Factors driving Adélie penguin chick size, mass and condition at colonies of different sizes in the Southern Ross Sea

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ABSTRACT: Body size, mass and condition can affect an organism's ability to cope with variation in resource availability or metabolic demand, particularly as juveniles reach independence. It follows that changes to parental provisioning efficiency (size and frequency of meals) through intraspecific competition or environmental conditions that affect prey availability may affect chick size, mass and condition and ultimately post-fledging survival. We examined how Adélie penguin chick size, mass and condition varied among colonies of different sizes on Ross Island during a 15 yr period of high environmental variability and varying intraspecific competition. Aiding the study was a natural experiment in which the presence of 2 giant icebergs midway through the study abnormally increased sea ice concentration (SIC), altering adults' access to food. Concurrently, the colonies were rapidly increasing in size; based on previous work, this indicated increased trophic competition near colonies, a trend likely indicating a changing food web in the greater region. Results showed that increased amounts of sea ice, which reduced the ability of adults to access food, had a negative effect on the size and mass of chicks. However, a greater proportion of fish (vs. krill) in the diet had a positive effect on chick size. Moreover, in some cases, increased intraspecific competition may be a more important driver of provisioning rate and chick size than abiotic factors, with chicks showing the effects of reduced food delivery at larger colonies. Understanding these patterns will allow better understanding of how factors such as climate change and altered food webs may affect Adélie penguin populations.

KEY WORDS: Adélie penguin · Chick growth · Diet variability · Provisioning efficiency · Intraspecific competition

INTRODUCTION

Energy reserves, as judged by the ratio of body mass to body size, may be important determinants of an organism's potential fitness and ultimately affect survivorship (Schulte-Hostedde et al. 2005). A high body mass or good condition may buffer against periods of low resource availability or high metabolic demand, enabling individuals to use stored energy reserves to survive short periods of stress (Ballard et al. 2010). Such effects may be particularly important for naïve juveniles when they first become independent of their parents and must learn to forage for themselves (Stienen & Brenninkmeijer 2002). In such situations, young that have a high body mass and/or are in good condition may be expected to have higher survival rates, and therefore be more likely to recruit into the breeding population (Sagar & Horning 1998, Kitaysky et al. 2006).

Body condition is likely to be strongly influenced by a range of abiotic (Schreiber 2001) and biotic (Lilliendahl 1998, Wanless et al. 2005) factors. For example, variable climatic regimes may be metabolically costly, with individuals using proportionally more energy for body maintenance and survival, thus reducing the energy that can be allocated to growth (Yoda & Ropert-Coudert 2007, Chapman et al. 2011). Periods of environmental perturbation may also change patterns of prey abundance, quality or accessibility, leading to reduced foraging efficiency (Ballard et al. 2010, Lescroël et al. 2010, 2014). Finally, reduction in the prevalence of both inter- and intraspecific trophic competitors can lead to increased availability of prey and thus increased foraging efficiency (Ainley et al. 2004, 2006, 2007, Lyver et al. 2011, Trathan et al. 2012). As noted in those studies and expanded below, changes in colony size as well as the increased prevalence of marine mammals foraging on the same prey can negatively alter provisioning efficiency (the amount of food delivered to chicks per unit time) and colony productivity.

Reduced provisioning efficiency has been shown to negatively impact chick meal sizes, chick growth, and fledging mass in some seabird species (e.g. Cruz & Cruz 1990, Williams & Croxall 1990, Wanless et al. 2005, Ballard et al. 2010) as adults prioritise self-maintenance over chick provisioning. However, there is also evidence that some species are able to compensate for stressful conditions by modifying adult or chick behaviours to maximise the benefits of available resources (Weimerskirch et al. 1995, Waugh et al. 2000, Ballard et al. 2010). Individuals may alter the timing of breeding, switch to alternate prey or change the timing or frequency at which chicks are fed to buffer the effects of environmental stress (Vinuela et al. 1996, Salihoglu et al. 2001, Chapman et al. 2011).

The foraging efficiency of Adélie penguins *Pygoscelis adeliae* is strongly influenced by changes in environmental conditions, particularly the sea ice concentration (SIC) within their foraging area (Emmerson & Southwell 2008, Ballard et al. 2010, Lescroël et al. 2010, 2014, Cottin et al. 2012). Adélie penguins are sea ice obligates, generally existing in areas of intermediate SIC where there is adequate ice for resting and facilitating the ice-associated food web, but not so much that individuals incur additional energetic cost associated with walking great distances between colonies and foraging areas (Ainley 2002, Emmerson & Southwell 2008). Indeed, adult Adélie penguins on Ross Island exhibit longer foraging trips and deliver less food to their chicks during periods of high SIC as a result of reduced access to prey (Ballard et al. 2010). Adélie penguin diet composition also varies with SIC, as crystal krill *Euphausia crystallorophias* are more prevalent than subadult silverfish *Pleuragramma antarcticum* when SIC is high (Ainley et al. 2003). Adult krill typically have a lower calorific value than subadult silverfish, which may further exacerbate the effects of reduced provisioning efficiency during periods of high SIC (Ainley et al. 2003).

Inter- and intraspecific competition can also affect prey availability to penguins. Parents make increasingly longer foraging trips throughout the breeding season at large colonies due to progressive prey depletion (Ainley et al. 2004, Ballance et al. 2009, Ford et al. 2014). Similarly, the arrival of cetaceans in the foraging areas correlates with longer penguin foraging trips as well as changes in penguin diet (Ainley et al. 2006). Finally, the removal of trophic competitors, such as minke whales *Balaenoptera bonaerensis* and more recently Antarctic toothfish *Dissostichus mawsoni*, correlates with periods of increased Adélie penguin population growth (Ainley et al. 2007, 2013, Lyver et al. 2014).

It has also been shown that Adélie penguin adults, particularly those beginning the breeding season in relatively better condition, may allocate a greater proportion of captured prey toward chick provisioning than to their own needs and thus sacrifice their own condition in favour of chick growth (Salihoglu et al. 2001, Ballard et al. 2010). Adults may alter the frequency of food delivery and food quality, while chicks can adjust metabolic processes to match provisioning rates (Salihoglu et al. 2001). Indeed, fledg-

ing mass of Adélie penguin chicks (2.8 to 3.2 kg) from colonies around Anvers Island, Antarctica, remained relatively constant over 25 yr despite significant variability in the abundance of their primary prey resource, Antarctic krill *Euphausia superba* (Salihoglu et al. 2001), indicating that compensatory mechanisms were likely important. In contrast, fledging mass of chicks gradually decreased over a 15 yr period at colonies farther north on the Antarctic Peninsula, in association with decreasing Adélie populations and a supposed decrease in krill availability (Hinke et al. 2007). The higher concentration of fish in the Anvers Island penguins' diet appeared to be a compensatory factor in chick provisioning (Chapman et al. 2011). Despite decreases in the population size of northern colonies, modelling has shown that there was sufficient abundance of krill, but perhaps not fish, necessary to maintain these Adélie penguin colonies along the western Antarctic Peninsula (Sailley et al. 2013).

In this study, we examined how Adélie penguin chick size, mass and condition varied among 3 breeding colonies of different sizes on Ross Island over 15 breeding seasons during a period of high environmental variability. We hypothesised that chick size, mass and condition would be dependent on environmental conditions and the intraspecific competition that adults experience while provisioning their chicks. Alternatively, the hypothesis that chick size, mass, or condition do not vary with environmental conditions or competition would imply that Adélie penguins are able to alter their chick provisioning behaviours and compensate for a wide range of conditions, as has been shown previously over shorter time periods (Salihoglu et al. 2001, Ballard et al. 2010). Herein, we follow Lewis et al. (2001) and subsequent authors in defining intraspecific competition as increased pressure on the availability of prey as a function of inter- and intra-colony variation in size.

