

CONSPECIFIC FOOD COMPETITION EXPLAINS VARIABILITY IN COLONY SIZE: A TEST IN MAGELLANIC PENGUINS

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Abstract. Food availability has been proposed as one of the main factors regulating population sizes in birds. Seabirds have provided evidence for the hypothesis that food depletion due to intraspecific competition explains variability in colony size. However, the predictions derived from this hypothesis have not been fully tested due mainly to the difficulties in measuring food availability in marine environments. We measured stable isotopes of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) in the blood of Magellanic Penguins (*Spheniscus magellanicus*), which reveal information about their consumed prey and foraging habits. We tested if conspecific competition causes food depletion, affecting penguin breeding performance and, ultimately, the size of the colonies. Blood $\delta^{15}\text{N}$ values of adults and chicks significantly decreased with increasing size of their colonies and with the number of conspecifics breeding within the parental foraging ranges. This suggests that high breeding densities provoke the depletion of high-quality prey (mainly anchovy). We also found positive relationships between $\delta^{13}\text{C}$ values and density of conspecifics within the parental foraging ranges, indicating that when competition for food is high, individuals tend to feed closer to the colony on prey of lower quality. Adult $\delta^{15}\text{N}$ values were positively correlated with breeding success at the colonies, which was negatively correlated with the density of conspecifics within foraging ranges. Moreover, $\delta^{15}\text{N}$ values of fledglings were positively correlated with their body condition but not with their T-cell mediated immune response considered as two measures of their survival prospects. This decreased breeding output was translated to the colony-size structure of the population, since colony size was negatively correlated with the number of conspecifics breeding within the parental foraging ranges. Therefore, we provide strong evidence suggesting that density-dependent food depletion determines the distribution of colony sizes in birds.

Key words: breeding success; colony size; intraspecific food depletion; Magellanic Penguin; offspring viability; Patagonia; population structure; seabirds; *Spheniscus magellanicus*; stable isotopes.

INTRODUCTION

Colonial breeding is widespread in birds, especially in some groups such as seabirds, where 98% of the species breed colonially (Rolland et al. 1998). Coloniality has attracted much research attention in recent decades, provoking an intense debate on its evolution and function (e.g., Brown and Brown 1996, Danchin and Wagner 1997, Tella et al. 1998). However, factors contributing to the variability in colony size within species have been scarcely examined (Brown et al. 1990, Brown and Brown 2000). Apart from the logical limitation imposed by available breeding sites, food availability has long been invoked to explain variability in colony size (Lack 1968). As far back as 1963, Ashmole proposed that the size of seabird colonies is limited by food availability during the breeding season,

when adults have to feed their chicks and themselves. Intraspecific competition at high densities and the resulting depletion of food around colonies may thus result in reduced rates of provisioning to chicks, which would influence reproductive output, recruitment rates, and finally colony dynamics.

There are several pieces of evidence supporting Ashmole's (1993) hypothesis. The assumption that colonial birds may deplete surrounding food resources was demonstrated by Birt et al. (1987) around two colonies of cormorants. On the other hand, colony size has been shown to be inversely related to chick growth rates and/or fledgling masses of seabirds (Gaston et al. 1983, Gaston 1985, Hunt et al. 1986), offspring traits that could affect juvenile survival and recruitment rates (see review in Magrath 1991). Less attention has been paid to the potential competition for food among conspecifics breeding in neighboring colonies. Food depletion around a colony may depend both on colony size and on the size of the population breeding around it. Tella

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et al. (2001) have recently shown that two aspects of offspring viability (body condition and cell-mediated immunocompetence) were inversely correlated with conspecific breeding density within the parental foraging range and with colony size in Magellanic Penguins (*Spheniscus magellanicus*). This intercolony competition for food may explain why the number of conspecific competitors from surrounding colonies is a good predictor of colony size, both in marine (Furness and Birkhead 1984) and in a terrestrial species (Griffin and Thomas 2000). Despite the above evidence, we are not aware of any study that simultaneously tested (1) that there is greater competition for food with increasing density of conspecifics, and (2) this competition explains variability in breeding output and colony size distribution in any bird species.

