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Faster growth and larger size at crèche onset are associated with higher offspring survival in Adélie Penguins

Scott Jennings,[1,a,] (iD) **Katie M. Dugger,**[2] **Grant Ballard,**[3] **and David G. Ainley**[4]

[1]Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries, Wildlife, and Conservation Sciences, Oregon State University, Corvallis, Oregon, USA
[2]U.S. Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries, Wildlife, and Conservation Sciences, Oregon State University, Corvallis, Oregon, USA
[3]Point Blue Conservation Science, Petaluma, California, USA
[4]H.T. Harvey and Associates Ecological Consultants, Los Gatos, California, USA
[a]Current address: Audubon Canyon Ranch, Cypress Grove Research Center, Marshall, California, USA
Corresponding author: scott.jennings@egret.org

ABSTRACT

We conducted the first assessment of Adélie Penguin (*Pygoscelis adeliae*) chick survival that accounts for imperfect resighting. We found that when chicks are larger in size when they enter the crèche stage (the period when both parents forage at the same time and chicks are left relatively unprotected), they have a higher probability of survival to fledging. We investigated the relationships between growth, crèche timing, and chick survival during one typical year and one year of reduced food availability. Chicks that hatched earlier in the season entered the crèche stage older, and chicks that both grew faster and crèched older entered the crèche at a larger size. These relationships were stronger in the year of reduced food availability. Thus, parents increased their chicks' chance of fledging if they provided sufficient food for faster growth rates and/or extended the length of the brood-guarding period. Early nest initiation (i.e., early hatching) provided parents with the opportunity to extend the guard period and increase chick survival. However, to extend the guard stage successfully, they must provide larger meals and maintain higher chick growth rates, even if just one parent at a time is foraging, which previous work has shown is not possible for all individuals. We show that the factors governing tradeoffs in chick-rearing behavior of Adélie Penguin parents may vary in accord with environmental conditions, a result from which we can better understand species' adaptations to environmental changes.

Key words: Adélie Penguin, brood guarding, crèche, growth, *Pygoscelis adeliae*, survival

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LAY SUMMARY

- When raising dependent young, animals must balance how much to invest in guarding the brood versus finding food for them. These so-called tradeoffs can influence how well the current brood grows and survives to independence.
- During two breeding seasons, one typical and one apparently food limited, we related Adélie Penguin chick survival rates to how fast they grew and the timing of a critical transition in brood-rearing when chicks switch from being guarded continuously by a parent to being left alone while both parents forage at the same time.
- We found that with a combination of early hatching and fast-growing, chicks entered the unguarded ("crèche") stage older and larger and, therefore, had a better chance of surviving to independence.
- Certain parents can manage tradeoffs to maximize breeding success even during unfavorable conditions. These results can help us understand how populations will respond to changing climate and habitats.

Un crecimiento más rápido y un tamaño más grande al inicio de la guardería se asocian con una mayor supervivencia de las crías en Pygoscelis adeliae

RESUMEN

Realizamos la primera evaluación de la supervivencia de los polluelos de Pygoscelis adeliae que consideran los re-avistamientos imperfectos. Encontramos que cuando los polluelos son más grandes en tamaño al momento de ingresar a la etapa de guardería (el período en el que ambos progenitores se alimentan al mismo tiempo y los polluelos quedan relativamente desprotegidos), tienen una mayor probabilidad de sobrevivir hasta emplumar. Investigamos las relaciones entre el crecimiento, el tiempo de guardería y la supervivencia de los polluelos durante un año típico y un año de disponibilidad reducida de alimentos. Los polluelos que nacieron más temprano en la temporada entraron en la etapa de guardería más viejos, y los polluelos que crecieron más rápido y comenzaron la guardería más viejos entraron a la guardería con un tamaño más grande. Estas relaciones fueron más fuertes en el año de menor disponibilidad de alimentos. En consecuencia, los padres aumentaban la posibilidad de que sus polluelos emplumaran si proporcionaban suficiente alimento para alcanzar tasas de crecimiento más rápidas y/o si extendían la duración del período de cuidado de la nidada. La iniciación temprana del nido (i.e., eclosión temprana) brindó a los progenitores la oportunidad de extender el período de cuidado y aumentar la supervivencia de los polluelos. Sin embargo, para extender la etapa de cuidado con éxito, deben proporcionar comidas más grandes y mantener tasas de crecimiento de los polluelos más altas, incluso si solo uno de los progenitores a la vez está buscando alimento, lo que no es posible para todos los individuos, según lo indicado por trabajos anteriores. Mostramos que los factores que rigen las soluciones de compromiso en el comportamiento de cría de los polluelos por parte de los progenitores de P. adeliae puede variar de acuerdo con las condiciones ambientales, un resultado a partir del cual podemos comprender mejor las adaptaciones de las especies a los cambios ambientales.