The presence of 2 giant icebergs (B-15 and C-16), the largest the size of Jamaica, grounded off the coast of Ross Island between January 2001 and July 2006 provided a large-scale 'natural experiment.' During this experiment, SIC increased to an unusual degree within the summer foraging areas of 2 of the colonies, where the SIC was already highly variable (Fig. 1a); the foraging areas, location of icebergs, and effect on SIC are shown by images in Dugger et al. (2014) and Ford et al. (2014). At the third colony, the presence of the giant icebergs precluded foraging within the marginal ice zone (MIZ) of the Ross Sea Polynya, a highly productive area (Ballard et al. 2010,

Dugger et al. 2014, Lescroël et al. 2014). In addition, a fishery for Antarctic toothfish (a direct trophic competitor of Adélie penguins for silverfish) was initiated in the first year of our study (peaking in catch around 2004, remaining relatively constant thereafter) and corresponded with the disappearance of large fish in southern Ross Sea waters (Ainley et al. 2013). We investigated whether the size, mass and condition of chicks varied with provisioning efficiency, diet composition (% fish), intraspecific competition among parents (colony size), breeding output (no. of chicks per pair), as well as abiotic environmental conditions (iceberg presence, SIC). The present paper and that by Dugger et al. (2014) are complementary, with the present paper addressing in much greater detail the subject of chick growth. We evaluated the following 3 general predictions, parsing each into specific predictions (see 'Materials and methods'): (1) Chick size and mass will be greater, and condition will be better, when provisioning efficiency is high, SIC is low, and fish are dominant in the diet. (2) Chick size and mass will be greater, and condition will be better, in breeding seasons with low intraspecific resource competition. We expect greater intraspecific resource competition among foraging parents to be associated with large breeding populations and high breeding output (more chicks produced per pair). (3) Sibling chicks will be most similar in size, mass and condition in breeding seasons with low intraspecific resource competition (measured as in prediction 2).

Understanding the mechanisms that determine the size, mass and condition of Adélie penguin chicks, and thus their subsequent survival and recruitment, will allow for better predictions of the future size and distribution of Adélie penguin colonies under rapidly changing environmental conditions in the Ross Sea (Ainley et al. 2010).

MATERIALS AND METHODS

Field site

Fieldwork was conducted at Cape Royds (77° 34′ S, 166° 11′ E), Cape Bird (77° 13′ S, 166° 28′ E) and Cape Crozier (77° 27′ S, 169° 23′ E) on Ross Island, southwestern Ross Sea (see maps in Ainley et al. 2004, Shepherd et al. 2005, Ford et al. 2014). These colonies comprise ~9% of the global Adélie penguin population (Lynch & LaRue 2014) and vary in size by 3 orders of magnitude (range in number of breeding pairs at each colony during this study: Cape Royds 1300 to 3900; Cape Bird 23 000 to 69 000; Cape
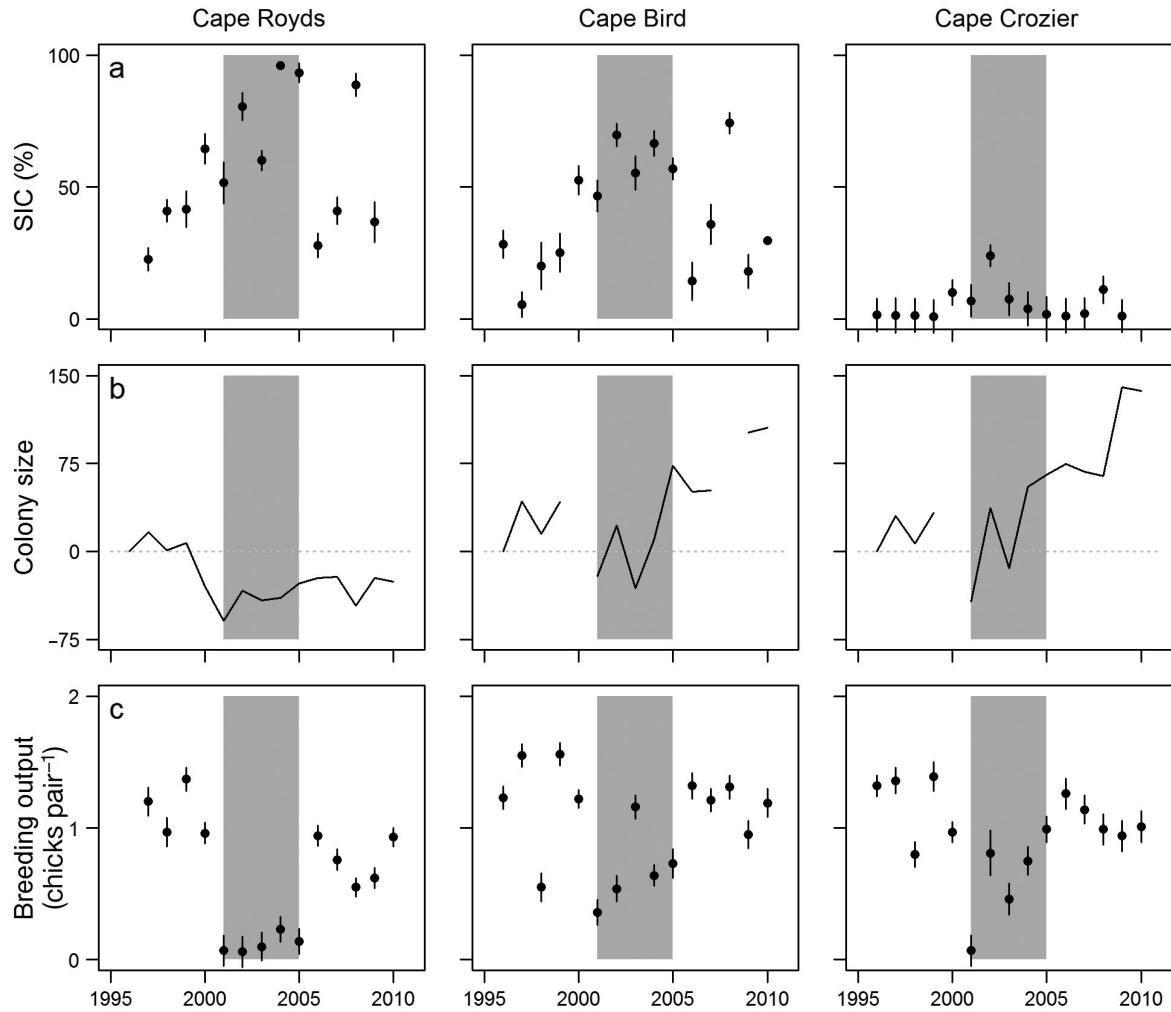
Fig. 1. Mean annual trends in (a) sea ice concentration (SIC), (b) colony size and (c) breeding output for Adélie penguins at 3 colonies on Ross Island. Colony size data represent the relative change in the number of breeding pairs at a given colony relative to 1996, with colonies arranged in order of increasing size from left to right (size in 1996: Cape Royds = 3378, Cape Bird = 33286, Cape Crozier = 117675 pairs). The presence of the giant icebergs is indicated by the shading. Error bars represent standard errors. Further details on each of the metrics can be found in Table 1 and 'Materials and methods'

Crozier 67 000 to 282 000; Fig. 1b, see also Lyver et al. 2014). Ainley (2002) summarized the annual cycle. Breeding Adélie penguins begin to arrive at Ross Island colonies in late October, with females typically laying 2 eggs by mid-November. Chicks hatch in mid-December and remain at the colony until mid-February. One parent remains with the chick(s) during the guard stage while the second parent forages at sea. Parents switch roles every 1 to 3 d, with chicks fed small meals by the guarding parent. Once chicks are approximately 3 wk old, they are left unguarded and begin to crèche (form groups of chicks independent of nests) as both parents need to forage to provide sufficient food. Chicks typically fledge when they are 7 to 8 wk old. Our study period included most of

chick-rearing, from the early guard stage (late December) through late crèche (late January), for 15 austral summers (1996–1997 to 2010–2011). Hereafter, we refer to austral summers using the initial year (i.e. 1996 refers to the breeding season beginning in October 1996 and ending in February 1997).