In this paper, we test the food depletion hypothesis using the Magellanic Penguin. This species breeds at highly variable densities (Yorio et al. 1998), and prey depletion as a cost of living at high densities has recently been suggested as an explanation of variability in offspring quality (Tella et al. 2001). A direct demonstration of this hypothesis would require an extensive marine sampling program, which is difficult to extend to a large number of colonies (Furness and Birkhead 1984, Birt et al. 1987). An alternative is to study the relationship between breeding densities and the relative proportion of preferred prey that individuals consume. Conventional methods for studying diet in birds (e.g., examination of stomach contents) have several sources of bias, including the rapid digestion of soft-bodied prey (see review in Duffy and Jackson 1986). Alternatively, stable-isotope ratios of nitrogen ($^{15}\text{N}/^{14}\text{N}$, expressed as $\delta^{15}\text{N}$) and carbon ($^{13}\text{C}/^{12}\text{C}$, $\delta^{13}\text{C}$) in the proteins of the consumer reflect those of their prey in a predictable manner (DeNiro and Epstein 1978, 1981). A great deal of dietary information can be obtained from the isotopic analysis of whole blood, which provides a dietary integration for a period of up to two months (Hobson and Clark 1992, 1993, Hobson et al. 1997). Analyses of $\delta^{15}\text{N}$ values in tissues of consumers and prey have been used largely to identify and quantify sources of dietary materials of individuals (Hobson 1993, Hobson et al. 1994, Sydeman et al. 1997, Szepanski et al. 1999, Thompson et al. 1999, Forero et al. 2002). Since a stepwise enrichment of tissue $\delta^{15}\text{N}$ values occurs with each trophic level (3–5%, Michener and Shell 1994), individuals with higher values of $\delta^{15}\text{N}$ generally feed on prey of higher trophic levels. In our study area, the Magellanic Penguin forages primarily on pelagic schooling fishes, mainly anchovy (*Engraulis anchoita*), and to a lesser extent on squid (*Loligo* and *Illex* sp.) (Scolaro et al. 1999). Forero et al. (2002) showed that anchovies have higher $\delta^{15}\text{N}$ signatures than squids (16.9‰ vs. 13.6‰). Thus Magellanic Penguins with higher blood $\delta^{15}\text{N}$ values are assumed to consume a higher proportion of anchovy (Forero et al. 2002), a prey with higher nutritive value than secondarily con-

sumed prey (Hislop et al. 1991, Scolaro et al. 1999). Using this technique, if conspecific competition is acting, we predicted lower $\delta^{15}\text{N}$ values in individuals living in large colonies and in colonies located in areas with higher densities of conspecifics breeding within the parental foraging ranges.

Our next prediction related to food depletion was that individuals from colonies located in areas with high density of conspecifics should compensate for food shortages by changing their foraging strategies. In a situation where there is a shortage of high-quality food, parents could adopt two different strategies: to expand their foraging so that their preferred prey could still be obtained (Monaghan et al. 1994, Kitaysky et al. 2000), or to forage closer to the colonies and thus increase provisioning rates to the chicks with prey of lower quality, to cover the higher energy demands during the chick-rearing stage (Furness and Monaghan 1987, Monaghan et al. 1992). Accurate determination of foraging ranges of seabirds requires the use of telemetry (e.g., Wilson et al. 1995). Alternatively, values of $\delta^{13}\text{C}$ can reveal spatial variation in feeding, including inshore vs. offshore foraging in marine habitats. Inshore or benthically linked food webs typically have higher $\delta^{13}\text{C}$ values than offshore or more pelagic foodwebs (Hobson et al. 1994, France 1995, Hobson et al. 1995, Thompson et al. 1999). Thus, we used blood $\delta^{13}\text{C}$ values as an approximate indicator of the zone of feeding about the colony. The relationship between $\delta^{13}\text{C}$ values and density of conspecifics at the foraging ranges would be negative or positive depending on the alternative responses explained above.

Life-history theory predicts that in long-lived species, such as seabirds, a decrease in food availability will affect fecundity before affecting adult survival (e.g., Hamer et al. 1991, Stearns 1992, Pons and Migot 1995, Oro et al. 1999). Therefore, we predicted a positive correlation between the proportion of high-quality prey in the diet of adults (as indicated by $\delta^{15}\text{N}$) and breeding success at the colonies, as well as positive relationships between $\delta^{15}\text{N}$ of chicks and two indicators of offspring viability, namely their body condition and cell-mediated immunocompetence (Magrath 1991, Tella et al. 2000). Consequently, we also predicted that breeding at high densities not only would compromise offspring quality (Tella et al. 2001), but also would result in poorer breeding success. Finally, if food depletion regulates the size and distribution of colonies in this seabird species through differential reproductive output and recruitment rates, we predicted a negative relationship between the size of colonies and number of conspecifics breeding at other colonies within their foraging ranges.

METHODS

Study area and species

We conducted this study in Chubut Province (Argentinean Patagonia) (Fig. 1), where the Magellanic

