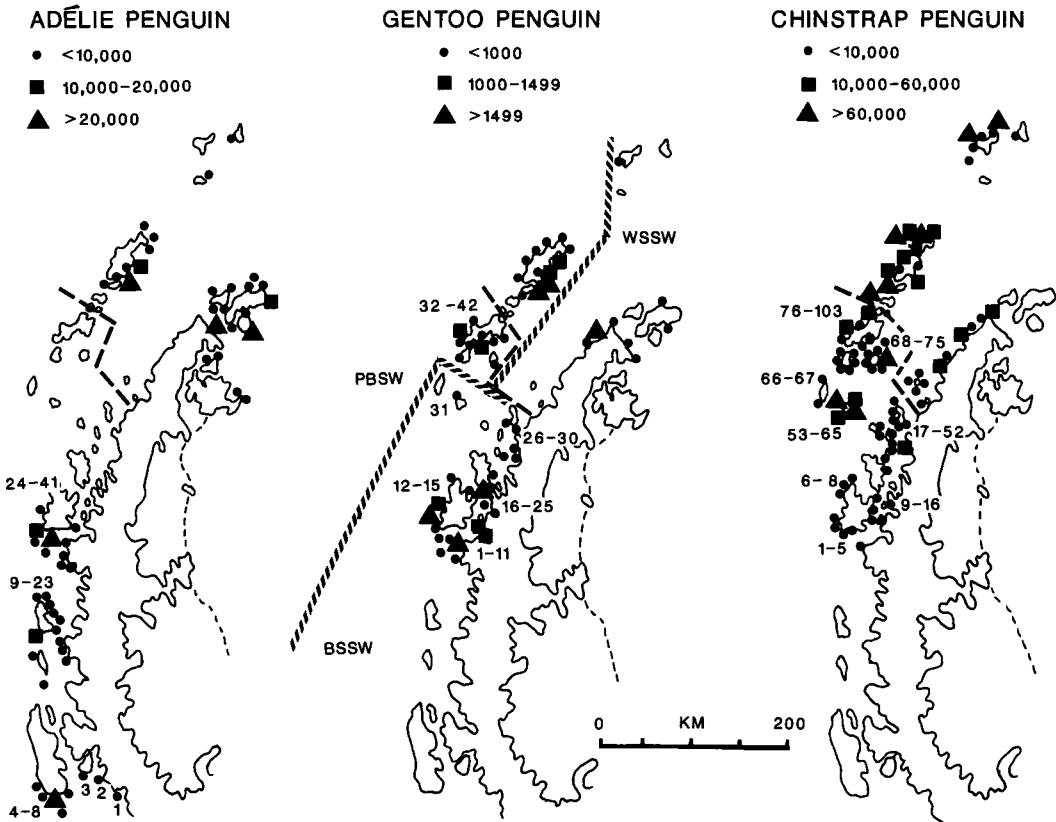


Fig. 3. Distribution and size of penguin colonies, numbered consecutively south to north along western side of Antarctic Peninsula: Adélie Penguin, clusters comprise colonies 1-8, 9-23, 24-41; Gentoo Penguin, clusters 16-25, 26-30, 31-37, and 38-42; and Chinstrap Penguin, clusters 1-5, 6-8, 9-16, 17-52, 53-66, 68-75, 76-85 (+67), and 86-103. Reference colonies against which correlations were applied are south of dashed lines; colonies to north included in analysis only if within 200 km foraging radius of a reference colony. Boundary of water masses indicated by hatched lines: Pacific Basin Surface Water (PBSW), Bellingshausen Sea Surface Water (BSSW), and Weddell Sea Surface Water (WSSW). Within densely colonized areas, not all colonies of less than 1,000 pairs for Gentoo Penguins or < 10,000 pairs for Chinstrap Penguins are shown by a dot (for detailed maps, see Woehler 1992).

0.1). Thus, the overall pattern exhibited by correlations with number of pairs and mean colony size was similar: a more positive value at 100 km compared to 50 km, followed by increasingly more negative values as distance increased. This is the same pattern shown among Adélie Penguins. For Gentoo Penguins, colony size did not correlate significantly with number of colonies at any distance. Neither was there a significant relationship between either colony size and nearest-neighbor colony size ($r = 0.090$, $P > 0.5$) or nearest-colony distance ($r = -0.130$, $P > 0.4$).