Weighing and measuring chicks

Once a week, beginning on 26 December at Cape Bird and between 1 and 3 January at Capes Crozier and Royds and ending 23 to 28 January, we selected approximately 50 Adélie penguin chicks (25 at the much smaller Royds) for inclusion in the study.

Chicks were selected randomly, with different parts of the colonies used during each sampling period; thus no chick was measured twice. During the first 2 wk chicks were in nests, and thereafter more and more chicks were in crèches. When 2 chicks were present in a nest, both chicks were captured for measurement, and their sibling status recorded. Captured chicks were weighed and had their left flipper measured before being returned to the nest or crèche. Sampling ended once 50 individuals had been processed. The actual age of sampled chicks was not known. Instead, we estimated the approximate age of chicks in each sampling period relative to the estimated date when 50% of nests within closely monitored reference colonies had hatched. Estimates of the median hatch date were calculated separately for each breeding season and colony and ranged from 13 December to 1 January, with chicks typically hatching first at Cape Crozier, then Cape Bird and finally Cape Royds (Dugger et al. 2014). Thus, the median age of chicks in a given sampling period is estimated in weeks since peak hatch ('week').

Calculating chick condition

We calculated chick condition using the Scaled Mass Index (SMI), a robust condition index that accounts for differences in the ratio of size to mass that may occur at different body sizes and which may be functionally important independent of an individual's energy stores (Peig & Green 2009). In this study we use flipper length as a proxy for skeletal size. We performed a standardised major axis regression (SMA) on log-transformed mass and flipper length. Then we used the slope from this regression to calculate condition using:

$$\text{SMI}_i = M_i \left[\frac{F_0}{F_i} \right]^{b_{\text{SMA}}} \quad (1)$$

where M_i and F_i are the body mass and flipper length, respectively, of individual i, b_{SMA} is the slope of the SMA regression of M on F, and F_0 is the mean flipper length of all sampled chicks. Therefore, the condition score of an individual chick (SMI_i) is their predicted body mass (g) when their flipper length has been standardized to F_0. High condition scores indicated individuals that were considered to be in good condition (i.e. they are heavier in mass than predicted for their structural size).

For all nests that contained 2 chicks at the time of measurement, we randomly selected the data from 1 chick to ensure there were no issues of dependence in the statistical analyses. In addition, we calculated the absolute differences in sibling size (size_{sib}), mass (mass_{sib}) and condition ($\text{condition}_{\text{sib}}$) for each nest. Siblings could not be identified once chicks reached the crèche stage.

Biotic explanatory variables

Parameters relating to adult provisioning efficiency at each of the 3 colonies were estimated from a small subcolony (~200 pairs) enclosed by a fence, where the only access in and out was over an automated weighbridge system consisting of a scale, direction sensor, and radio-frequency identification reader connected to a data logger (see Ballard et al. 2001 for more details). A subset of breeding individuals (25 to 59 individuals at Cape Crozier, 3 to 93 at Cape Bird, and 16 to 74 at Cape Royds, depending on breeding season) within each of these subcolonies were implanted with passively integrated transponders, providing unique identification. If sample size was low at the beginning of a breeding season, we implanted transponders in additional, randomly selected individuals as needed. Each time a penguin crossed the weighbridge, the bird identification, date and time, direction of travel, and body mass were recorded automatically (Ballard et al. 2001). These data provided a measure of the frequency with which parents visited their chicks as well as the amount of food delivered, allowing the calculation of provisioning efficiency. For each parental foraging trip, provisioning efficiency was calculated as the amount of food (g) brought back to the colony by an adult (calculated as a parent's incoming mass minus its mass on the subsequent departure, i.e. including both the food delivered to the chicks and the food digested by the adult when attending the nest) divided by the duration of the foraging trip (min) (also referred to as catch per unit effort in previous publications; see Ballard et al. 2010, Lescroël et al. 2010, 2014 for more details). As the latter studies note, over the course of the breeding season parent mass does change, but not radically within the time of a single foraging trip. Parents that return quickly from foraging feed their chicks more often (Salihoglu et al. 2001, Chapman et al. 2011). This is especially true once chicks are in the crèche, with parents returning to sea immediately after feeding their chick(s) once, rather than small sequential feeds when guarding smaller chicks. These data were summarised to provide a weekly mean estimate of provisioning efficiency for each

breeding season and colony corresponding to the same time periods in which the chicks were measured. Provisioning efficiency data were only available from 1996 through 2006.

Diet composition was estimated using data obtained by multiple methods: (1) stomach flushing samples (1996 to 2005; n = 4 to 56 colony^{-1} breeding season^{-1}), (2) observing chick feeding events using binoculars to assess prey species (fish: grey colour; krill: pink) passed from adult to chick (2001 to 2010; n = 2 to 541 colony^{-1} breeding season^{-1}), (3) dissecting the stomachs of chicks killed by south polar skuas *Stercorarius maccormicki* (2000 to 2010; n = 1 to 78 colony^{-1} breeding season^{-1}), and (4) noting food spilt around nests (2000 to 2010; n = 1 to 95 colony^{-1} breeding season^{-1}) (see Ainley et al. 2003, 2006 for further details). The stomach sampling and chick stomach dissections indicated that >95% of the diet was composed of Antarctic silverfish and crystal krill, making the more general results of the visual sampling suitable for our purposes (approximate proportion of fish vs. krill, also confirmed by stable isotope analysis of chick tissues: Ainley et al. 2003). These data were summarised to provide a weekly mean approximation of the proportion of fish ('fish') in the diet for each breeding season and colony.

The mean number of chicks produced per pair at each colony was estimated each breeding season as a measure of breeding output (Dugger et al. 2014). The number of breeding pairs on active nests in a specified set of subcolonies was counted during late incubation (25 November to 8 December), when a minimum number of adults are present (Taylor et al. 1990, Ainley 2002). We then counted the number of chicks present in the same subcolonies once most chicks had entered crèche (15 to 20 January). Breeding output in each subcolony was calculated as the ratio of chicks to active nests, with mean values estimated for each colony in each breeding season ('breeding output').

We used aerial photography to estimate the number of occupied territories present at each colony ('colony size'; Lyver et al. 2014). The colonies were overflown by helicopter and photographed; the resulting images were of sufficient resolution to clearly identify individual penguins. Flights were carried out within a few days of 1 December (depending on weather; 25 November to 8 December) when the population was composed of single birds incubating eggs and very few non-breeders (Taylor et al. 1990, Ainley 2002). The number of occupied territories were counted to provide an index of the breeding pairs present at the colony.