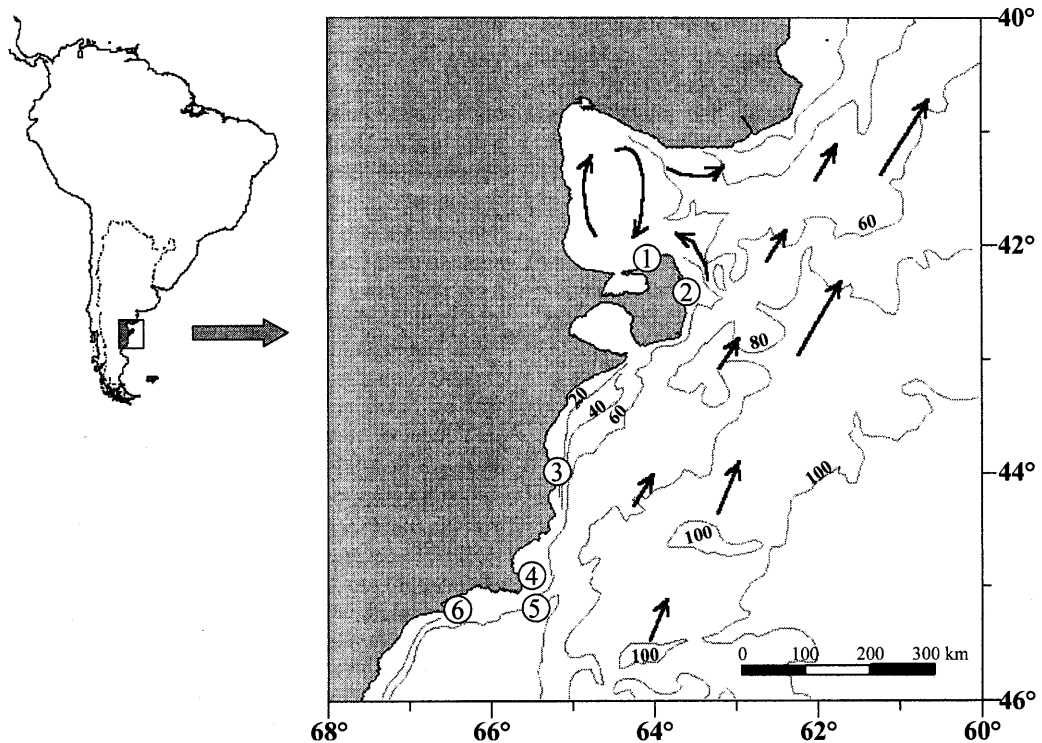


FIG. 1. Location of sampled colonies and bathymetry of the Chubut area. Major circulation patterns are indicated. Major currents are the Patagonian current and Malvinas current. Due to the scale and proximity of sampled colonies, numbers 1 and 2 encompass two and three colonies respectively.

Penguin constitutes 84% of the seabird community in terms of number of breeding pairs (Yorio et al. 1998). A total of 527 463 pairs breed in 29 colonies, constituting 49% of the penguin colonies and 55% of the pairs breeding on the Atlantic coast of South America. Median colony size in Chubut was 3165 breeding pairs (range 47–175 000), and variability in colony size closely resembles that for the entire distribution of the species (Tella et al. 2001). By selecting this study area we minimized the potential influences of large-scale variation in food supplies between areas due to different oceanography and productivity (Furness and Birkhead 1984). Magellanic Penguins arrive at their breeding colonies in late August, and during the chick-rearing period (November–February) both parents provide food to the young (Boersma et al. 1990). An important segregation in the diet exists between chicks and parents and between male and female adults, which is probably imposed by the nutritive requirements of chicks during development and by sexual size dimorphism in adults, respectively (Forero et al. 2001, 2002).

Field procedures

To evaluate if high conspecific densities cause the depletion of high-quality prey, we sampled adults and chicks at eight colonies ranging in size from 483 to 175 000 breeding pairs (Fig. 1). We visited colonies at the end of the breeding season (1999–2000), when the

chicks were ~70 d old (i.e., close to leaving the nest; Tella et al. 2001). All adults and fledglings were sampled from different nests randomly distributed through each colony. We restricted sampling to a minimum that we expected could show isotopic differences among colonies, based on a previous study that showed statistical differences among sexes and age classes of Magellanic Penguins in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values when analyzing smaller sample sizes by group within each colony (Forero et al. 2002; see also Hobson and Schwarzc 1985). Final sample sizes by colony varied slightly due to some losses during processing. We extracted ~1 mL of blood from each penguin, which was used for both isotope analyses (see below) and for sexing the individuals through molecular procedures after DNA extraction (Ellegren 1996).

Breeding success, body condition, and immune response were measured in six of the colonies studied in 1999. We recorded external measurements and body mass from each fledgling sampled for isotopes. Since body mass was influenced by sex, age, and size of fledglings (Tella et al. 2001), we obtained an index of body condition by taking the residuals from an ANCOVA with log body mass as the dependent variable, sex as a factor, and log-transformed flipper and bill lengths as covariates ($r^2 = 0.36$, $F_{3,58} = 10.42$, $P < 0.001$). We challenged the immune system of these chicks through the subcutaneous injection of phyto-

haemagglutinin (PHA), a technique that measures *in vivo* cell-mediated immunity (e.g., Moreno et al. 1998, Smits et al. 1999, Tella et al. 2000). We injected 0.1 mL of 2 mg/mL PHA (Sigma Pharmaceuticals, South Croydon, Australia) in phosphate-buffered saline in a marked site of the right external food web (Moreno et al. 1998), and measured the immune response 24 h later (see Tella et al. 2001 for more details). Breeding success was estimated as brood size at fledging time, since we could not determine whether most of the empty nests were not occupied by breeding pairs or they failed early in the breeding season. We recorded brood size in the nests located within a band of 2 m wide in a walked line transect perpendicular from each focal nest to the sea ($n = 3252$ nests, range = 218–1148 nests per colony).