Chinstrap Penguin along the Antarctic Peninsula.—The population in the study area comprised 593,990 pairs in 103 colonies, or 5,766

pairs per colony (Poncet and Poncet 1987, Shuford and Spear 1988; Fig. 3); no Chinstrap Penguins breed in Victoria Land (Woehler 1992). Nearest-colony distance averaged 5.5 ± 0.6 km. Clustering was not clearly discernible, but neither were colonies evenly distributed: rather, clusters of small colonies existed around large ones at Alcock Island (22), and capes Wallace and Gary on Low Island (55, 60), all within BSSW. Additional clusters occurred around Bailey Head on Deception Island (68), and Cape Shirreff (88), both within PBSW. Much suitable nesting habitat exists in the region occupied by this species, at least in the southern portion (pers. obs.). Although Figure 3 by itself does not present a convincing case for size structur-

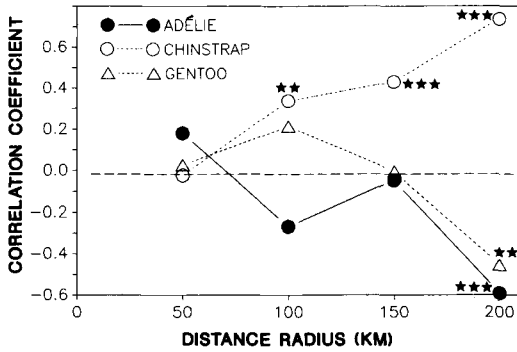


Fig. 4. Correlation coefficients between mean colony size and total number of other colonies at incremental foraging radii for three penguin species of the Antarctic Peninsula. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

ing of Chinstrap Penguin colonies, statistical evidence indicates otherwise (see below).

The observed relations between colony size and different characteristics of spatial structure were markedly different in the Chinstrap Penguin compared to the previous two species. First, the total number of pairs within 50 km of the reference colony showed a significant positive correlation with colony size, but no significant correlations existed for greater distances (Fig. 2). The same was true between colony size and mean size of other colonies. In general, for mean colony size and number of pairs, correlations diminished with increasing distance from the reference colony. Correlations of colony size with the number of colonies were not significant at any distance.

A second unique result for Chinstrap Penguins was that the size of the nearest colony was positively related ($r = 0.232$, $P = 0.018$) to colony size (although distance to nearest colony was not; $r = -0.063$, $P > 0.5$). That is, the larger the reference colony, the larger was its neighbor, a relationship contradictory to that predicted by the prey-depletion hypothesis.

Further insight into the difference in distribution pattern between Chinstrap Penguins, on the one hand, and Adélie and Gentoo penguins, on the other, is provided by considering the relationship between number of colonies within specified range and the mean size of these colonies (Fig. 4). For Chinstrap Penguins, as the number of colonies increased so did mean colony size (the correlation was significantly positive at 100, 150, and 200 km). In contrast, for Adélie and Gentoo penguins, as the number of

colonies increased their size decreased; the relationship was significant for these two species at 200 km. Moreover, the regression coefficient relating number and size of Chinstrap Penguin colonies was significantly greater ($P < 0.01$) than the respective coefficients for Adélie and Gentoo colonies. In summary, Chinstrap Penguins were found either in many large colonies that were near to one another or a few small ones, whereas for Adélie and Gentoo Penguins, individuals tended to occur either in several large colonies or many small colonies, but usually the two size classes were not in the same vicinity.

DISCUSSION

Size structuring and prey depletion.—For each of the three species, we found evidence of geographic structuring of populations. In Adélie and Gentoo penguins, size of colony was significantly and inversely related to the number of breeding pairs and mean size of other colonies; mean colony size relative to number of other colonies within a specified area was also significantly and negatively correlated. We refer to such a pattern, the same observed by Furness and Birkhead (1984), as "negative size structuring." For Chinstrap Penguins, there was a significant positive relationship between colony size and number of pairs or mean colony size; also, the size and number of colonies within a specified range was positively correlated. We refer to this pattern as "positive size structuring."

Negative size structuring is consistent with the prey-depletion hypothesis. Nevertheless, we maintain that, even in Adélie and Gentoo penguins, the prey-depletion hypothesis is not confirmed for several reasons. (1) The distance at which negative size structuring is apparent is beyond the TMFR of parents feeding chicks. Conversely, (2) at distances within the TMFR, there were no significant negative correlations between colony size and number of breeding pairs. We would expect, under the prey-depletion hypothesis, that the number of foraging birds breeding close to the colony (e.g. <50 km) should have a greater impact on colony growth than would the number of birds breeding up to 200 km away, yet we observed the opposite for Adélie and Gentoo penguins. (3) The average size of outlying colonies predicted reference colony size as well as or better than did the total number of breeding pairs. (4) No sig-

nificant negative correlations existed between colony size and size of, or distance to, the nearest neighbor. Finally (5), the number of colonies within foraging range was not correlated with size of the reference colony.