Abiotic explanatory variables

Sea ice concentration (SIC) was calculated as the % ice cover within the potential foraging area of each colony (Ballard et al. 2010) as measured weekly by passive microwave imagery using the Special Sensor Microwave/Image (SSMI, Cavalieri & Comiso 2004). The potential foraging area was determined as the polygon that contained 95% of at-sea positions of provisioning parents as determined by radio and satellite telemetry from 1997 to 2006 (Ainley et al. 2004, 2006, D. G. Ainley unpubl. data). These are shown visually in Dugger et al. (2014) and Ford et al. (2014). The area that the giant icebergs (B-15 and C-16; Robinson & Williams 2012) occupied within the foraging area was omitted from the SIC calculation because this area was never available for foraging, and because the presence/absence of the giant icebergs in each breeding season was accounted for using a separate explanatory variable. The icebergs did not arrive until after the crèche period in the 2000 breeding season (see maps in Ainley et al. 2004, Shepherd et al. 2005, Ballard et al. 2010), thus we considered this breeding season to be a 'non-iceberg season'. The icebergs departed in July 2006, and thus 2006 was the first breeding season free of their presence.

Statistical analyses

Our specific predictions were tested by evaluating the relationships between dependent and explanatory variables (Table 1) using mixed effects models constructed with the 'nlme' package (Pinheiro et al. 2012) in R v.2.15.0 (R Development Core Team 2012). Further details of the specific predictions and models are given below and in Table 2. Prior to analysis, we assessed the relationships between all explanatory variables to ensure that they were not correlated. We examined all possible additive combinations of the fixed explanatory variables for each prediction using the 'MuMIn' package (Barton 2012), ranking the models by their corrected Akaike's Information Criterion (AIC$_c$) score. Models within 2 AIC$_c$ (Δ_i) of the best model value (referred to herein as the top model set) were deemed to be potentially relevant and examined for alternate explanations. Given that different combinations of parameters may have varying ecological interpretations, we only report effect sizes for the best fitting model (i.e. the lowest AIC$_c$ score) rather than model-averaged estimates, thus identifying the best combination of parameters that described each dependent variable. Due to the diffi-

Table 1. Parameters measured and included in models describing Adélie penguin chick condition and mass on Ross Island. Means ± SE and ranges for the earliest to latest weekly measurements are calculated across all colonies and breeding seasons. Further information about how each parameter was calculated is provided in 'Materials and methods'

Parameter	Description	Mean ± SE (Range)
Response variables		
Size	Flipper length of Adélie penguin chicks (mm)	138.7 ± 0.5 (25, 216)
Mass	Mass of Adélie penguin chicks (g)	1984.8 ± 12.3 (50, 5000)
Condition	Condition of Adélie penguin chicks calculated using the scaled mass index, SMI (g)	1789.1 ± 3.8 (786, 2803)
$Size_{sib}$	Difference in flipper length between siblings from the same nest (mm)	14.7 ± 0.4 (0, 77)
$Mass_{sib}$	Difference in mass between siblings from the same nest (g)	256.1 ± 7.0 (0, 1400)
$Condition_{sib}$	Difference in condition between siblings from the same nest (g)	270.7 ± 7.6 (0, 1986)
Food availability and quality		
Provisioning efficiency	Mean catch per unit effort at each colony per week (g min^{-1})	0.46 ± 0.003 (0.02, 1.58)
Fish	Mean proportion of the diet comprised of silverfish per week (%)	43.8 ± 0.4 (0.0, 100.0)
Competition		
Colony size	Number of breeding pairs present at each colony each breeding season	65 270 ± 8409 (1367, 282 515)
Breeding output	Mean number of chicks produced per pair in each breeding season (chicks pair^{-1})	0.89 ± 0.07 (0.06, 1.56)
Environmental conditions		
Sea ice concentration (SIC)	SIC per week (% of foraging area at each colony covered by sea ice)	33.5 ± 2.2 (0.0, 99.8)
Iceberg	Y/N, whether giant icebergs were present	Present: 2001−2005

Table 2. Predictions regarding relationships between dependent variables and covariates for Adélie penguin chicks at 3 colonies on Ross Island, Antarctica. Detailed explanations of the parameters are given in Table 1 and 'Materials and methods'

General prediction	Specific prediction: dependent variables	Predicted effects
1. Chick size and mass will be greater, and condition better, when provisioning efficiency is high, SIC is low and fish are dominant in the diet	1.1 Size 1.2 Mass 1.3 Condition	$\beta_{provisioning\ efficiency} > 0$ $\beta_{fish} > 0$ $\beta_{ln(SIC)} < 0$ $\beta_{age} > 0$ β_{colony} (variable) $\beta_{colony} \times \beta_{ln(SIC)}$ (variable) Random variable: week since peak hatch|breeding season
2. Chick size and mass will be greater, and condition better, in breeding seasons with low intraspecific resource competition	2.1 Size 2.2 Mass 2.3 Condition	$\beta_{iceberg} < 0$ $\beta_{colony\ size} < 0$ $\beta_{breeding\ output} < 0$ Random variable: week since peak hatch
3. Siblings will be most similar in size, mass and condition, in breeding seasons with low intraspecific resource competition	3.1 $Size_{sib}$ 3.2 $Mass_{sib}$ 3.3 $Condition_{sib}$	$\beta_{iceberg} < 0$ $\beta_{colony\ size} < 0$ $\beta_{breeding\ output} < 0$ Random variable: week since peak hatch

culty in correctly estimating residual degrees of freedom in mixed effects models, we used 95% confidence intervals, and whether or not they included zero, to evaluate strength and direction of effects (Bolker et al. 2009). Throughout this paper, all means are provided ±SE.

Prediction 1: Chick size (1.1) and mass (1.2) will be greater, and condition (1.3) will be better when provisioning efficiency is high, SIC is low and fish are dom-inant in the diet. We evaluated whether chick size, mass and condition varied weekly with the adult provisioning efficiency and diet quality ('fish'), as well as the role of SIC (ln[SIC]) and SIC–colony interactions (ln[SIC]:colony), in modifying the relationships. We included week since peak hatch within breeding season as a random effect. These analyses were restricted to data collected between 1998 and 2006 due to missing data in the provisioning efficiency dataset.
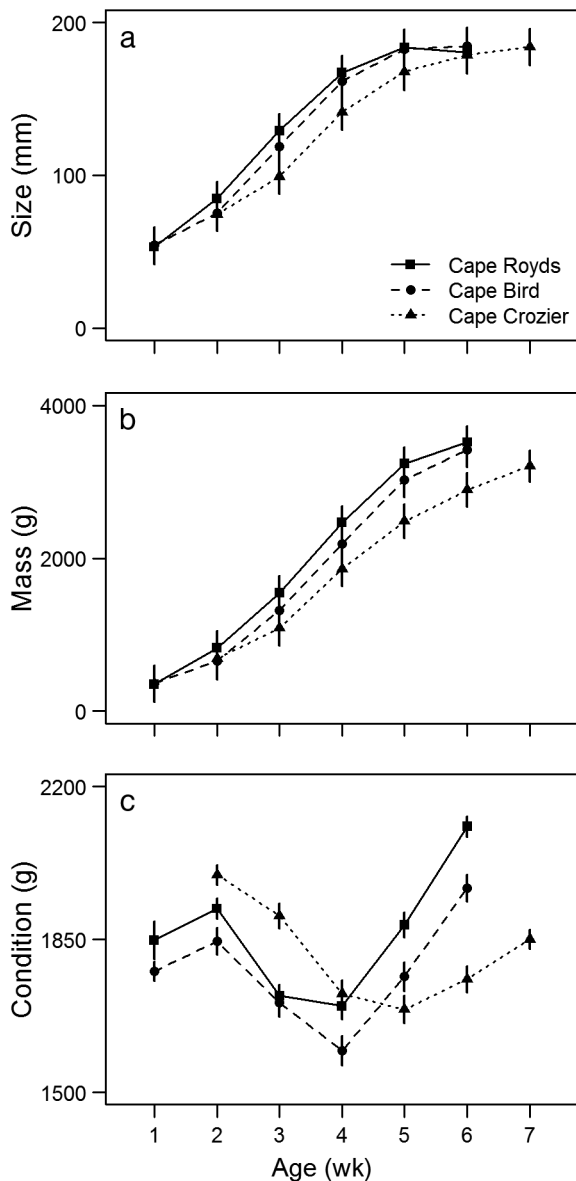
Fig. 2. Mean weekly relationships between (a) size (as measured by flipper length), (b) mass and (c) condition of Adélie penguin chicks. Data are summarised by age (week since peak hatch) across all breeding seasons sampled. Error bars: ± SE. Further details on each of the metrics can be found in Table 1 and 'Materials and methods'