Stable isotope analyses

Blood was mixed with 1.5 mL of 70% ethanol (Hobson et al. 1997) and stored at room temperature (20°–25°C) until stable isotope analysis. Whole blood stored in solution was freeze-dried to remove ethanol and then powdered. Stable-carbon and nitrogen isotope assays were performed on 1 mg subsamples of homogenized materials by loading into tin cups and combusting at 1800°C in a Robo-Prep elemental analyzer (MWG Biotech Ag., D85560 Ebersberg, Germany). Resultant CO₂ and N₂ gases were then analyzed using an interfaced Europa 20:20 continuous-flow isotope ratio mass spectrometer (CFIRMS; PDZ Europe, Northwich, Cheshire, UK) with every five unknowns separated by two laboratory standards (egg albumen). Isotope abundances were expressed in δ notation as the deviation from standards in parts per thousand (‰) according to the following equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where $X = {}^{15}\text{N}$ or ${}^{13}\text{C}$, and R = the corresponding ratio ${}^{15}\text{N}/{}^{14}\text{N}$ or ${}^{13}\text{C}/{}^{12}\text{C}$. The R_{standard} for ${}^{15}\text{N}$ is that for atmospheric N₂ (AIR) and for ${}^{13}\text{C}$ is that for Pee Dee Belemnite (PDB). Based on numerous measurements of organic standards (albumen and collagen) the analytical precision (± 1 SD) of these measurements is estimated to be $\pm 0.1\text{‰}$ and $\pm 0.3\text{‰}$ for carbon and nitrogen, respectively (Hobson et al. 1994).

Colony sizes, foraging ranges, and number of potential competitors

The distribution and size of the 29 colonies located in Chubut were extracted from Yorio et al. (1998). A telemetry study conducted at one of these colonies determined that adults regularly foraged 117 km from the colony during the incubation period (range 0–303 km; Wilson et al. 1995). Estimates of foraging ranges for the chick-rearing period, based on chick-feeding intervals and mean swimming speeds, are ~ 30 km (Scolaro 1984, Wilson et al. 1995). In addition, the number of conspecifics breeding within circles of 100 km radius

negatively affected offspring body condition of chicks (Tella et al. 2001). Based on this information, we calculated the number of potential competitors using circles of 30, 100, and 300 km radius from the focal colony. As in previous studies (Furness and Birkhead 1984, Griffin and Thomas 2000), we considered that each breeding colony extends its feeding range in a circle out to the same distance as every other colony and that penguins are equally likely to forage in all parts of this range. However, mean oceanic productivity in temperate regions may not be as uniform as previously believed (Furness and Birkhead 1984), and colony foraging ranges may be irregularly shaped or unevenly used (Cairns 1989). In any case, these potential caveats should increase statistical noise and reduce the strength of actual relationships (Furness and Birkhead 1984, Griffin and Thomas 2000). The area of overlap in foraging area was calculated for each colony and for each foraging distance. The proportion of overlap in the foraging area (without considering land overlap) was then multiplied by the pair numbers at neighboring colonies to obtain the number of pairs likely to forage within the range of the focal colony. The resulting number of potential competitors was summed for each colony in turn for all the neighboring colonies within which they overlapped (Griffin and Thomas 2000, Tella et al. 2001).

The availability of nesting habitat could influence colony size. Several colonies were located on pristine seacoast, where nesting habitat seems to be unlimited. However, colony size was positively correlated with island size ($r_s = 0.79$, $P < 0.001$, $n = 14$; data from Yorio et al. 1998). Nonetheless, we calculated the saturation level of these colonies following Forbes et al. (2000). For that we estimated the potential number of breeding pairs that could be accommodated on a given island considering its size and the mean observed breeding density for the species in the densest colony of our study area (Punta Tombo, 644 pairs/ha, from Yorio et al. 1998). All islands had lower numbers of breeding pairs than those they could accommodate in relation to their size (Wilcoxon matched-pairs rank test, $Z = -3.30$, $P = 0.001$). While the effect of island size constraining colony size is thus unclear, it is expected to reduce the strength of the potential relationship between colony size and density of conspecifics.

Statistical analyses

We used Generalized Linear Mixed Models (GLMM) to assess variability in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in relation to colony size and conspecific densities. GLMM allows one to incorporate random effects in the models and thus to generalize results to the whole population, not only to the data set analyzed (Littell et al. 1996). In our case, since some individuals belonged to the same colonies, we fitted colony as a random term in GLMM using SAS Macro program GLIMMIX (Littell et al. 1996). Previous research showed that $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$

values did not differ between the two years, but significant sexual differences existed in adults but not in chicks (Forero et al. 2002). Therefore, sex was included in the models for adults. Latitudinal trends in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values have been previously reported, with both isotopes decreasing with the latitude in northern and southern oceans (Rau et al. 1982, Best and Schell 1996). Although our sampled colonies were within a narrower range of latitude, the effect of this variable was tested by including it in the models. The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were normally distributed and thus were modeled using normal distribution of errors and the identity link function. Each explanatory variable (latitude, colony size, and densities of conspecifics measured at different foraging ranges) and their interactions were fitted to the observed data by following a forward stepwise procedure, which results in the most adequate model for explaining variation in the response variable where only significant effects are retained (e.g., Tella et al. 2001). Influences of diet quality on breeding success, offspring body condition, and immune response were tested by Spearman rank correlations between within-colonies mean values of $\delta^{15}\text{N}$ and the corresponding mean values of breeding performance. The same statistical test was used to assess the relationship between overall conspecific breeding densities and breeding success, and between colony size and density of conspecifics within different foraging ranges. Given the directionality of our predictions, we used one-tailed tests, except for the analyses of $\delta^{13}\text{C}$ values where a bi-directional response would be plausible (see *Introduction*).