Palabras clave: crecimiento, cuidado de la nidada, guardería, Pingüino de Adelia, Pygoscelis adeliae, supervivencia

INTRODUCTION

Tradeoffs in behavior and energy expenditure are a central component of life history theory (Stearns 1989), and tradeoffs during reproduction can have a large impact on an individual's lifetime fitness (Bell 1980). Evaluating these tradeoffs from the perspective of the parents' fitness (i.e., how much to invest in current vs. future reproductive efforts) has received considerable attention (Williams and Fowler 2015). However, the effect of variation in parents' behavior on the future survival of their offspring is also an important component of these reproductive tradeoffs (Stearns 1989). Both parental effort and offspring growth rates are adaptively flexible, and where growth rate is plastic, there are often tradeoffs between growth rate and risk of mortality (Abrams et al. 1996, Ghalambor et al. 2013). Furthermore, parental tradeoffs often become more critical when resources are limited and offspring are exposed to greater restriction of provisioning or guarding as parents devote more of their time and energy to self-care (Clutton-Brock et al. 1985, Beauplet et al. 2005, Rowland et al. 2007).

It has long been recognized that food availability is a key determinant in avian reproductive timing and output (Lack 1968, Drent and Daan 1980). However, risks to young from predation or inclement weather can also strongly impact reproductive success, necessitating that avian parents can identify changes in predation risk and adjust reproductive investment accordingly (Komdeur 1999, Dillon and Conway 2018). When acquiring food is difficult and requires more time away from the nest, and there is a risk to offspring that can be minimized by parental guarding, an important tradeoff exists in how parents allocate their time (Ghalambor et al. 2013). There may also be constraints on parents who need to begin replenishing their own resources before onset of molt or winter weather (Ballard et al. 2010), with parents adjusting their breeding investment based on their own energetic needs (Erikstad et al. 1997, Jodice et al. 2002).

Several colonial-nesting avian species partially mitigate predation and exposure risks to unguarded chicks by chicks from multiple nests gathering in protective groups called crèches while both parents are away foraging (Munro and Bédard 1977, Evans 1984, Wanker et al. 1996). Variation in the duration of the guarded period appears to be an adaptive response to parent, chick, and environmental conditions (Ims 1990, Tveraa et al. 1998, Catry et al. 2006, Rothenbach and Kelly 2012, Dupont et al. 2021). However, increased predation or other environmental risks to young may extend the brood-guarding period, while food shortages or other constraints on parents' foraging effort may lead to earlier crèche onset (Tenaza 1971, Catry et al. 2009). Chicks are often most at risk during the first few days of the unguarded (crèche) stage, but this risk may be mitigated when chicks are left alone older or larger (Davis 1982, Catry et al. 2006, 2010).

Although theory, supported by empirical work, predicts tradeoffs between the competing offspring needs of fast growth and protection, there is also evidence that these tradeoffs do not exist for all parents or in all circumstances. The impact of parental tradeoffs may vary as environmental conditions and resource availability shift (Stearns 1989), and it appears that some high-quality individuals can maximize multiple life-history traits simultaneously, sometimes even under challenging conditions (Lescroël et al. 2009, Williams and Fowler 2015). However, the extent to which parents tradeoff between chick provisioning and chick defense under varying environmental conditions, and how these tradeoffs influence offspring outcomes, remain poorly studied.

