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Effects of Diet and Provisioning Behavior on Chick Growth in Adélie Penguins (*Pygoscelis Adeliae*)

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Abstract.—When provisioning chicks, parents trade-off their time, energy, and other resources to maximize reproductive success. As parents adjust investment to maximize their fitness, impacts on offspring growth can occur. We investigated provisioning and chick growth of Adélie Penguins (*Pygoscelis adeliae*) at one of the largest colonies (~175,000 pairs), during one year of normal chick growth and survival and in a year which, by chance, was characterized by low chick growth and survival ("difficult" year). We measured daily average amount and quality of food delivered, as well as foraging-trip duration, and compared them to chick mass and skeletal growth during two years of contrasting conditions. We used mixed-effects models to test the prediction that increased parental investment would lead to increased growth rates, while accounting for confounding effects. There was no evidence of an effect of parent age. All provisioning measures predicted growth of at least one morphological character but, especially during the year of normal reproductive success, no provisioning measure strongly predicted growth across most morphological characters. However, during the difficult year parental investment positively affected growth rates, especially for males that were fed relatively more fish. The observed variation in growth rates between males and females, and between years of contrasting apparent resource availability, was large enough to lead to size differences that may subsequently affect post-fledging survival and ultimately population processes. Received 29 January 2020, accepted 3 September 2020.

Key words.—Adélie Penguin, chick growth, chick provisioning, diet, stable isotopes, parental investment

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Growth during the juvenile stage can have important implications for subsequent survival and fitness, especially among vertebrates (Arendt 1997). Variability in food availability and quality, predation pressure, weather and other factors can affect parents' ability to deliver calories to offspring, providing a mechanism for trade-offs between parents maintaining their own condition and that of their offspring (Stearns 1989). If variation in parental investment can affect the subsequent size or performance of offspring once they become adults, and if the reproductive success of one sex is more sensitive to variation in individual size (males in many vertebrates but sometimes females), then parents may bias their investment toward offspring of one sex or the other based on parent condition (Trivers and Willard 1973). The Trivers-Willard hypothesis can

be extended to include variation in environmental conditions (not just parent condition) to predict that where male offspring exhibit faster growth rates and thus have greater nutritional requirements, parents may underinvest in or even abandon male offspring under challenging conditions (Clutton-Brock *et al.* 1985).

Colonial seabirds are suitable for studying the impacts of parental investment on reproductive success owing to efficient collection of behavior and productivity data from a large number of individuals facing the same environmental conditions (Ashmole 1971; Ydenberg and Bertram 1989). The amount of food seabird parents deliver to their chicks per unit time generally decreases as foraging trip duration increases, because parents utilize more of the resources acquired for their own maintenance dur-

ing longer trips (Weimerskirch *et al.* 1994; Ainley *et al.* 1998; Granadeiro *et al.* 1998). Seabird chicks grow faster and attain larger size when they receive larger and more frequent and/or higher quality meals (Salihoglu *et al.* 2001; Chapman *et al.* 2011), although mass and skeletal growth may respond differently to variation in diet (Lyons and Roby 2011). Despite these general patterns across seabirds, there is substantial variability in the degree to which parent condition, offspring condition, and environmental conditions may interact to influence parental care and offspring growth, both within and between species (e.g. Weimerskirch *et al.* 1995; Tveraa *et al.* 1998; Wendeln and Becker 1999).

We investigated the relationships between provisioning and chick growth rates of Adélie Penguins (*Pygoscelis adeliae*) in one of the largest colonies known for the species (~175,000 breeding pairs at the time of the study), during two years which, by chance, were characterized by contrasting reproductive success at the colony scale. We selected three aspects of chick provisioning that represent tradeoffs between parental investment and benefits to chicks: (1) the proportion of high-energy fish in the diet provisioned to chicks; (2) the average amount of food delivered to chicks per day (increased food delivery represents increased parental investment); and (3) the length of foraging trips (shorter foraging trips, less time between feedings, and therefore greater chick feeding frequency, represents greater parental investment). Increased food delivery and shorter foraging trip duration were both previously shown in this species to lead to larger chicks (Chapman *et al.* 2010), but also to represent increased parental investment in reproduction, in which parents provisioning chicks with larger and more frequent meals lost more of their own body mass through the season than parents who provisioned smaller, less frequent meals (Ballard *et al.* 2010). The diet of adults and chicks at this colony during the chick-provisioning period has two main components: crystal krill (*Euphausia crystallorophias*) and Antarctic silverfish (*Pleuragramma antarcticum*). Differences between krill and fish in relative

abundance, predator-avoidance capabilities, and density of aggregations (O'Brien 1987; Fuiman *et al.* 2002) may all contribute to the relative efficiency at which parent penguins can acquire prey. Silverfish have a higher lipid content or energy density than krill (Ainley *et al.* 2003; Chapman *et al.* 2011), and Adélie Penguins may preferentially choose higher lipid foods, which can be important for chick growth (Chapman *et al.* 2010; Ainley *et al.* 2018). However, krill availability has nevertheless been linked to Adélie Penguin population dynamics (in this case the larger Antarctic krill (*Euphausia superba*), Trivelpiece *et al.* 2011; Kohut *et al.* 2014; but see Sailley *et al.* 2013), and it appears that no Adélie population forages exclusively on silverfish during the breeding season (summary of diets by location in Ainley 2002). Thus, although krill is clearly an important component of Adélie diet during breeding, penguin breeding productivity and chick fledging mass can be increased by replacing krill with fish in the diet (Ainley *et al.* 2018) but provisioning exclusively with fish may be more costly to parents owing to increased effort, i.e., diving deeper (Ainley *et al.* 2015). In this context it is reasonable to propose that more fish in the diet represents higher parental investment in reproduction among Adélie Penguins, but it is also reasonable to postulate that a higher proportion of fish in the diet indicates lower krill availability.