RESULTS

Food depletion

Blood $\delta^{15}\text{N}$ values were available for 141 adults (71 males, 70 females). The GLMM for $\delta^{15}\text{N}$ values of adults showed that its variability was explained by sex ($F_{1,132} = 7.22, P = 0.004$), colony size ($F_{1,132} = 9.06, P = 0.001$), density of conspecifics within 100 km radius ($F_{1,132} = 13.68, P = 0.0001$) and the interaction between density of conspecifics and colony size ($F_{1,132} = 8.0, P = 0.002$), after controlling for birds sharing colonies. This model explained 34.4% of the original deviance, although alternative models substituting density of conspecifics at 100 km radius by density of conspecifics at 30 or 300 km were also significant and produced a change in the explained deviance of only 0.25%. These results show that the proportion of prey of high quality obtained by adults (as indicated by $\delta^{15}\text{N}$ values) decreased as both colony size and the density of conspecifics increased. In addition, the interaction in the model shows that differences in $\delta^{15}\text{N}$ values by colony size were lower in areas with high density of conspecifics (Fig. 2a).

The GLMM for $\delta^{15}\text{N}$ values in 98 fledglings revealed that, after controlling for birds sharing colonies, these

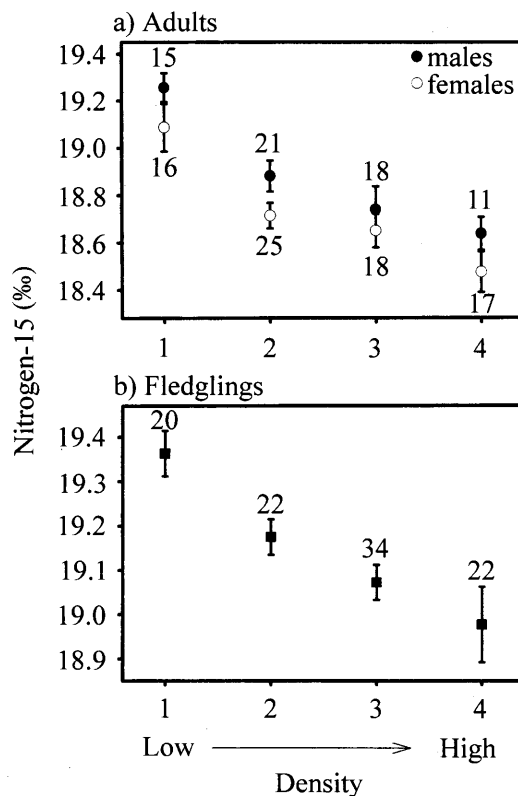


FIG. 2. Mean $\delta^{15}\text{N}$ values (± 1 SE) of (a) adults and (b) fledglings in relation to different intensity of conspecific competition. Categories of conspecific competition were calculated considering values lower and higher than the medians for colony size and conspecific breeding densities at 100 km radius as follows: numbers 1 and 3 = small colonies located in areas of low and high conspecific breeding density, respectively; 2 and 4 = large colonies located in areas of low and high conspecific breeding density, respectively.

values were negatively related to colony size ($F_{1,90} = 6.33, P = 0.007$) and to density of conspecifics at 100 km of foraging range ($F_{1,90} = 11.83, P = 0.0005$), with the interaction also significant ($F_{1,90} = 4.92, P = 0.01$). Fledglings raised in large colonies within areas of high conspecific density had the lowest $\delta^{15}\text{N}$ values, and differences in quality of diet between colonies of different sizes were smaller in areas of high density of conspecifics (Fig. 2b). This model explained 26.4% of the original deviance, being slightly higher than that explained by alternative significant models for density of conspecifics at 30 km (23.7%) and 300 km radius (25.6%). For adults and chicks latitude had no effect on their nitrogen isotope signatures ($P = 0.31$ and $P = 0.89$, respectively, in multivariate analyses).