We used data from a large nesting colony of the Adélie Penguin (*Pygoscelis adeliae*) to evaluate evidence supporting tradeoffs between brood-guarding duration and chick growth rate. We also evaluated the consequences of growth rate and guard stage duration variability on chick survival. The Adélie Penguin raises 1 or 2 chicks, which crèche 15–30 days after hatching (Davis 1982). Chicks grow faster when they are fed more frequently and with higher quality food (Chapman et al. 2011, Jennings et al. 2021), and they receive more food and grow faster when both parents forage simultaneously during the crèche stage (Culik 1994, Salihoglu et al. 2001). Prior studies have shown that crèche stage survival is variable ranging from low to high (Taylor 1962, Volkman and Trivelpiece 1980, Clarke et al. 2002). However, where small colony size or clement environmental factors mean parent foraging trips are short and chicks are well fed, crèching frequently does not occur (Ainley et al. 2018). This indicates that there are chick survival costs to crèching, especially with the time pressure to reach sufficient size for survival caused by the short Antarctic breeding season (Ainley et al. 1983). Adélie Penguin chick mortality is mostly due to skua (*Stercorarius* spp.) predation and exposure to harsh weather (especially wetting when temperatures rise above freezing), and chicks generally become less susceptible to these risks as they grow larger (Davis 1982, Salihoglu et al. 2001). Thus, there appear to be 2 conflicting pressures that determine the length of brood guarding: Shorter guard period with greater risk but faster growth rate
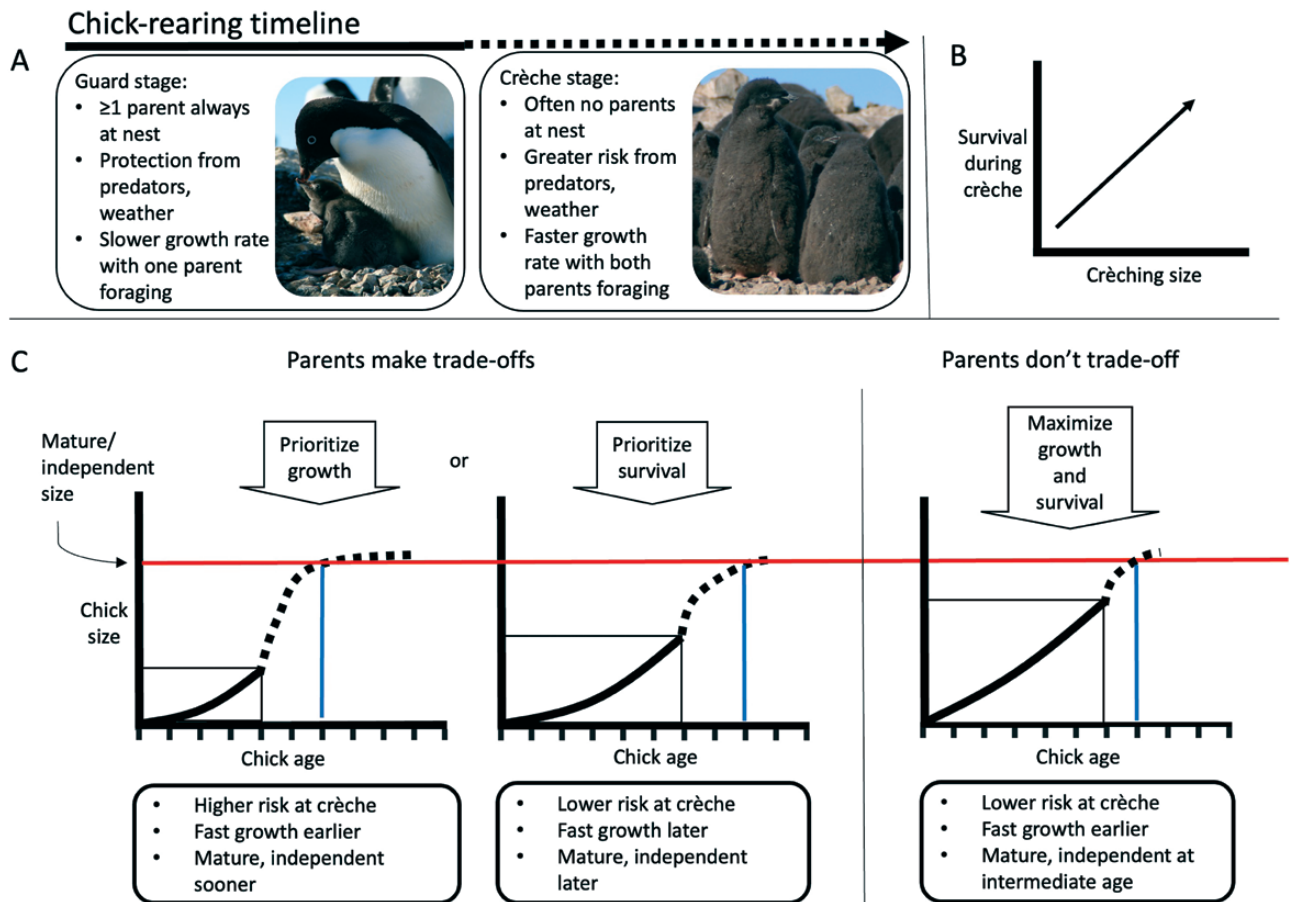
FIGURE 1. Conceptual diagram related to hypotheses and predictions about Adélie Penguin chick growth and survival at Cape Crozier, Ross Island, Antarctica, during the Austral summers of 2012–13 and 2013–14. (A) Overview of the timeline and main components of the two main stages of chick rearing. (B) Hypothesized relationship between chick survival during the crèche stage and the size at which they enter the crèche stage. (C) Predictions related to hypothesized tradeoffs between prioritizing chick growth (left panel) vs chick survival (middle panel); in contrast, if parents do not trade-off, we predict they can maximize chick growth and guarding duration. In panels (A) and (C), the solid line indicates guard stage and dashed line indicated crèche stage. In (C), the horizontal line crossing all sub plots indicates the size at which chicks are mature/independent and can fledge (leave the colony), vertical lines at the intersection of the growth curve and mature/independent lines indicate the age at which this size is reached under the different hypothesized strategies, and the thin lines aid comparing the size and age at crèche onset.