Prediction 2: Chick size (*2.1*) *and mass* (*2.2*) *will be greater, and condition* (*2.3*) *will be better in breeding seasons with low intraspecific resource competition.* We evaluated how chick size, mass and condition varied between breeding seasons, using colony size, breeding output and iceberg presence as proxies for resource competition among parents. We included week as a random effect to account for variable peak hatch date.

Prediction 3: Sibling chicks will be most similar in size (*3.1*), *mass* (*3.2*) *and condition* (*3.3*) *in breeding seasons with low intraspecific resource competition.* We evaluated whether differences in sibling size, mass and condition varied between breeding seasons using colony size, breeding output and iceberg presence used as proxies for resource competition. We included week as a random effect to account for variable peak hatch date.

RESULTS

A total of 8693 Adélie penguin chicks were weighed and measured among the 3 colonies on Ross Island between 1 January 1997 and 28 January 2011 (Royds: 1801, Bird: 3588, Crozier: 3304). Chick mass ranged from 50 to 5000 g (mean ± SE: 1758.0 ± 18.3 g) over the length of the breeding season, while size (measured as flipper length) varied from 25 to 216 mm (138.7 ± 0.5 mm; Table 1, Fig. 2). Using the mean flipper length as F_0, our estimates of condition based on the SMI ranged from 786 to 2803 g (1733.8 ± 6.8 g) over the entire breeding season. Just prior to fledging when chicks were approximately 5 wk old, chick size ranged from 71 to 216 mm (176 ± 0.4 mm), with chicks being a similar size at all 3 colonies (Fig. 2). Chick mass varied from 500 to 4850 g (2589 ± 17.2 g), with chicks notably smaller at Cape Crozier than the other sites. Similarly, chick condition at 6 wk was lowest at Cape Crozier and highest at Cape Royds, with condition pooled across the sites ranging from 806 to 2801 g (1761 ± 7.4).

Prediction 1.1: Chick size will be greater when provisioning efficiency is high, SIC is low and fish are dominant in the diet. Chick size varied among colonies, with chicks smaller for their age at Cape Crozier compared with Capes Bird and Royds (Table 3). Chick size was negatively correlated with ln(SIC), with this effect strongest at Cape Bird and Cape Royds. The proportion of fish in the diet had a positive effect on chick size, independent of the fact that a greater proportion of the diet was composed of fish later in the breeding season when chicks were necessarily larger. Provisioning efficiency had a positive effect on chick size in several competitive models (<2 AIC$_c$) but was not included in the best model (see the Appendix).

Prediction 1.2: Chick mass will be greater when provisioning efficiency is high, SIC is low and fish are dominant in the diet. (Fig. 2, Table 3). There was a negative relationship between chick mass and ln(SIC), and this relationship was strongest at Cape

Table 3. Estimates of parameter coefficients from the top model for each predic-tion. Detailed explanations of the parameters and predictions are given in Tables 1 & 2 and 'Materials and methods'. For Models 1.1, 1.2, and 1.3, colony coeffi-cients are presented relative to Cape Crozier, whose mean value for a given dependent variable is therefore given by the intercept coefficient. SIC: Sea ice concentration; Y: yes (i.e. iceberg present)

Model	Parameter	Coefficient	SE	95% CI
1.1 Size	Intercept	100.46	6.94	86.86, 114.07
	ln(SIC)	−13.22	1.47	−16.09, −10.35
	Fish	0.063	0.031	0.002, 0.124
	Colony = Bird	60.55	4.59	51.55, 69.55
	Colony = Royds	66.08	6.09	54.14, 78.02
	ln(SIC):colony = Bird	−11.27	2.25	−15.68, −6.86
	ln(SIC):colony = Royds	−8.26	2.74	−13.64, −2.89
1.2 Mass	Intercept	744.92	165.23	420.93, 1068.1
	ln(SIC)	−34.96	4.35	−43.49, −26.44
	Colony = Bird	1184.09	114.68	959.22, 1408.95
	Colony = Royds	1294.15	127.90	1043.36, 1544.95
	ln(SIC):colony = Bird	21.70	3.33	15.16, 28.23
	ln(SIC):colony = Royds	25.91	3.87	18.32, 33.50
1.3 Condition	Intercept	1896.12	46.39	1805.16, 1987.08
	Colony = Bird	−398.02	54.68	−505.25, −290.8
	Colony = Royds	−214.89	74.67	−361.30, −68.48
	ln(SIC)	74.89	16.53	42.48, 107.30
	Provisioning efficiency	−195.35	68.32	−329.31, −61.39
	ln(SIC):colony = Bird	111.95	29.62	53.87, 170.03
	ln(SIC):colony = Royds	−57.16	35.09	−125.96, 11.65
2.1 Size	Intercept	138.92	21.56	96.67, 181.18
	Iceberg = Y	−9.81	0.82	−11.42, −8.21
	Colony size	−0.000113	0.000004	−0.00012, −0.00011
	Breeding output	3.46	1.00	1.51, 5.42
2.2 Mass	Intercept	2083.55	485.97	1130.90, 3036.20
	Iceberg = Y	−343.50	21.03	−384.73, −302.27
	Colony size	−0.0032	0.0001	−0.0033, −0.0030
	Breeding output	−127.76	25.56	−177.86, −77.66
2.3 Condition	Intercept	1820.29	30.21	1761.07, 1879.50
	Iceberg = Y	−86.05	12.02	−109.60, −62.49
	Breeding output	−174.37	14.31	−202.42, −146.31
3.1 $Size_{sib}$	Intercept	13.87	1.84	10.27, 17.48
	Breeding output	4.06	0.97	2.16, 5.97
3.2 $Mass_{sib}$	Intercept	299.85	50.62	200.51, 399.20
	Iceberg = Y	−44.96	14.92	−74.24, −15.68
3.3 $Condition_{sib}$	Intercept	261.20	22.88	216.31, 306.10
	Colony size	0.00024	0.00012	0.00013, 0.00048

Royds and weakest at Cape Crozier. Several compet-itive models (AIC_c <2) indicated that provisioning efficiency had a negative relationship with chick mass, while the proportion of fish in the diet was pos-itively associated with chick mass. However, neither variable was included in the best model (see the Appendix).