We predicted that a higher parental investment would be correlated with more rapid chick growth. We evaluated the relative ability of the three aspects of provisioning (size, frequency, and composition of provisioned meals), as indices of parental investment, to explain observed variation in growth rates of male and female chicks in two years of contrasting productivity at the colony scale. Our analysis included parent age to account for possible age-related differences in foraging performance and parenting capability (Cam and Monnat 2000; Daunt *et al.* 2007), and also accounted for differences in growth rates related to brood size and hatching order (Ainley and Schlatter 1972; Becker and Wink 2003).

METHODS

Study Species and System

We studied Adélie Penguin provisioning and chick growth during the austral summers of 2012-13 and 2013-14 (hereafter "2012" and "2013", respectively) at Cape Crozier, Ross Island, Antarctica (77° 27' 15.00"S, 169° 13' 45.00"E). This is one of the largest colonies of this species with approximately 175,000 breeding pairs at the time of this study (Dugger *et al.* 2010; Lynch and LaRue 2014). Adélie Penguins regularly raise two chicks at least to crèching, that occurs mid-way in a 55 day post-hatch period (Ainley 2002). On Ross Island, the proportion of fish in the Adélie Penguin diet increases as the chick provisioning period progresses, likely due to depletion of krill but possibly also related to chick needs (Ainley *et al.* 2018). At the colony scale, chick growth, or at least fledging mass, is positively related to the amount of fish in the diet (Whitehead *et al.* 2015; Jennings *et al.* 2016).

Our first year of study, 2012, was normal in terms of chick growth and reproductive success. By chance, 2013 appeared to be atypical because parents were limited in their ability to provision their young, though we do not know the cause of this. Not only were overall chick growth rates lower, but there were fewer two-chick broods (% broods with two chicks in nests that we monitored: 83% in 2012, 44% in 2013). Calculated at the colony scale, 2013 was also characterized by lower-than-average breeding productivity (chicks per nest: 2012 = 0.94, 2013 = 0.85; 2006-2012 mean = 1.05; G. Ballard, D. G. Ainley and K. M. Dugger, unpubl. data).

This research involved nests from two different groups of adult Adélie Penguin that have been individually-marked as part of long-term research. The first group, known-age parents (hereafter "KA"; see Dugger *et al.* 2006 for description of long-term banding program), were banded just prior to fledging; thus age during subsequent returns to the colony was known. The second group, weighbridge parents (hereafter "WB"), nest in one sub-colony that is fenced with the only access over a weighbridge (an electronic scale coupled with a direction sensor and Radio Frequency Identification antenna). These birds were implanted with a passively-interrogated transponder (PIT tag). The weighbridge records the identity, direction of travel, mass, date, and time of WB parents as they go back and forth provisioning chicks (for full WB design and usage see Ballard *et al.* 2010). The WB was operated from early egg-laying (November) through most of the chick-rearing period (late January).

WB nests were studied during both years. During 2013, we included KA nests to address the possible contribution of parent age to chick provisioning and subsequent growth rates. Nests from both groups of parents were selected systematically during early- to mid-incubation to represent a range of characteristics of both the parents and the nest site (interior vs. edge of subcolonies). We selected WB nests having at least

one PIT-tagged parent (identified during incubation using a handheld reader). We monitored nests every 1-3 day during incubation to determine hatching day for all eggs.

Morphological Measurements

At 10 days post-hatching for the first-hatched chick of each brood we began to collect morphological measurements and individually marked each chick with a T-bar fish tag (Floy Tags Inc., USA). If present, the second-hatched chick was also measured and tagged on the same day to avoid disturbing the nest again 1-2 days later when it reached 10 days old. Thereafter, we repeated morphological measurements at 5-day intervals for the remainder of the 50-55 day chick rearing period. Because mass, and skeletal and bill growth rates may respond differently to restricted caloric intake (Lyons and Roby 2011), we collected five morphological measurements to represent growth: mass (g) and lengths (mm) of tibiotarsus, foot, flipper and bill (measurement methods described in Jennings *et al.* 2016). Fish tags were removed at the end of the monitoring period (> 50 day).