and possibly larger fledging size, or longer guard stage with less risk but also slower growth rate and perhaps fledging smaller.

Our specific goals were to determine if Adélie Penguin parents vary in their ability to make tradeoffs between chick guarding and chick provisioning, and how that might influence pre-fledging chick survival. We hypothesized that chick survival during the crèche stage would be positively related to chick age and size at crèching, with smaller crèching or younger crèching chicks initially at higher risk but also growing faster with both parents simultaneously provisioning. Alternatively, larger crèching or older crèching chicks would experience lower predation or weather risk but would exhibit slower growth (Figure 1). We used data from 2 years that appeared to have contrasting food availability but similar weather and predation risk (see "Methods"), and we expected tradeoffs to be stronger during the more challenging year. Because we wanted to establish how survival changed during the chick-rearing period, and specifically upon the transition to crèche stage, we first investigated chick survival during the entire chick-provisioning period (guarding and crèche stages). We then investigated chick survival only during the crèche

stage to test our prediction that chicks entering the crèche older and/or larger will have a higher probability of surviving to fledge (Figure 1B). Finally, we investigated how chick growth rates and crèche-timing related to chick age and size at crèche onset to understand the degree to which parents can balance tradeoffs between provisioning chicks (maximize growth) and defending them (Figure 1C). If our hypothesized tradeoffs between growth and brood guarding were true, we expected to observe a negative relationship between growth and crèche timing, and crèching age alone would be the best predictor of crèching size. In contrast, if crèching size is best predicted by growth rate and crèching age together, this would support the idea that (at least some) parents can simultaneously maximize both, even under trying conditions.