Prediction 1.3: Chick condition will be better when provisioning efficiency is high, SIC is low and fish are dominant in the diet. Chick condition varied among colonies, with chicks at Cape Crozier in better condi-tion than those at Capes Bird and Royds (Fig. 2). The relationship between chick condition and ln(SIC) var-

ied between colonies, being positive at Crozier and Bird but constant at Royds. In contrast to our predictions, there was a negative relationship between chick condition and provi-sioning efficiency, with chicks in poorer condition when provisioning efficiency was high. The proportion of fish in the diet had a positive ef-fect on chick condition in the second best model (AIC_c = 1.08) but was not included in the best model (Appen-dix, Table 3).

Prediction 2.1: Chick size will be greater in breeding seasons with low intraspecific resource compe-tition. Mean chick size varied among breeding seasons in re-sponse to the presence of the giant icebergs, colony size and breeding output (Appendix, Table 3). As pre-dicted, chicks were smaller at larger colonies (Fig. 3a) and in the pres-ence of the icebergs (Fig. 4a). How-ever, in contrast to our predictions, high breeding output was associ-ated with larger chicks (Table 3).

Prediction 2.2: Chick mass will be greater in breeding seasons with low intraspecific resource compe-tition. Mean chick mass varied among breeding seasons in re-sponse to the presence of the giant icebergs, colony size and breeding output (Appendix, Table 3). As pre-dicted, chicks were lighter at larger colonies (Fig. 3b) and when breed-ing output was high, while the pres-ence of the icebergs reduced mean chick mass by 344 ± 21 g (Fig. 4b).

Prediction 2.3: Chick condition will be better in breeding seasons with low intraspecific resource competition. Mean chick condition varied among breeding seasons in response to iceberg presence, with chicks on average 77 ± 12 g lighter than ex-pected for their body size when the icebergs were present (Fig. 4c, Table 3). As predicted, high intra-specific competition negatively affected chick condi-tion, with chicks in poorer condition when breeding output was high (Appendix, Table 3). Colony size had a negative impact on chick condition in the sec-ond best model (AIC_c = 0.47) but was not included in the best model (see the Appendix).
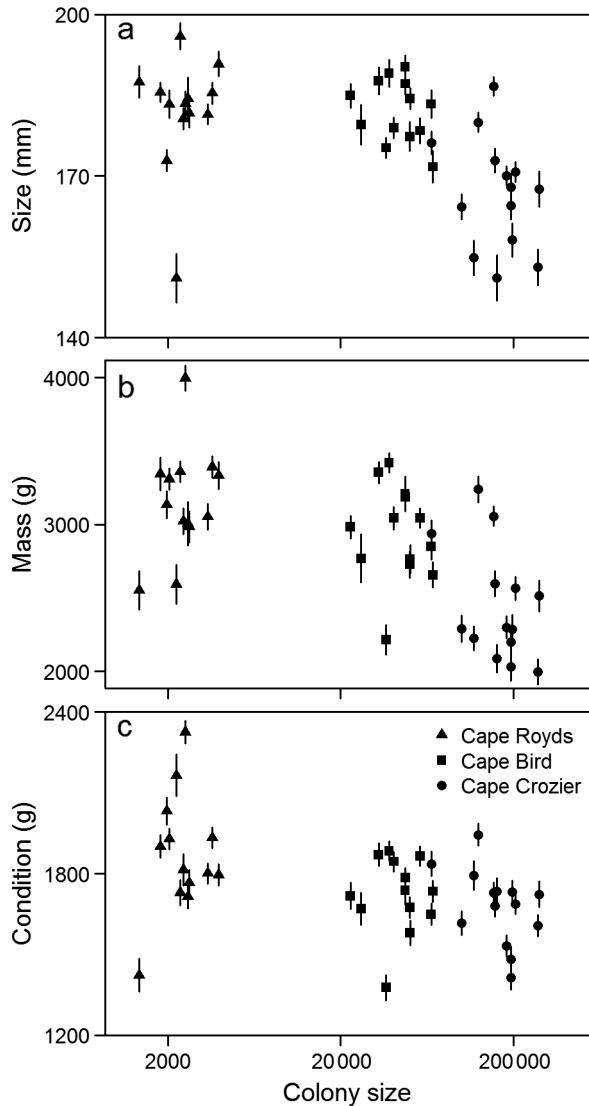
Fig. 3. Relationship between colony size and (a) mean size (as measured by flipper length), (b) mass and (c) condition of Adélie penguin chicks. Data are summarised for chicks approximately 5 wk old;. Error bars: ± SE. Further details on each of the metrics can be found in Table 1 and 'Materials and methods'

Prediction 3.1: Sibling chicks will be most similar in size in breeding seasons with low intraspecific resource competition. As predicted, variation in size between sibling chicks from the same nest was greater when breeding output was high (i.e. more parents with 2-chick broods; Table 3). Iceberg presence was included in the second best mode (AIC$_c$ = 0.61), with the difference in size between sibling chicks tending to be smaller when the icebergs were present (Fig. 4d, Appendix).

Prediction 3.2: Sibling chicks will be most similar in mass in breeding seasons with low intraspecific re-

source competition. The mean difference in the mass of sibling chicks from the same nest was affected by the presence of the giant icebergs (Table 3). Differences in sibling mass of up to 1400 g were observed, with large differences in sibling mass less prevalent when the icebergs were present (Fig. 4e). The breeding output and colony size were both included in several competitive models (AIC$_c$ < 2; Appendix), with high values of these variables tending to result in greater differences in sibling mass.

Prediction 3.3: Sibling chicks will be most similar in condition in breeding seasons with low intraspecific resource competition. Differences in sibling condition were best explained by colony size, with greater differences in sibling condition observed at larger colonies (Appendix, Table 3). Iceberg presence and breeding output were both included in several competitive models (AIC$_c$ < 2; Appendix), with iceberg presence and higher breeding output tending to result in greater differences in condition between sibling chicks.

DISCUSSION

Our study clearly showed that the size, mass and condition of Adélie penguin chicks varies with environmental conditions and intraspecific competition among their parents, indicating that adult penguins are unable to fully compensate and provide sufficient resources during periods when assumed prey quality and/or availability is low. Our results indicate that altering the amount and quality of food (specifically the proportion of fish) fed to chicks can affect growth, as has previously been shown for Adélie penguins (Salihoglu et al. 2001, Takahashi et al. 2003, Ballard et al. 2010, Chapman et al. 2011) and other seabird species (e.g. Wanless et al. 2005, Kitaysky et al. 2006). In fact, it appears that the inclusion of more fish in the diet may offset reduced access to food (i.e. when SIC is too high). This could be the reason we did not detect a significant effect of provisioning efficiency on chick size and mass.