Weighbridge Data

We used WB data to determine two variables: the average daily provisioning rate to each chick (FOOD), and averaged foraging trip duration (FTD). If both adults from a nest had a PIT tag (24 of 45 nests), we lumped their provisioning data to obtain a single, average FOOD and FTD for the nest. We calculated FOOD as the mass of total food (g) delivered to the nest divided by the duration of the foraging trip and the number of chicks present in the nest at the time of parental arrival. We assumed no parental digestion of stomach contents during their relatively short visits (Clarke *et al.* 2002) to the nest (~50% of nest visits during this study were < 1 day; ~66% were < 2 days); thus, the amount of food delivered to the nest was calculated as the difference in parent mass (g) between an incoming trip and the subsequent outgoing trip (Ballard *et al.* 2001). Because we lacked a method to estimate allocation of food between siblings, we assumed it was evenly distributed. This assumption was consistent with previous observations of equal division of food loads amongst siblings in Adélie Penguins except in circumstances of resource limitation (Spurr 1975; Lishman 1985). We averaged FTD (to the nearest 0.1 d) across the entire chick rearing period for each nest. We included foraging trip duration as a component of FOOD, and FTD alone, to differentiate the effects of larger, less frequent feedings from regular small meals.

Diet Composition

Stable isotope values from feathers can provide information on diet within ~2 weeks prior to, and during, feather growth (Bearhop *et al.* 2010). Adélie Penguin chicks grow two plumages during chick rearing, at 12-17 day and 25-35 day post hatch, both of which are distinguishable from each other and from natal feathers (Taylor 1962; Ainley 2002). We evaluated isotope values

in the feathers that were grown post-hatching, to represent diet of chicks during the provisioning period. We combined material from 3-5 feathers collected from the abdomen for each generation, and averaged isotope values across plumages for chicks from which we collected two samples. We focused on $\delta^{15}\text{N}$ (the ratio of the heavy and light nitrogen isotopes, ^{15}N and ^{14}N ; analysis conducted by the Stable Isotope Facility, University of California Davis), rather than other isotopic elements, because previous work has shown that a positive relationship between $\delta^{15}\text{N}$ and the proportion of fish in the diet exists at the colony scale on Ross Island (Ainley *et al.* 2003). DNA was also extracted from the feathers to determine sex of each chick by molecular means (Griffiths *et al.* 1998).

Data Analysis

We used the two-sample *t*-test to compare the average values of the primary explanatory variables of interest ($\delta^{15}\text{N}$, FOOD and FTD) between the two years of the study to provide additional context for the results of the modelling described below. We conducted separate analysis for each morphological character and started by estimating the daily growth rate of each chick during the linear phase of growth. Growth for all morphological characters appeared to be in the linear phase at the onset of measurements (10 days old), as reported elsewhere for mass growth (Ainley and Schlatter 1972; Culik 1994; Chapman *et al.* 2010). To identify the age at which linear growth ceased for each measurement, we fit a series of linear models (morphological measurement ~ age) to the data of each chick, beginning with the entire dataset, then using reduced data sets that incrementally excluded measurements from the end of the sample period (e.g., full measurement period: 10-55 days; measurements through day 50 only: 10-50 days; measurements through day 45 only: 10-45 days, etc.). For each morphological character, we selected the time interval for which R^2 values were maximized across the majority of chicks and verified

this selection by visually examining the fitted lines plotted against the raw data. The linear phase of growth was thus determined to be 10-40 day for mass and flipper, 10-35 day for tibiotarsus and foot, and 10-55 days (end of measurements) for bill. The slope coefficients from these models were taken as an estimate of the daily growth rate, during the linear phase, for each measurement for each chick.

We then explored the relationships between daily growth rate and the explanatory variables of interest (Table 1). For nests from WB parents, we had data on FOOD, FTD, and $\delta^{15}\text{N}$; while for nests from KA parents, we had data on parent age and $\delta^{15}\text{N}$. Thus, we could not compare the relative importance of all variables in the same candidate model set, and analysis proceeded in three iterations. First, we used the entire dataset to evaluate the relationships between growth rates and $\delta^{15}\text{N}$, utilizing the largest possible sample size. Next, we used the WB subset of data to evaluate the relative importance of $\delta^{15}\text{N}$, FOOD and FTD in predicting growth rates. Finally, we used the KA data subset to account for the relative effect of parent age versus $\delta^{15}\text{N}$ in predicting growth. Because age-related changes in parental quality may not be simply linear, we also included candidate models having the quadratic effects of parent age. The correlations between predictor variables were small enough that we determined all could be considered together in the same model.

We developed candidate model sets with all additive combinations of these primary variables of interest plus chick sex, year, and hatch order (A, B or S [singleton]). Based on field observations and evidence of faster growth in male chicks (Jennings *et al.* 2016), we also included some 2- and 3-way interactions involving year, sex and $\delta^{15}\text{N}$. However, 3-way interactions were not included in candidate model sets for the WB and KA subsets due to sample size considerations. All continuous covariates were deemed appropriate to include together as fixed effects in candidate models (absolute value of correlation between all pairs ≤ 0.5). Candidate

Table 1. Names and brief description of covariates used to model Adélie Penguin (*Pygoscelis adeliae*) chick growth at Cape Crozier, Ross Island, Antarctica during 2012 and 2013. Variables were continuous unless otherwise noted. For two level categorical variables the level coded as 0 was the reference level. WB stands for weighbridge and KA stands for Known-age; both abbreviations refer to subsets of the data.