METHODS

Study System

This study was conducted on Cape Crozier, Ross Island, Antarctica (77°27′15.00″S, 169°13′45.00″E) during the summers of 2012–2013 and 2013–2014 (hereafter 2012 and 2013, respectively). Cape Crozier is the largest Adélie Penguin

colony in the southern Ross Sea and one of the largest for the species (Lynch and LaRue 2014). It is surrounded by hundreds of nesting South Polar Skuas (*Stercorarius maccormicki*), with most of the colony within skua foraging territories (Wilson et al. 2017). Our study included 43 chicks in 2012 and 69 chicks in 2013 (112 total). Across both years, 84 chicks survived to the crèche stage and could be used to model crèching size and age and survival during that period. The mean crèching age was 21.3 days (SE = 0.46, range: 15–26, *n* = 33) in 2012, and 18.9 days (SE = 0.41, range: 10–25, *n* = 51) in 2013.

Across the entire colony, not just study chicks, we observed that substantially more chicks died from apparent starvation in 2013 than in 2012. Although the average amount of food delivered to chicks per day was similar between the 2 years, in 2013 there was a longer interval between food deliveries, indicating that parents required more time foraging to provision their chicks (Jennings et al. 2021). Chick fledging mass in 2013 (mean ± SD = 2,741 ± 483 g, *n* = 110) was the lowest recorded between 2000 and 2016, but in 2012 (2,948 ± 626 g, *n* = 206) it was approximately average for that time period (Ainley et al. 2018). Similar patterns in chick mortality and fledging size were observed at Cape Crozier during 2001–2005 when large icebergs made ocean access more difficult and increased the duration of foraging trips, leading to lower chick feeding rate (Ballard et al. 2010, Dugger et al. 2014). During the present study, in 2013, chick carcasses accumulated at a rate to indicate the supply of carrion was apparently greater than the skua demand, and most of these carcasses had empty stomachs and no sign of predation or scavenging, neither of which was not observed in 2012. Although we did not collect data to quantify annual variation in skua population size or predation pressure during our study, we did not observe any evidence of differences between 2012 and 2013. Nor did frequency of high wind events or temperatures differ between the 2 years (Supplementary Figure S1). Thus, chick-raising challenges of 2013 apparently resulted from food availability and not predation pressure or weather.

Beyond provisioning and brood guarding, other Adélie Penguin parental behaviors and characteristics can influence chick growth rates and outcomes. Older and more experienced parents start breeding earlier in the spring (Ainley et al. 1983) and are generally more successful (Taylor 1962, Lescroël et al. 2009, Kappes et al. 2021), although parent age is a poor predictor of chick growth rate for this species (Jennings et al. 2021). However, earlier nesting allows chicks and parents more time to gain weight before the onset of molt and winter weather (Ainley 2002, Chapman et al. 2011). Nests on the colony edge, adjacent to skua territories, experience higher predation risk and are guarded longer (Ainley et al. 1983, Davis and Mccaffrey 1986). First-hatched chicks and those without siblings grow faster than second-hatched ones (Ainley 2002, Jennings et al. 2021), and male chicks average faster growth than females (Jennings et al. 2016).

Data Collection
We systematically selected nests to represent a range of parent ages and nest positions (edge vs. interior). We checked nests every 1–3 days during incubation and chick-rearing to determine hatch day, the first day of crèche stage, and chick fate. On 5-day intervals from 10 days old through the end of the chick-rearing period (50–55 days old; Ainley and Schlatter 1972, Chapman et al. 2011), we measured mass (to nearest 25 g),

and lengths of flipper and tibiotarsus (to 1 mm; Jennings et al. 2016). We individually marked chicks with a T-bar fish tag (Floy Tags Inc., USA) attached to the loose skin on the nape to facilitate individual identification without recapture. Tags were light gray to match the color of juvenal plumage and were removed just before fledging. We determined chick sex molecularly from feather samples (Fridolfsson and Ellegren 1999).