Foraging strategy

The GLMM for $\delta^{13}\text{C}$ of adults included sex of individuals ($F_{1,131} = 7.05, P = 0.009$) after controlling for birds sharing colonies. In addition, adults from colonies in areas with high density of conspecifics at 300

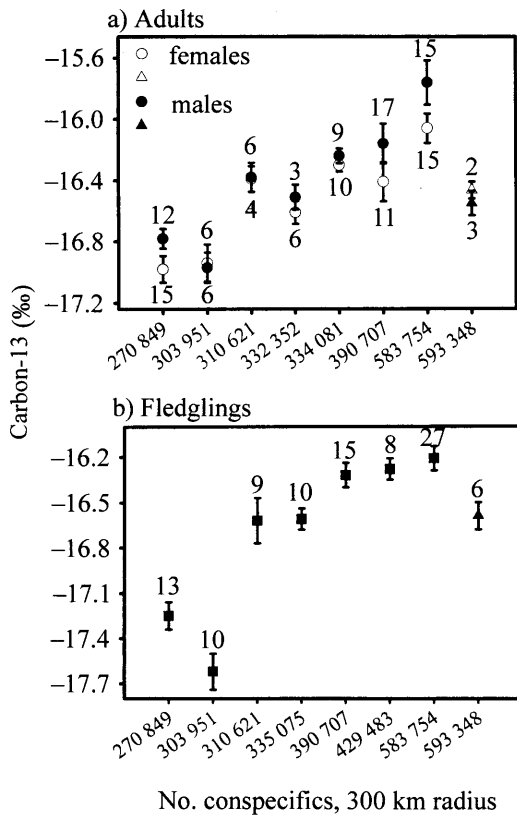


FIG. 3. Mean $\delta^{13}C$ values (± 1 SE) of (a) adults and (b) fledglings in relation to conspecific breeding density at 300 km radius. Individuals from Isla Arce are represented by triangles.

km radius foraged for themselves and their chicks more inshore (as indicated by higher $\delta^{13}C$ values of adults and chicks, respectively), although this tendency was only marginally significant ($F_{1,131} = 3.68$, $P = 0.057$ and $F_{1,90} = 3.60$, $P = 0.06$ for adults and fledglings, respectively). However, these trends were masked by the only sampled colony located on an offshore island (Isla Arce, Fig. 3), which clearly gave lower $\delta^{13}C$ values (France 1995, Hobson et al. 1995). When this colony was excluded, sex remained significant for adults ($F_{1,127} = 7.62$, $P = 0.006$) and the effect of density of conspecifics at 300 km was highly significant both for adults ($F_{1,127} = 10.91$, $P = 0.001$; Fig. 3a) and fledglings ($F_{1,85} = 5.19$, $P = 0.02$; Fig. 3b). These models explained 53.5% and 68.0% of the original deviance, respectively. Alternative, significant models including densities at 30 and 100 km radius were nearly identical, resulting in changes in the explained deviance of only 0.1%. As occurred for nitrogen, latitude did not influence carbon isotope values of adults and chicks ($P = 0.45$ and $P = 0.88$, respectively, in multivariate analyses).

Breeding performance

We found a positive correlation between within-colony means of breeding success and $\delta^{15}N$ values of

adults ($r_s = 0.77$, $P = 0.036$, $n = 6$ colonies) (Fig. 4a). In addition, within-colony means of body condition of fledglings strongly correlated with their $\delta^{15}N$ values ($r_s = 0.94$, $P = 0.002$) (Fig. 4b), indicating that those chicks fed with higher quality diets fledged with a better body condition. However, although we found a positive relationship between mean colony $\delta^{15}N$ values and within-colony means of cell-mediated immune response of fledglings, this relationship was not significant ($r_s = 0.26$, $P = 0.31$). Finally, we found that breeding at high densities negatively affected breeding success as revealed by negative correlations between breeding success and the overall conspecific breeding density, which were significant beyond 100 km radius (30 km: $r_s = -0.580$, $P = 0.114$; 100 km: $r_s = -0.912$, $P = 0.006$; 300 km: $r_s = -0.943$, $P = 0.002$).

Distribution and size of colonies

Initially, we found a negative correlation between colony size and number of conspecifics only at 300 km of foraging range ($r_s = -0.36$, $P = 0.03$, $n = 29$) (Fig. 5c). For shorter ranges the correlations tended towards zero (30 km: $r_s = 0.05$, $P = 0.40$; 100 km: $r_s = -0.18$, $P = 0.18$) (Fig. 5a, b). However, there were some small-to-medium size colonies sited in areas with low population breeding density (Fig. 5). These groups of colonies were those located in Península Valdés and Caleta Malaespina areas, respectively, which formed relative-

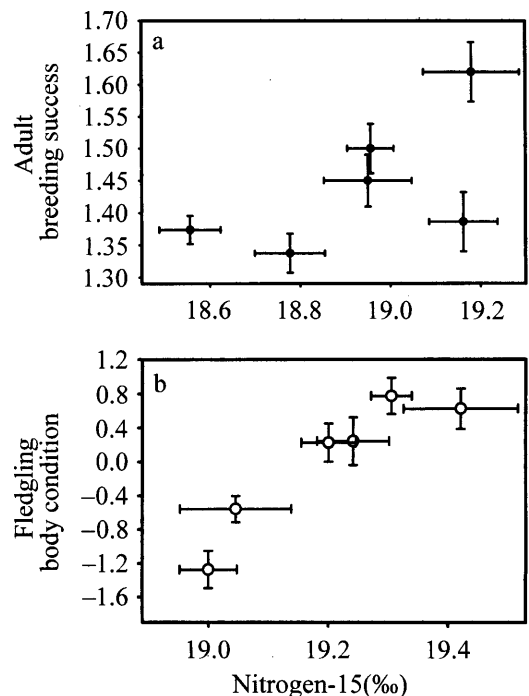


FIG. 4. Relationships between (a) within-colony mean $\delta^{15}N$ values of adults and mean breeding success by colony, and (b) within-colony mean $\delta^{15}N$ values of fledglings and their mean body condition. Means ± 1 SE are represented for each variable.