Model	Variable name	Description
Fixed effects	$\delta^{15}\text{N}$	Delta ^{15}N itrogen; the ratio of ^{15}N to ^{14}N , measured in ‰. A larger value indicates a greater proportion of diet composed of fish vs. krill.
	FOOD	Average amount of food delivered per chick day ⁻¹ (g); WB data subset
	FTD	Average foraging trip duration (h); WB data subset; same date ranges as FOOD
	Parent age	Parent age in years; KA data subset
	Sex	Sex of chick; categorical; female coded as reference level
	Year	Austral summer; categorical; 2012 coded as reference level
	Hatch order	Categorical; coded as two dummy variables representing whether chick was hatched 2 nd (B) or was from a single chick nest (S), with 1 st hatched coded as the reference level
Random effects	NEST	Nest identification code; categorical; chicks from the same nest received the same code

models also included Nest ID as a random effect to account for lack of independence between chicks from the same nest.

Model selection began by fitting a linear mixed-effect model with the most saturated fixed-effects structure (i.e., the most complicated interactions considered plus all remaining additive variables) and the Nest ID random effect. This model was fitted with Restricted Maximum Likelihood estimation to determine importance of the random effect (Zuur *et al.* 2009). Nest ID was deemed unimportant in explaining growth rates if the estimated random-effect variance was > 2 orders of magnitude smaller than the residual variance. If the random effect was supported as important in the most saturated model, we fit the entire candidate model set with Maximum Likelihood Estimation to determine the best fixed-effect structure and evaluate the relative importance of the fixed effects. If the random effect was deemed unimportant, the candidate model set was re-generated as regular linear models.

To select the best fixed-effect model structure, we used an information theoretic approach and multi-model inference (Burnham and Anderson 2002). We selected the model having the lowest AIC_c value (AIC value corrected for small sample size) as the model best-supported by the data. We evaluated the explanatory power of the best-supported models with conditional R^2 (Nakagawa and Schielzeth 2013) or adjusted R^2 values for models with and without the random effect for Nest ID, respectively. We evaluated the strength of relationships between growth rates and variables in the best model based on the degree to which 95% confidence intervals (CI; bootstrapped for mixed effects models) for the coefficients of these variables did or did not overlap zero. All analyses were conducted in R version 3.6.0 (R Core Team 2019) and the lme4 package (Bates *et al.* 2014). Year, sex, hatch order and nest ID were treated as categorical (coding in Table 1), and all other variables were treated as linear continuous variables. Unless otherwise noted, means are expressed with standard error.

RESULTS

Data summary

We measured growth of 38 chicks in 2012 and 53 chicks in 2013, including 49 chicks of WB parents across both years, and 42 of KA parents in 2013 (Table 2). There was no difference in ^{15}N values between the two years (2012: 10.8 ± 0.07 , 2013: 10.9 ± 0.09 ‰; two-sided P -value = 0.08). Average FTD was longer (31.0 ± 0.07 vs. 47.8 ± 0.09 h; two-sided P -value < 0.001) and FOOD was greater (160.5 ± 17.41 vs. 257.3 ± 36.74 g d⁻¹; two-sided P -value = 0.011) in 2013. However, the pattern in FOOD was driven by mostly small values

Table 2. Number of Adélie Penguin (*Pygoscelis adeliae*) chicks measured for each data subset defined by sex and study year at Cape Crozier, Ross Island, Antarctica during 2012 and 2013. WB stands for weighbridge and KA stands for Known-age; both abbreviations refer to subsets of the data.

Data subset	WB		KA	
	2012	2013	2012	2013
Year				
Male	19	8	na	21
Female	19	3	na	21
Total	38	11		42

in 2012 and a single large but still biologically-reasonable value (585 g day⁻¹) for FOOD in 2013; all other 2013 values were within the range of values observed during 2012. There was no evidence that the amount of food delivered per day decreased with increasing FTD in either year (for the linear model FOOD~FTD*year, FTD: = -1.129, 95% CI = -5.000 to 2.742; year: = 132.736, 95% CI = -115.995 to 381.468; FTD*year: = -0.356, = -6.129 to 5.417). Rather, as parents made longer trips, they brought back larger food loads to maintain roughly the same average food delivered per day.

Evaluating the effect of ^{15}N , data from all chicks together were used to evaluate the relationship between growth rates and ^{15}N value (higher value indicating diet with more fish), while accounting for the effects of sex, year, hatch order, and nest ID. The effect of ^{15}N was included in the best supported models for mass, flipper and tibiotarsus growth, and the conditional R^2 (explanatory power of fixed and random variables) or R^2 for these ranged from 0.66 to 0.15 (Table 3). ^{15}N was less important in explaining bill and foot growth (i.e., not in the best-supported model, but in models with $0 < \text{AIC}_c \leq 2$; online Appendix Table A1).