We estimated growth rate for each morphological measurement as the slope coefficient of regression of size on age, fitted to data for the period of linear growth [full details in Jennings et al. (2021)]. Linear growth lasted until 40 days old (mass and flipper) or 35 days old (tibiotarsus). Because chicks crèched when 10–26 days old, our growth rate estimate reflected parental behavior during the guard stage and the beginning of the crèche stage. Adélie Penguin chick growth rate declines and in some cases reverses in the final week or so before fledging (Ainley and Schlatter 1972), and this could be important to overall chick outcomes. However, we only used growth during the linear phase because (1) slope estimates for linear models fitted during this period provided a straightforward and intuitive way to compare growth rate among chicks, and (2) growth during this period was more pertinent to our parameter of interest (crèching size) than growth late in the crèche stage.

We only recaptured chicks every 5 days for measurement. If crèching happened on a scheduled measurement day then crèching size was measured directly, otherwise, it was calculated using the linear model described above (Jennings et al. 2021). We checked chick fate every 2–3 days, identifying their tag with binoculars from ~5 m. We searched for crèched chicks in a radius of ≤25 m around their respective nest. On each attempted resighting we searched until we found the chick (alive or dead) or for 15 min, whichever came first. If a chick was not resighted, we returned and repeated these methods for 4–5 days. If a chick was not detected by day 5, searches were discontinued, and we assumed it had died and was scavenged. Toward the end of the chick-rearing period, as chicks neared fledging age and spent more time closer to beaches, we also conducted several systematic searches for marked chicks along beaches and heavily trafficked routes between nests and beaches.

Analysis
We used prior research and knowledge of the study system to develop an a *priori* model set containing variables to test each of our specific predictions while accounting for the effects of 2 additional variables we thought might have important effects on our response variables. These extra variables were chick sex and relative hatch date (calculated as the difference in days between the hatch date of each chick and the mean hatch date each year). Our sample size limited the number of variables we could include in our models, so we did not include separate variables for parent age, experience, or quality, nor for nest position (see Lescroël et al. 2009). However, the systematic selection of nests from a mix of parent ages and interior vs. edge nest positions ensured our data reflected the average population response across both these factors. In addition, we accounted for any remaining variation in parental quality by including relative hatch date as a covariate and we used relative rather than absolute hatch date to account for

TABLE 1. Names and descriptions of covariates considered in models to estimate the daily survival of Adélie Penguin chicks at Cape Crozier, Ross Island, Antarctica over the entire chick-rearing period (49 days) and over the crèche period only (39 days) during the 2012/2013 and 2013/2014 breeding seasons. Model parameters indicate whether covariate was used for modeling crèche timing (cr), survival (φ), and resighting probability (*p*).

Variable name	Variable description	Model parameters
Year	2012–2013 (0) or 2013–2014 (1)	cr, φ, *p*
Sex	Female (0) or Male (1)	cr, φ, *p*
Time constraints		
t	General time dependence (e.g., variable daily survival within years)	φ, *p*
T	Linear time trend in daily survival within years	φ, *p*
TT	Quadratic time trend in daily survival within years	φ, *p*
ln*T*	Log-linear time trend in daily survival within years.	φ, *p*
Growth rates		
Mass growth	Mass growth rate (g d^{-1})	cr, φ
Flipper growth	Flipper length growth rate (mm d^{-1})	cr, φ
Tibiotarsus growth	Tibiotarsus length growth rate (mm d^{-1})	cr, φ
Crèche size and age[a]		
Crèching mass	Mass on day when entered crèche stage	φ
Crèching flipper	Flipper length on day when entered crèche	φ
Crèching tibio	Tibiotarsus length on day when entered crèche	φ
Crèching age	Age when entered crèche	φ
Time-varying individual covariates		
Crèched	Whether or not a chick is in the crèche stage on a given day within the 49-day monitoring period	φ
Other		
Hatch date	Relative hatch date; calculated separately for each year. Negative value indicates hatch date earlier than yearly average	cr, φ

[a]Note, the crèche size and age variables were response variables in the crèche-timing analysis, and predictors in the survival analysis.

any population level differences in nesting phenology between the 2 years.