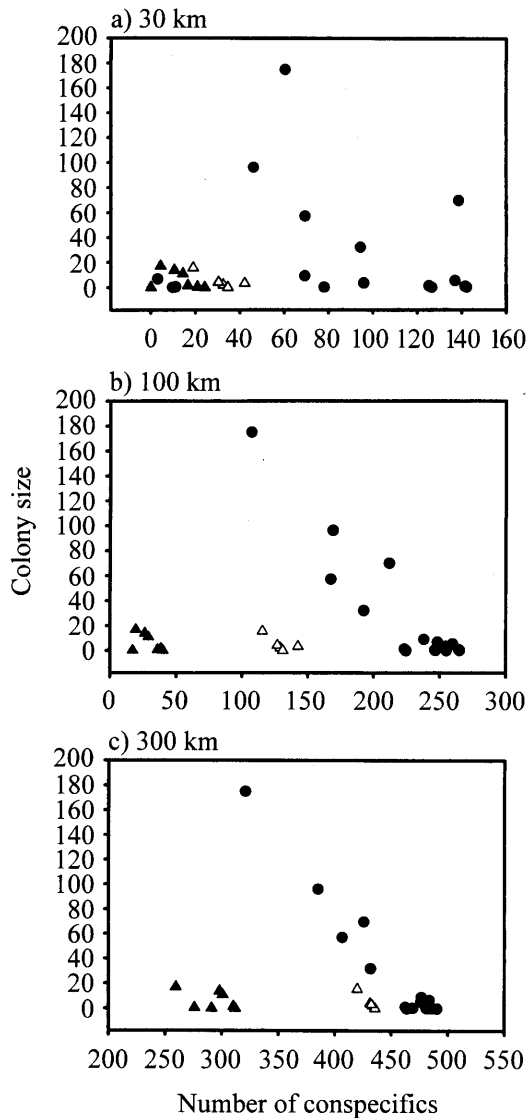


FIG. 5. Relationships between colony size (number of breeding pairs) and conspecific breeding density within foraging ranges at (a) 30 km, (b) 100 km, and (c) 300 km. Solid and open triangles correspond to colonies of Península Valdés and Caleta Malaespina, respectively. Both variables are indicated as total number of breeding pairs divided by 10^3 .

ly recently and have increased in size during the last two decades (Carribero et al. 1995, Yorio et al. 1998, P. Yorio, *personal communication*). Following Furness and Birkhead (1984), we repeated the analyses excluding these colonies, as they are too young and are probably well below a size that balances the number of conspecific competitors, which could mask the previous correlations. With this exclusion, correlation coefficients were negative for all foraging ranges (30 km: $r_s = -0.21$, $P = 0.22$, $n = 16$), being highly significant at 100 km ($r_s = -0.68$, $P = 0.002$, $n = 16$) and 300 km ($r_s = -0.72$, $P = 0.001$, $n = 16$) (Fig. 5). Moreover, within each one of these groups of growing colonies

the correlations between colony size and density of conspecifics at different foraging ranges were always negative for Península Valdés (range of $r_s = -0.43$ to -0.46 , range of $P = 0.15$ – 0.17 , $n = 7$ colonies) and even statistically significant for Caleta Malaespina ($r_s = -0.66$ to 1.00 , $P = 0.000$ – 0.08 , $n = 6$).

DISCUSSION

Here we provide strong evidence that conspecific competition for food affected the size and distribution of breeding colonies in a colonial bird, supporting Ashmole's hypothesis (1963). The first, and more novel, finding of our research is the evidence of depletion of high-quality food around colonies as revealed by $\delta^{15}\text{N}$ values. Although applications of this technique in ecological studies are increasing (e.g., Michener and Schell 1994, Hobson 1999, Kelly 2000), ours is the first one to test the food depletion hypothesis. Both colony size and density of conspecifics at different foraging ranges explained variability in $\delta^{15}\text{N}$ values in Magellanic Penguins. Higher values of $\delta^{15}\text{N}$ indicate that individuals are including in their diet a higher proportion of anchovy (Forero et al. 2002), a prey with shorter time for digestion, as well as a higher energy value and more protein than squid and other potential prey (Hislop et al. 1991, Cherel and Ridoux 1992, Hilton et al. 1998). Therefore, Magellanic Penguins living in large colonies and in colonies situated in areas with a high density of conspecifics tend to feed their offspring and themselves with prey of inferior quality. Differences in $\delta^{15}\text{N}$ values by colony size were slightly greater in areas of low than in areas of high population density. Therefore, at higher densities, where levels of conspecific competition could be above a given threshold, colony size could be less important in determining variation in the availability of high-quality prey. On the other hand, we found very small differences both in adults and chicks in the foraging ranges at which density of conspecifics determined the proportion of high-quality prey they included in their diet. Thus, depletion of food through conspecific competition is important at both short and long foraging distances, and affects both age classes of the population.