Across the three morphological characters with ^{15}N in the best model, there were some similarities in the relationships between ^{15}N and growth rates (Fig. 1). First, the strongest effect (as judged by magnitude of coefficient and slope of line for estimates in Fig. 1) was a positive relationship between ^{15}N and both mass and tibiotarsus growth in males during 2013, the year we observed slower chick growth and lower breeding

Table 3. Model selection results for the relationships between provisioning and growth rates of Adélie Penguin (*Pygoscelis adeliae*) chicks at Cape Crozier, Ross Island, Antarctica during 2012 and 2013. Fixed effect structure of the best supported model for each morphological feature for each data subset. Models with * also had Nest ID as a random effect. w_i is the AICc model weight. R^2 or conditional R^2 (for mixed effects models) is shown where the variables for inference (in bold) were included in the best model. WB stands for weighbridge and KA stands for Known-age; both abbreviations refer to subsets of the data. $\delta^{15}\text{N}$ refers to the ratio of ^{15}N to ^{14}N , FTD = Foraging Trip Duration, FOOD refers to mass of food delivered per chick per day.

WB and KA combined Morphometric feature	Model structure*	w_i	R^2
Mass *	Sex * $\delta^{15}\text{N}$ * Year + Hatch order	0.483	0.66
Flipper *	Sex * $\delta^{15}\text{N}$ + Year	0.124	0.27
Tibiotarsus	Sex * $\delta^{15}\text{N}$ * Year	0.383	0.15
Bill	Sex * Year	0.301	—
Foot	Sex	0.133	—
WB group Morphometric feature	Model structure*	w_i	R^2
Mass *	Sex + Year + FOOD	0.280	0.45
Flipper *	Sex + Year * $\delta^{15}\text{N}$	0.08	—
Tibiotarsus	Year * $\delta^{15}\text{N}$ + FOOD	0.093	0.12
Bill	Sex + Year	0.214	—
Foot	Sex + FTD	0.11	0.07
KA group Morphometric feature	Model structure	w_i	R^2
Mass	Hatch order	0.263	—
Flipper	$\delta^{15}\text{N}$ + Hatch order	0.174	—
Tibiotarsus	Sex * $\delta^{15}\text{N}$	0.439	—
Bill	Parent age	0.195	0.1
Foot	Sex * $\delta^{15}\text{N}$ + Parent age + Parent age ²	0.232	0.28

*Model also included Nest ID as a random effect.

success at the colony-scale. For both mass and tibiotarsus, the coefficient for the 3-way sex:year: ^{15}N interaction was positive, and the 95% CI excluded (mass) or just barely included (tibiotarsus) zero (online Appendix Table A2). Recall that the reference levels sex and year were female and 2012, so this coefficient represents the strong positive relationship between ^{15}N and growth for males in 2013.

A second similarity among these three morphological characters was the negative relationship between ^{15}N and growth rates for females in one (2013 only for mass) or both years (Fig. 1). For mass and tibiotarsus the 95% CI's associated with the coefficients for females included zero (online Appendix Table A2), and the plotted slopes were relatively flat (Fig. 1), indicating less support and weaker effects for these negative relationships than for the positive relationships observed for mass and tibiotarsus growth for males in 2013. Similarly, there was only weak support for the relationship between

^{15}N and growth for males in 2012. However, there was stronger evidence for the negative relationship between ^{15}N and female flipper growth in 2013 (95% CI not including zero).

Comparing the effect of ^{15}N to food delivery

The WB data subset included data from both years and was used to evaluate the importance of FOOD and FTD, relative to ^{15}N , in predicting chick growth rates. WB variables were included in the best model for mass, tibiotarsus and foot growth (Table 3). However, explanatory power for the best tibiotarsus and foot growth models was low (Table 3), and several models (including the intercept-only model) were highly competitive, indicating covariate effects in the best models for these dependent variables were not strongly supported (online Appendix Table A1).

In contrast to other morphological characters, the best-supported model for mass growth had 3 times more support than the 2nd and 3rd ranked models (online Appendix Table A1) and a conditional R^2 value of 0.45. In this mod-