The major contribution of this study is the identification of mechanisms that drive provisioning and growth of Adélie penguins chicks in the southern Ross Sea, with both environmental conditions and intraspecific competition shown to be important. Our study indicates that the iceberg presence led to smaller and lighter chicks, who were ultimately in poorer condition (see also Ainley et al. 2004, Dugger et al. 2014). While SIC increased at Capes Royds and Bird due to iceberg presence, the location of the ice-
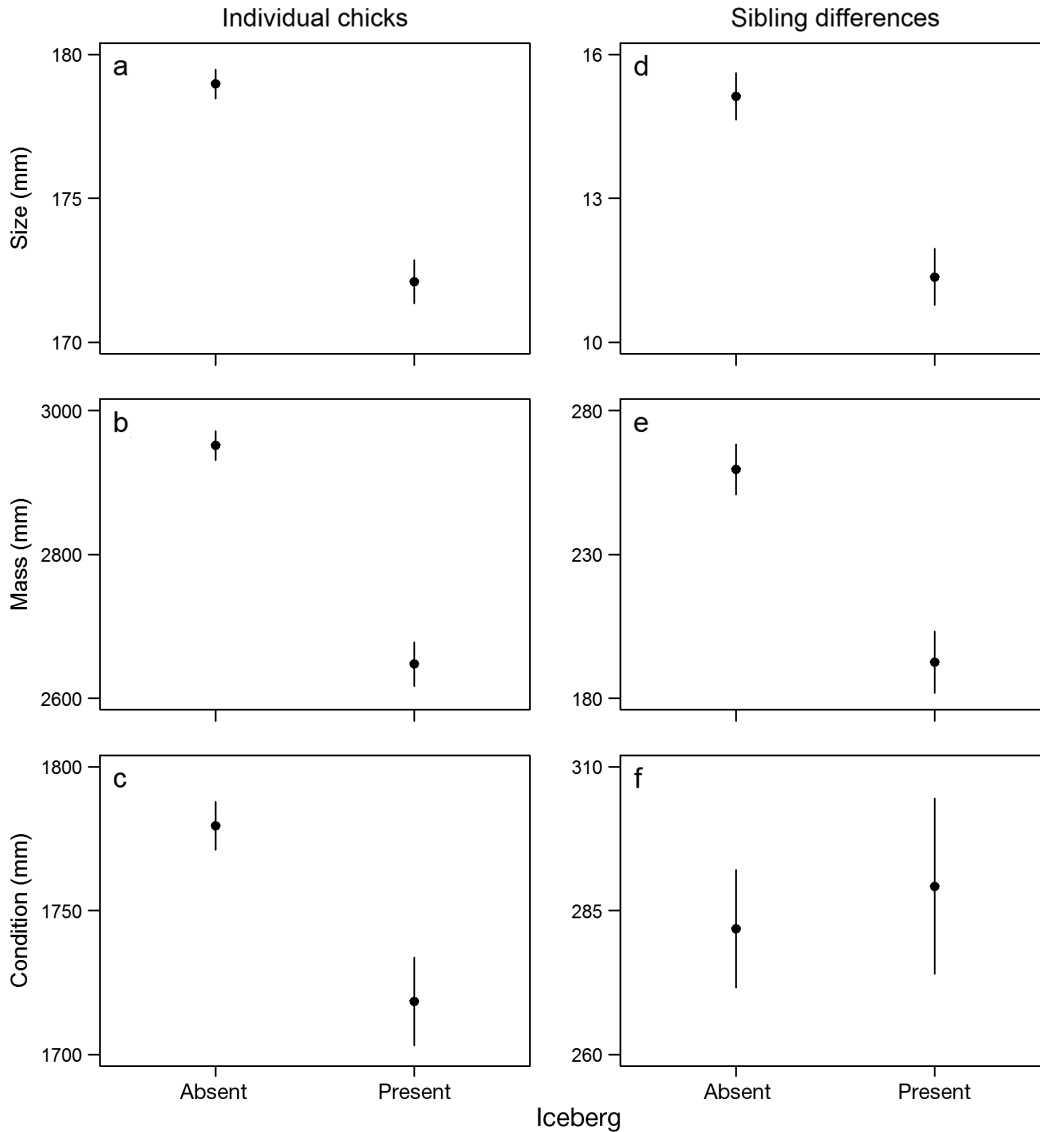
Fig. 4. Mean size, mass and condition of Adélie penguin chicks in the presence and absence of the giant icebergs. The left panels depict the mean (±SE) across all colonies at approximately 5 wk of age. The right panels depict the mean (±SE) difference between individuals from the same nest at approximately 3 wk of age. Further details on each of the metrics can be found in Table 1 and 'Materials and methods'

bergs meant that foraging penguins at Cape Crozier were prevented from foraging in the productive MIZ of the Ross Sea Polynya, where they otherwise forage in non-iceberg years (Dugger et al. 2014, Lescroël et al. 2014). Thus, the mechanism by which iceberg presence affected foraging differed between the colonies, although the impacts on chick size, mass and condition were similar. Adult Adélie penguins are known to provide less food to chicks during periods of greater intraspecific competition (Ballard et al. 2010), as well as greater interspecific competition (cetaceans; Ainley et al. 2006). Indeed, as colonies grew in size (especially Cape Crozier) in the later

breeding seasons of our study, chick size and condition decreased. Chick size and condition were also lower during breeding seasons of greater breeding output when there is likely to be greater intraspecific competition among foraging parents (Lewis et al. 2001). Overall, chicks tended to be larger but lighter and in poorer condition when there was a greater proportion of 2-chick broods (competition among chicks). However, we also observed greater differences between sibling chicks in terms of size and mass when there was a greater proportion of 2-chick broods, despite the fact that Adélie penguins provide more food to chicks in such nests (Ballard et al. 2010).

Previous studies at Cape Crozier have shown that 6 to 15% SIC in the foraging range is optimal for foraging efficiency (and ultimately chick size and mass) in this high latitude penguin species (Ballard et al. 2010, Lescroël et al. 2010, 2014). This is consistent with penguins foraging in the MIZ of polynyas, where SIC rapidly increases with distance away from the polynya edge (see Ainley et al. 1998). Sea ice concentration affects access to prey and possibly (but not necessarily) prey abundance. The presence of the giant icebergs led to increased SIC during those breeding seasons. This was particularly evident close to Capes Royds and Bird, although the proximity of Cape Crozier to the Ross Sea Polynya meant that the SIC remained relatively low during this period. As noted above, an important effect of the icebergs on Cape Crozier penguins was blocked access to the MIZ.

Nest desertion was more common at Capes Royds and Bird when SIC was high, probably because foraging trips took longer and mates were unable to return before the brooding or guarding mate abandoned the nest to ensure its own survival (Ballard et al. 2010). Thus, overall breeding success was lower in these breeding seasons. What may have resulted was essentially a selection for pairs in which both members had learned (or were predisposed) to forage in nearby ice cracks in the otherwise almost complete ice cover (D. G. Ainley pers. obs. at Royds and from helicopter overflights). For those few pairs in which both members foraged in cracks near the colony, the chicks were well fed and were in better condition than in non-iceberg breeding seasons. Clearly the ice cracks would not have been able to support large populations, with intraspecific competition for food among adults likely high within a few largely enclosed spaces (Watanuki et al. 1993). Foraging in cracks is common for the very small colony of Adélie penguins (<1000 pairs) investigated by Watanuki et al. (1993, 2003), a colony restricted in size due to poor access to foraging habitat. Such a situation speaks greatly to the power of polynyas for enhancing penguin colony size and even colony existence (Ainley 2002, Arrigo & van Dijken 2003).

Chick size and mass were lower during periods of high SIC, with the greatest declines observed at Cape Crozier. These relationships seem somewhat counter-intuitive when considering SIC only. However, they become clearer when viewed in the context of intraspecific competition among foraging parents. Most remarkable in our results was the fact that the colonies at Cape Bird, and especially Cape Crozier, began to increase in size after 2004, well before the large icebergs departed in winter 2006,

and have continued to grow at an irregular rate in subsequent breeding seasons (Lyver et al. 2014). Accordingly, with the presumed increase in foraging competition, chick size, mass and condition decreased at Cape Crozier. The pattern is counter-intuitive because decreased chick size and condition should result in decreased probability of surviving once chicks begin provisioning themselves (Perrins et al. 1973, Coulson & Porter 1985, Magrath 1991, Sagar & Horning 1998). Being quite speculative (but under investigation using ocean glider studies), what may be indicated is that despite food being depleted close to colonies, food availability not far beyond the colony 'halo' of intense foraging (Ballance et al. 2009) was adequate for chicks to forage successfully post-fledging. On the other hand, the time lag between fledging and recruitment into the breeding population may mean that we have yet to see colony growth be affected by a lower survival rate for chicks fledging in poor condition.