We conclude that the prey-depletion hypothesis, at least as it applies to foraging of parents feeding chicks, is supported by none of the penguin species, a conclusion in agreement with Furness and Birkhead (1984), who cited the summer superabundance of food in polar regions as the hypothetical reason for the absence of prey depletion. At the same time, Adélie and Gentoo penguins showed size structuring qualitatively similar to that observed by Furness and Birkhead. Thus, we conclude that prey depletion during the chick provisioning period is not a necessary condition for negative size structuring of seabird colony distribution.

Natal philopatry and the metapopulation.—We observed that colonies of all three species tended to be clustered, where within each cluster, several smaller colonies centered around one or two large ones. This geographic pattern, too, is contrary to one structured by prey depletion alone; all else being equal, colonies should not be large and should be as evenly spaced as possible to maximize distance between colonies and reduce potential effects of resource depletion. Because the observed pattern is one that would magnify the effect of prey depletion, we suggest that factors favoring aggregation play an important role in affecting colony size and distribution among Antarctic penguins (and perhaps other seabirds as well). We also suggest that each cluster of colonies constitutes a metapopulation (see Gilpin and Hanski 1991), with outlying smaller colonies seeded by recruits from the initially founded and larger colony, as a result of philopatric tendencies among recruits.

The effects of natal philopatry are expressed in two ways. First, in a philopatric species, individuals tend to breed in their natal colony even if that colony is already large, thus counteracting a tendency to disperse to avoid prey depletion (we call this path A). Secondly, if they do disperse, individuals are constrained to settle near their natal colony (path B). Structuring by path A resists prey depletion and would not lead to the negative correlation postulated by the prey-depletion hypothesis. Structuring by path B produces a pattern resembling that predicted by prey depletion, but it is not predicated on foraging range. If the effect of natal philo-

patry is applicable in a given seabird species, colony distribution would reflect constraints exerted by habitat availability and would be directly related to the degree of philopatry; clustering would be weak in the least philopatric species and vice versa. In our analysis, the weaker clustering exhibited by Chinstrap Penguins indicates that natal philopatry may be less well developed than in the other two species. In the only study of natal philopatry in penguins, Ainley et al. (1983) showed that Adélie Penguins are indeed highly philopatric.

In our view, natal philopatry is a constraint required in models of the geographic structuring of seabird populations, be they nest-site or prey limited, a belief expressed also in the reviews of avian coloniality by Wittenberger and Hunt (1985; see also Burger and Gochfeld 1990). Philopatry resists the ideal-free distribution of seabirds hypothesized to exist by Cairns (1989) and implied but not stated by Furness and Birkhead (1984). These authors did not consider whether factors favoring aggregation affected their results, but such factors might well have been considered. Other than the point that nest sites were limited in their study area, neither Furness and Birkhead or Cairns offered further explanation for why seabirds nest in a highly clumped (i.e. colonial) fashion in the first place. Whereas suitable, ice-free habitat is rare in a large-scale view of the Antarctic coastline, enough is available in our study areas that colony size should have equilibrated unless aggregating factors are important in the structuring process.

The initial settling of first-time breeders and the redistribution of experienced breeders (i.e. emigration and immigration) reflect not only philopatric tendencies, but also the importance of breeding density at prospective colonies as revealed by European Shags (*Phalacrocorax aristotelis*; Potts 1969, Potts et al. 1980), Herring Gulls (*Larus argentatus*) and Lesser Black-backed Gulls (*L. fuscus*; Coulson et al. 1982, Coulson 1991). Future recruits are attracted to larger colonies (Birkhead 1977), but if breeding density becomes too high (negative influences are encountered), prospecting birds will more likely recruit to a smaller colony nearby, thus increasing emigration to and colonization of nearby colonies. Remaining to be determined is whether or not these emigrants are avoiding the increased commotion (i.e. interference competition), reduced availability of optimal nest sites

(exploitative competition), or other factors such as prey depletion (interference or exploitative). In several regional studies, population changes have been shown to be much greater at small colonies, while the larger ones have changed little or not at all (e.g. King Penguin [*Aptenodytes patagonicus*] in the Crozet Islands [Jouventin and Weimerskirch 1990]; Adélie Penguin in the Ross Sea [Taylor et al. 1990]; Black-legged Kittiwake [*Rissa tridactyla*] in Britain [Coulson 1983]; and Common Murre [*Uria aalge*] in central California [Takekawa et al. 1990]).

Role of metapopulations in geographic structuring.—While the pattern we observed does not support prey depletion as an important phenomenon among Antarctic penguins during the chick-provisioning period, it does indicate that colony distribution is nevertheless structured and that a re-evaluation of factors regulating the dynamics of intercolony structure is warranted (see also Wittenberger and Hunt 1985). Indeed, the geographic structuring among colonies of the three Antarctic penguin species may reflect social forces mentioned above (and see below) without any contribution from prey depletion. Alternatively, there may be an effect of prey depletion (in addition to social forces), but one that acts at distances beyond the TMFR of adults provisioning chicks. Below we describe the argument for such a mechanism, relying on our observations that: (1) colony size does not appear to have a negative impact on the closest colony; (2) the influence of colonies within the TMFR of adults provisioning chicks on reference colony size appears weak (neither strongly positive nor negative); and (3) the influence of colonies at greater than TMFR on reference colony size appears significantly negative (or at least less positive, in the case of Chinstrap Penguins). These three patterns can be explained by forces acting on a spatial scale smaller and greater than the TMFR of parents with chicks.