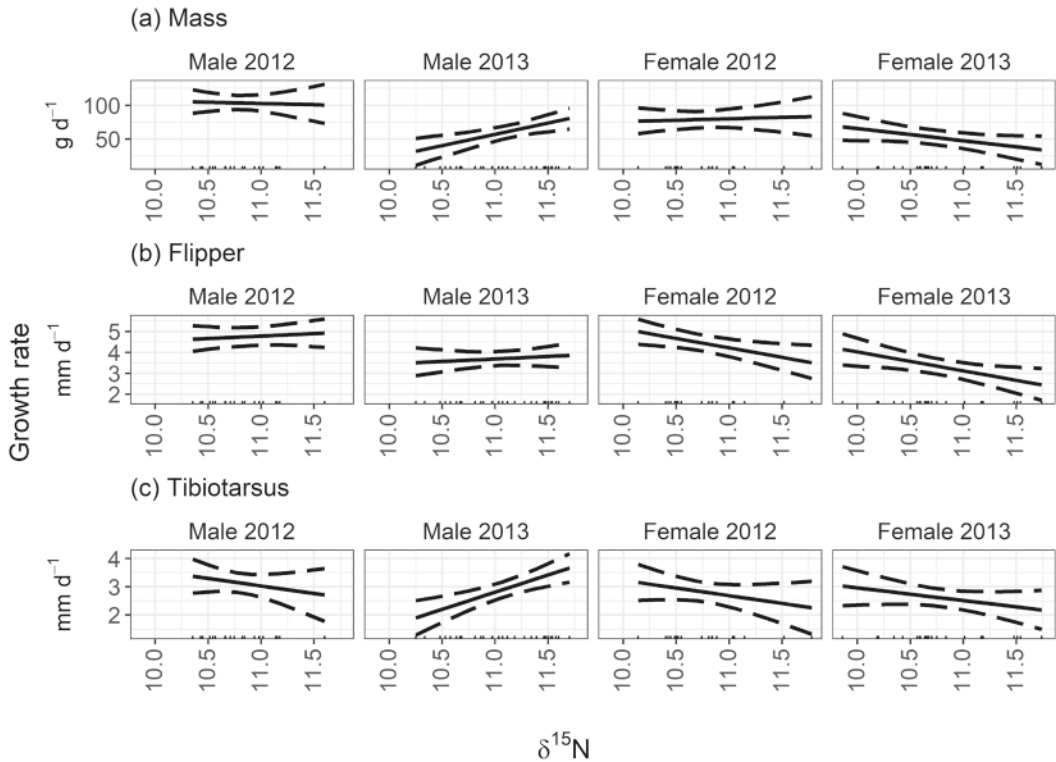


Figure 1. Relationships between growth rates (mass, flipper and tibiotarsus) and $\delta^{15}\text{N}$ (ratio of ^{15}N to ^{14}N ; higher value indicates higher proportion of fish in the diet) for all Adélie Penguin (*Pygoscelis adeliae*) chicks measured at Cape Crozier, Ross Island, Antarctica, during 2012 and 2013. Estimates (solid line) and 95% CI (dashed lines) are from the best model, across the range of $\delta^{15}\text{N}$ values observed for each sex-year group. Hash marks along the x axis represent raw data. Note different units and scales for y-axes.

el, the coefficient for the effect of FOOD was positive and had 95% CI that did not include zero, indicating strong support for a relationship between mass growth and FOOD. In this case, each additional gram of food delivered per chick per day was associated with an increase in mass growth rate of 0.08 g day^{-1} (online Appendix Table A2) and this relationship was the same for both sexes in both years (Fig. 2). It should be noted that there were only three females in the WB sample during 2013, so there was limited information to detect a sex-by-year interaction if it existed.

Comparing the effect of ^{15}N to parent age

The KA data subset was used to evaluate the importance of parent age, relative to ^{15}N , in predicting chick growth rates during 2013 (data only available for this year). Parent age was supported as an important variable in predicting foot and bill growth rates but was not

included in top models for growth of any of the other morphological characters (Table 3; online Appendix Table A1). For both of these morphological characters the relationship between growth and parent age was contrary to what we predicted; foot growth initially decreased with increasing parent age before increasing slightly in the oldest parents, and bill growth was slower in chicks with older parents (Fig. 3). Although parent age was included in competitive models for tibiotarsus and flipper growth (online Appendix Table A1), the model ranking nonetheless indicated more support for ^{15}N than parent age in predicting growth of these 3 morphological characters.

DISCUSSION

We measured three aspects of parental investment during chick rearing: 1) average food delivered chick $^{-1} \text{ d}^{-1}$ (FOOD; more