Increasing food availability beyond the colony foraging 'halo' could be a function of the decreased prevalence of a major penguin competitor in the southern Ross Sea. Large Antarctic toothfish, which forage for silverfish in the water column (Eastman 1985), have disappeared in waters around Ross Island, possibly the result of a fishery that has grown since 1997 (Ainley et al. 2013). This reduction in large toothfish may lead to an increase in the availability of energy-rich silverfish, which is likely to result in larger Adélie penguin chicks (see also Salihoglu et al. 2001, Chapman et al. 2011) .

At present, we do not fully understand the demographic mechanisms that influence Adélie penguin juvenile survival, particularly the effects of mass and condition at fledging (but this is under investigation). On average, near-fledging chicks from Cape Crozier were ~700 g lighter than those from Cape Royds, yet the Cape Crozier population has been exhibiting rapid growth whereas Cape Royds has not. A fledgling with higher body condition (greater lipid and protein reserves though structurally smaller) may have greater fasting endurance and therefore more potential to develop successful foraging strategies, increasing their chances of survival (Millar & Hickling 1990, Schulte-Hostedde et al. 2001, Kitaysky et al. 2006). However, it is also possible that larger and heavier chicks, such as those at Cape Royds, might be less efficient foragers than their smaller counterparts at Cape Crozier due to increased buoyancy. Underwater swimming speeds may be lower and required dive depths more difficult to attain, with the ability to evade predators also compromised. Alternatively,

even if provisioning is equal between different-sized chicks, larger chicks may be at a disadvantage under difficult foraging conditions due to their greater overall energetic requirements (Volkman & Trivelpiece 1980). If our research persists long enough to estimate chick survival as a function of fledging size, mass and condition (measurement of the mass of near-fledged chicks at banding began in 2006), it may eventually be possible to obtain sufficient data to identify links between chick condition at fledgling, subsequent recruitment and trends in population size.

Understanding the relative effects of biotic and abiotic drivers on population dynamics, and the interactions between them, is a key component in understanding the factors driving changes in animal populations. We have shown that the size, mass and condition of Adélie penguin chicks is greater during times when environmental conditions allow for more efficient parental foraging. In addition, we have shown that in some cases, increased intraspecific competition may be a more important driver of chick size than abiotic factors. If we are to better understand the effects of climate change and altered food web structures on penguins and other upper level marine organisms, a more complete understanding about how biotic and abiotic factors interact to influence population and ecosystem dynamics is required (Estes 2014, Springer & van Vliet 2014).

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Appendix. Model selection results for each prediction as evaluated by comparing corrected Akaike's Information Criterion (AIC_c). All possible combinations of terms that were included in each model set (different for each prediction; see Table 2) were evaluated but only the models contributing 95% of the Akaike weights, as well as 'intercept only' models, are shown. The model with the lowest AIC_c value for each prediction was chosen as the best model, and coefficients for the top model for each prediction are reported in Table 3. The number of observations (n) and estimated parameters (K), differences in model AIC_c value from the best model (ΔAIC_c) and Akaike weights (*w*) are shown for each model. Detailed explanations of the parameters are given in Table 1 and 'Materials and methods'

Model	K	Log likelihood	AIC_c	ΔAIC_c	*w*
1.1 Size (n = 2689)					
Colony + ln(SIC) + fish + ln(SIC):colony	10	−12439.3	24898.65	0.00	0.358
Colony + ln(SIC) + provisioning efficiency + ln(SIC):colony	10	−12439.4	24898.97	0.33	0.304
Colony + ln(SIC) + provisioning efficiency + fish +ln(SIC):colony	11	−12438.8	24899.67	1.02	0.215
Colony + ln(SIC) + ln(SIC):colony	9	−12441.4	24900.79	2.14	0.123
Intercept only	4	−12559.1	25126.25	227.6	0.000
1.2 Mass (n = 2689)					
Colony + ln(SIC) + ln(SIC):colony	9	−20813.9	41645.82	0.00	0.471
Colony + ln(SIC) + fish + ln(SIC):colony	10	−20813.6	41647.19	1.38	0.237
Colony + ln(SIC) + provisioning efficiency + ln(SIC):colony	10	−20813.9	41647.78	1.96	0.176
Colony + ln(SIC) + provisioning efficiency + fish + ln(SIC):colony	11	−20813.3	41648.61	2.79	0.117
Intercept only	4	−20894.3	41796.53	150.71	0.000
1.3 Condition (n = 2689)					
Colony + ln(SIC) + provisioning efficiency + ln(SIC):colony	10	−19249.3	38518.76	0.00	0.616
Colony + ln(SIC) + provisioning efficiency + fish + ln(SIC):colony	11	−19248.9	38519.95	1.20	0.339
Intercept only	4	−19282.1	38572.13	53.37	0.000
2.1 Size (n = 7011)					
Breeding output + iceberg + colony size	6	−32007.1	64026.26	0.00	0.994
Intercept only	3	−32593.8	65193.51	1167.25	0.000
2.2 Mass (n = 7011)					
Breeding output + iceberg + colony size	6	−54758.0	109528.04	0.00	1.000
Intercept only	3	−55444.0	110894.06	1366.02	0.000
2.3 Condition (n = 7011)					
Breeding output + iceberg	5	−50856.3	101722.65	0.00	0.558
Breeding output + iceberg + colony size	6	−50855.6	101723.12	0.47	0.442
Intercept only	3	−50931.5	101868.96	146.31	0.000
3.1 Size$_{sib}$ (n = 981)					
Breeding output	4	−3815.7	7639.39	0.00	0.402
Breeding output + iceberg	5	−3815.0	7640.00	0.61	0.296
Breeding output + colony size	5	−3815.7	7641.41	2.02	0.146
Breeding output + iceberg + colony size	6	−3815.0	7642.02	2.63	0.108
Intercept only	3	−3824.4	7654.75	15.36	0.000
3.2 Mass$_{sib}$ (n = 981)					
Iceberg	4	−6689.5	13386.94	0.00	0.260
Breeding output + iceberg	5	−6688.6	13387.17	0.23	0.232
Breeding output	4	−6689.7	13387.45	0.50	0.202
Iceberg + colony size	5	−6689.3	13388.56	1.62	0.116
Breeding output + iceberg + colony size	6	−6688.5	13389.01	2.06	0.093
Breeding output + colony size	5	−6689.6	13389.21	2.26	0.084
Intercept only	3	−6694.0	13393.95	7.01	0.008
3.3 Condition$_{sib}$ (n = 981)					
Colony size	4	−6804.6	13617.17	0.00	0.366
Breeding output + colony size	5	−6804.2	13618.49	1.32	0.189
Iceberg + colony size	5	−6804.4	13618.93	1.76	0.152
Intercept only	3	−6806.7	13619.45	2.27	0.118
Breeding output + iceberg + colony size	6	−6804.2	13620.52	3.34	0.069
Breeding output	4	−6806.7	13621.35	4.17	0.045
Iceberg	4	−6806.7	13621.45	4.28	0.043