If foraging parents affect prey availability, either by exploitative or interference competition, our results imply that philopatry and other aggregating factors override avoidance of such competition close to a colony. This pattern is consistent with the correlation of colony size and number of adults in the region being weak and even positive near to the reference colony. Presumably, individuals benefit from recruiting as closely as possible to breeding and foraging habitat "proved" to be favorable (i.e. the

location from which they fledged). In an evolutionary context, beneficial aggregating factors for penguins that would lead to philopatry include: (1) antipredator strategies (e.g. swamping the predator; in the case of Antarctic penguins, skuas [*Catharacta* spp.] and seals [*Hydrurga leptonyx*]); (2) social facilitation, which leads to breeding synchrony (itself an antipredator strategy) and mate choice (the rapidity of pair formation being critical where summers are short; see Ainley et al. 1983); and (3) spatial heterogeneity of high-quality breeding or foraging habitat (i.e. the possible limitation on ice-free terrain on which to nest; see also Wittenberger and Hunt 1985). We can reasonably expect that the original colonists in a region chose the best breeding area available at the time (as postulated by Wittenberger and Hunt 1985, Cairns 1989). In seabirds that do not forage on or near their breeding territories, such a choice is a compromise between optimal breeding habitat and access to more distant food.

Farther from the colony (assuming that prey abundance is constant over an area beyond the foraging range of parents), perhaps nearer to the maximum foraging range for a given colony, we would expect that prey depletion, if a factor, begins to override the influence of philopatry. Beyond the foraging range of parents feeding chicks, but within the general vicinity of natal colonies, a large number of prebreeders and nonbreeders have been noted among Adélie Penguins (Ainley et al. 1984) and other seabird species (e.g. Briggs et al. 1987, Spear 1988, Weavers 1992, Veit 1995). Nonbreeders, including juveniles, lack the constraint to forage within range of a chick, but nevertheless congregate near natal colonies (Ainley et al. 1984:fig. 15; also see Weavers [1992] for telemetric studies of breeding and nonbreeding Little Penguins [*Eudyptula minor*]). These larger populations—breeders plus the nonbreeders of a colony cluster—constitute the metapopulation.

Exploitative or interference competition caused by individuals of the metapopulation, if food availability was affected, could have negative effects on the size and distribution of colonies at distances beyond parental foraging range, as may be the case in the penguins. Also affected may be the ultimate limit to the size of the metapopulation (due to decreased feeding success leading to poorer fitness) and ultimately the breeding portion of it. Furthermore, the critical time of year when foraging by the me-

tapopulation exerts its greatest influence may be the early spring when potential breeders begin to move toward and concentrate near colonies to re-establish or prospect for territories and mates rather than during the late spring/summer, a time when a bloom of prey materializes (see review of breeding phenology and prey availability, including studies on penguins, in Ainley and Boekelheide 1990). Superabundance of food during the chick-rearing period does not rule out food limitation earlier in the breeding season. Even for breeders, especially in studies of penguins, it is well established that foraging range during this early nesting period (through the incubation period) is much greater than during chick provisioning as demonstrated by nest-relief intervals and telemetry (e.g. Taylor 1962, Trivelpiece et al. 1987, Sadleir and Lay 1990, Clarke and Kerry 1992). We hypothesize that this greater foraging radius overlaps the distance range in which we observed the significant negative correlations between colony size and the size/distribution of neighboring colonies (i.e. at 200 km, but not closer than 150 km in the species we studied).

In a study of Little Penguins, Dann et al. (1992) found that annual mortality of breeders correlated with body-fat levels (and mass) attained during the incubation period (i.e. early in breeding season) rather than the chick-provisioning period or any other time of the year. We suggest, thus, that not just breeding distribution but also breeding population size in penguins (and other seabirds), through factors affecting the metapopulation, may be determined by prey availability during late winter/early spring before the chick-provisioning period. Obviously, much work is required: on the ecology of seabird at the scale of metapopulations (see also Wooller et al. 1992); on the relationship to metapopulations of their respective breeding portions; and, as noted by Wittenberger and Hunt (1985), on the factors affecting and effected by coloniality in seabirds, specifically the factors that affect different rates of growth of colonies within one region (e.g. Taylor et al. 1990).

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