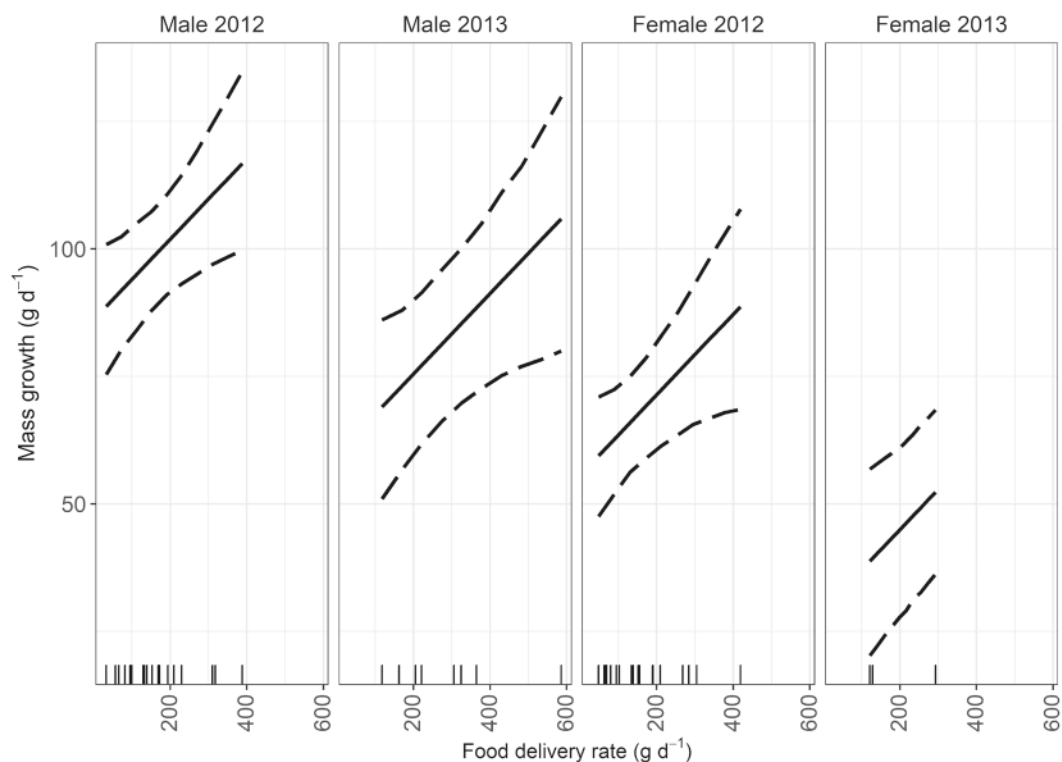


Figure 2. Relationships between mass growth rate and food delivery rate for Adélie Penguin (*Pygoscelis adeliae*) chicks in the Weighbridge data subset at Cape Crozier, Ross Island, Antarctica, during 2012 and 2013. Estimates (solid line) and 95% CI (dashed lines) are from the best-supported model. Hash marks along the x axis represent raw data.

= higher investment); 2) average foraging trip duration (FTD; shorter = higher investment); and 3) relative caloric value of food provided to chicks (as estimated by ^{15}N ; higher = greater fish:krill ratio = higher investment). We predicted that greater parental investment would be associated with faster growth rates, and this prediction was partially supported by our data. FOOD was positively associated with mass growth rates for chicks of both sexes during both years. FTD was negatively related to foot growth rates. And a diet containing more fish (higher caloric value) was positively related to male chick mass and flipper growth during the year of reduced reproductive success (2013). We also predicted faster growth of chicks raised by older parents, but our data indicated that chicks from younger parents grew faster than chicks from older parents. This is perhaps suggestive of senescence in older parents (but see foot growth of chicks

from very old parents, Fig. 3a) or a loss of phenotypes that over-invest in reproduction as the population ages (Lescroël *et al.* 2010; Kappes *et al.* 2021).

Male Adélie Penguin chicks in this study grew faster than females, and in a separate analysis of single sex broods only appeared to have been provisioned with more fish than females (Jennings *et al.* 2016). Average FTD was longer in 2013, and it may be that a diet having more fish was required to maintain the faster male growth rates when there was a greater time between individual feedings, perhaps due to lower availability of krill. These conclusions at least partially agree with the energetic modelling of Chapman *et al.* (2011), who found that the addition of higher lipid silverfish can compensate for reduced overall provisioning rate. Female chicks, with their overall slower growth rates, may have been less sensitive to increased time between feedings, and

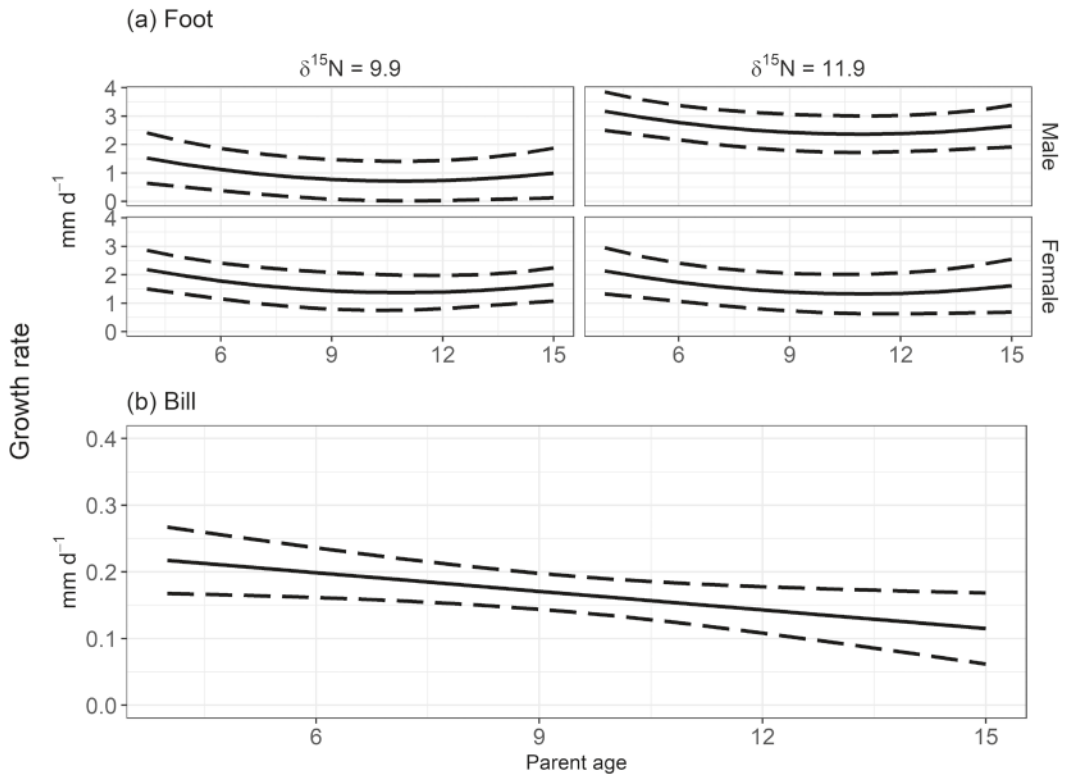


Figure 3. Relationship between estimated growth rates (foot and bill) and parent age for Adélie Penguin (*Pygoscelis adeliae*) chicks in the known-age data subset at Cape Crozier, Ross Island, Antarctica, during 2012 and 2013. Estimates (solid line) and 95% CI (dashed lines) are from the best models, across the range of observed parent age values and for both years combined. Hash marks along the x-axis represent raw data. For foot, estimates are shown at 2 values for $\delta^{15}\text{N}$ that represented the observed range for this variable, and the hash marks for each sub-plot show all the data.