Magellanic Penguins living in areas of high densities of conspecifics showed more inshore foraging habits, as revealed by their higher $\delta^{13}\text{C}$ values. Although $\delta^{13}\text{C}$ analysis does not provide an exact measurement of foraging range, this trend could be explained by a constraint imposed by depletion of food at large foraging ranges. For other seabird species, it has been shown that in years of low food availability, individuals tend to forage farther from the colony (Monaghan et al. 1994). However, in Magellanic Penguins, 300 km could be the maximum distance that they could travel (Wilson et al. 1995), especially during the chick-rearing period, when food requirements are higher than during incubation. Thus, in areas with high conspecific breeding density, by foraging closer to the colonies on prey of

lower quality, adults could partially counterbalance the shortage of high-quality diet (as indicated by lower $\delta^{15}\text{N}$ values) with higher feeding frequencies (Monaghan et al. 1992). However, this reasoning should be considered with caution because our results could be influenced by potential geographic variation of $\delta^{13}\text{C}$ values of prey in relation to the distance from the colony.

The foraging range distance at which density of conspecifics more clearly provoked food depletion (up to 300 km) was much larger than the previously supposed mean distance of foraging for adults feeding their chicks (30 km, Wilson et al. 1995). However, Wilson et al. (1995) showed that foraging ranges during the incubation period extended up to 300 km. Therefore, the food depletion we have detected at fledging time may result from conspecifics foraging all along the breeding cycle, which extends for more than five months (Boersma et al. 1990).

Food depletion influenced two critical components of the breeding performance of individuals, namely the number and quality of offspring raised. Mean number of fledged chicks by colony was negatively affected by the proportion of diet of high quality that parents consumed, which was determined by the number of breeding conspecifics feeding within the parental foraging ranges. In other penguin species diet quality has been identified as a factor influencing growth rates (Heath and Randall 1985, van Heezik and Davis 1990). Tella et al. (2001) showed that large breeding densities within a 100 km radius in the same penguin population resulted in a reduction in fledgling body condition. We have determined now that these results are a direct consequence of depletion of high-quality food, as indicated by the negative relationship between penguin $\delta^{15}\text{N}$ values and density of conspecifics and the positive relationship between body condition of fledglings and $\delta^{15}\text{N}$ values. Tella et al. (2001) also suggested that the negative relationship they found between cell-mediated immune response and colony size could be due to depletion of high-quality food around the colonies. We found no support for this hypothesis, since the positive correlation between this measure of immunocompetence and $\delta^{15}\text{N}$ values in fledglings did not reach statistical significance. Therefore, other factors apart from food depletion associated with larger colonies, such as increased social stress, could also compromise the immunocompetence of fledglings (Tella et al. 2001). Initially, the negative relationship we found between body condition and $\delta^{15}\text{N}$ values could seem contradictory to the results found by Hobson et al. (1993). These authors showed that dietary stress in birds, both captive and in natural conditions, produced an increase in $\delta^{15}\text{N}$ values with food deprivation and stress. However, conditions of that study were of extreme stress, and in our population individuals probably are below the threshold that provokes body protein breakdown or catabolism

and the consequent increase of nitrogen isotope values in extremely stressed individuals (Hobson et al. 1993).

Conspecific food depletion was a previously untested mechanism, which was assumed to cause the negative relationships between colony size and conspecific population density found in birds (Furness and Birkhead 1984, Griffin and Thomas 2000). This negative relationship was also found in Antarctic penguins (Ainley et al. 1995), although these authors argued against the prey depletion hypothesis as the cause of this population structure because, contrary to more temperate regions, food supplies during the breeding season are supposed to be superabundant in the South Polar region. We have demonstrated that food depletion resulting from conspecific competition occurs around penguin colonies in a temperate region, and that it affects breeding performance of individuals. Despite the lack of accurate data on fledgling survival, dispersal, and recruitment rates for this species, in a scenario of high philopatry (as generally suggested for penguins, Williams 1995), differences in breeding success and offspring viability among colonies, ultimately driven by food depletion, could explain the actual colony size structure in this population. Accordingly, colony sizes of Magellanic Penguins vary inversely with the number of conspecifics breeding within parental foraging ranges, being highly significant at 100 and 300 km radius. Additionally, we found evidence that food depletion could be beginning to act in two groups of colonies of recent formation.

To our knowledge, this study is the first to show a link between conspecific food depletion, breeding performance, and the resulting population structure in colonial birds. This finding is not only important for a better understanding of both population regulation in seabirds and variability in avian colony size, but also has potential implications in conservation. Given the increasing interference of commercial fisheries with seabird trophic requirements (e.g., Furness and Cooper 1982, Furness and Tasker 2000), fishing activities intended to be compatible with seabird conservation should take into account not only their potential effects on the nearest colonies, but also on the whole metapopulation where conspecific food depletion is acting.

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