less needy of a higher lipid diet, although the overall negative effect of a higher proportion of fish in their diet on their growth rates, especially flipper growth, suggests a potential trade off in parental investment (preferentially feeding male, or perhaps larger chicks that happened to be males). It appears that flipper growth continues well after fledging from the colony (Jennings *et al.* 2016), so it is unclear what effect this reduced flipper growth may have had on foraging or survival of recently fledged females in 2013. Our results indicate that some parents may have underinvested in offspring of the more expensive sex during the challenging year (male chicks fed less fish had the slowest mass and tibiotarsus growth rates of any chicks in the study), which at least partially agrees with the Trivers-Willard hypothesis. Adult male Adélie Penguins are responsible

for early-season territory initiation and defense, and larger individuals appear to have an advantage in territorial contests (Ainley 2002). It appears that adult males also have a diet higher in fish (Massaro *et al.* 2020), so these sex related differences in dietary requirements may persist through life. Parents who cannot increase investment in male chicks during challenging conditions may “cut their losses” because males may never achieve adequate reproductive success to warrant even normal effort. However, our results and interpretations on sex-based differences related to FOOD and FTD during the challenging year should be taken as preliminary, owing to the smaller sample size of WB nests that year (including only three female chicks). It should also be noted that our assumption of equal food distribution among siblings may not have held if parents were

limited in their ability to provision two-chick broods. In Wandering Albatross (*Diomedea exulans*) male chicks also grow faster but they are also fed more (Weimerskirch *et al.* 2000). However, we believe that, if present, this phenomenon would lessen the strength of the relationships we found.

The relationships we observed between provisioning and growth rates are likely to be relevant not just to eventual reproductive success, but also to chicks' post-fledging survival and fitness. In the western Antarctic Peninsula, a difference in mean fledging mass of only 117 g (~5% of fledging mass) separated chicks that returned to recruit into the breeding population and those that did not (Chapman *et al.* 2010). In the Ross Island Adélie Penguin population, the average difference between the two groups during 2001-2012 was 220 g (~6.5%) and chicks fledging at a heavier mass did have a higher probability of surviving (Ainley *et al.* 2018). The differences observed here in estimated daily growth rates of chicks that were provisioned differently (more often, with more food, or with a proportionally greater contribution of fish) were great enough to achieve such differences in fledging mass (Whitehead *et al.* 2015).

Our results also have important implications for understanding how parents modulate their own condition during breeding. The variation in FTD and FOOD we observed are of a magnitude that has been linked to meaningful variation in parent condition throughout the breeding season. The upper values for both variables are associated with loss of parent mass throughout the provisioning period, while lower values were associated with mass gain (Ballard *et al.* 2010), and a 1‰ increase in $\delta^{15}\text{N}$ corresponded to an approximate 10% increase in the proportion of chicks' diet contributed by fish (Ainley *et al.* 2003). While no data exist to directly compare the relative costs to parents of provisioning with krill vs. fish, this difference in proportion of fish may be costly to parents, as securing fish may involve deeper diving (Ainley *et al.* 2015). Thus, these

results identify a possible mechanism for variation in parent fitness based on parental foraging ability (Lescroël *et al.* 2010). While FTD was longer in 2013 than 2012, perhaps related to food limitation, it was not longer than is generally thought to be sufficient to maintain chick growth in this species (~1-2 days; Clarke *et al.* 2002; Ballard *et al.* 2010). Thus, conditions during 2013 were evidently still within the range of variability to which this species is adapted, though apparently not all parents could cope equally well (Lescroël *et al.* 2019 and citations therein for further treatment of differences in individual breeding capacity) but quality in the context of environmental variability has rarely been evaluated. We investigated the demographic responses of a long-lived seabird, the Adélie penguin (*Pygoscelis adeliae*). It appears that the parents in our sample who were able to breed during 2013 compensated for apparent reduced food-availability by making slightly longer-duration foraging trips while maintaining sufficient food delivered per day, and their chicks grew faster if fed more fish.

We showed that increasing parental care (with likely impact on parent condition) in a long-lived seabird species appeared to have a stronger influence on chick growth in times of apparent resource limitation, and that offspring sex may play a role in the trade-off between these optimizations. This greater understanding of the consequences for offspring growth of the interaction between parental effort and environmental variability can be particularly important for the management and conservation of species living in high latitudes or other areas with increasingly unpredictable food availability. Perhaps with a higher quality diet (more fish), Adélie Penguins are better able to cope with years of generally lowered prey availability, and mitigating these 'troughs' could be one of the factors behind their rapidly increasing populations in the southern Ross Sea (Lyver *et al.* 2014) and disappearance from western Antarctic Peninsula where they have only krill to eat (Schofield *et al.* 2010; Sailley *et al.* 2013; Cimino *et al.* 2014).

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