We used an information theoretic approach to weigh relative evidence for each model in each model set. We used Akaike Information Criteria (AIC) values corrected for small sample size (AIC$_c$) and for extra binomial variation (QAIC$_c$) to judge the relative support for each candidate model by comparing its value to that of the model with the lowest value (ΔAIC$_c$ or ΔQAIC$_c$; Burnham and Anderson 2002). We used the "build-up" strategy advocated by Morin et al. (2020) to evaluate variable importance while limiting the number of models considered. We first fitted candidate models with additive combinations of year, sex, and relative hatch date and we included the year * sex interaction based on previously established relationships between provisioning and growth rates (Jennings et al. 2021). We retained model structures if they had ΔAIC$_c$ or ΔQAIC$_c$ values ≤5 and no uninformative parameters (95% confidence limits overlapping zero; Arnold 2010). We then added covariates to these competitive structures to answer our research questions (see Supplementary Tables for full candidate models).

Survival.

We used the Cormack-Jolly-Seber open population model (Lebreton et al. 1992) to evaluate relationships between daily survival rates and the predictor variables of interest (Table 1). The Cormack-Jolly-Seber model allowed us to account for a decrease in resighting probabilities over the course of the season as chick mobility increased. We estimated the

overdispersion factor (ĉ) as 1.16, and used this value to adjust variance for estimated model coefficients and calculate Quasi-likelihood AIC$_c$ (QAIC$_c$) values for use in model comparison.

We wanted to estimate: (1) survival across the entire chick-rearing period including the guard-crèche transition (through 49 days to avoid fledged chicks being represented as dead), and (2) the effect of crèching age and size on subsequent survival to fledging during the crèche stage only (final 39 days of chick rearing). Because these 2 objectives required different datasets (not all chicks survived long enough for objective 2), we did a similar but separate model selection procedure for each. For both objectives, we first found competitive structures for daily survival rate (φ) and resighting (*p*) probabilities, while holding *p* and φ, respectively, at a general structure that represented the most complicated combination of covariates we thought might be important sources of variation in resighting or survival (Year × Sex + *t*). Here, "*t*" is the general variation in daily survival (i.e., survival varies independently by day). In addition to the year, sex, and hatch date variables, we also evaluated temporal variation in φ, including linear (T), quadratic (TT), and natural log (ln*T*) trends within each season. We compared competitive structures from these first 2 model sets to arrive at the φ and *p* structures that would be used to evaluate variables of interest (candidate sets for the first and second survival objectives in Supplementary Tables S1 and S3, respectively). Then our model sets diverged to address our 2 objectives. To evaluate overall patterns of daily survival probability and how survival probability changed upon crèche onset (first objective in survival analysis), we added

the time-varying individual covariate for whether a chick was in the crèche stage on a particular day (coded 1 = crèched, 0 = guarded, candidate models in Supplementary Table S2). For survival during crèche stage only (objective 2), we added individual covariates representing the size and age at which each chick entered the crèche stage to the best base model structures for ϕ and p (candidate models in Supplementary Table S4). However, we found that hatch date and crèching age were correlated (Pearson correlation $r = -0.63$), so we did not consider any models that contained both predictors.

Growth rates and crèche timing.

We used separate model sets to answer the 4 questions of interest: (1) does mass, flipper, or tibiotarsus growth rate predict age at crèching, (2) does mass growth rate predict mass at crèching, (3) does flipper growth rate predict flipper length at crèching, and (4) does tibiotarsus growth rate predict tibiotarsus length at crèching? We initially accounted for lack of independence between siblings with mixed effects models with a random effect for Nest ID. However, the estimated random effect variance was zero or very small relative to the residual variance, so we used linear models with fixed effects only (Zuur et al. 2009). For all four questions, we first determined the competitive year, sex, and hatch date structure, then we added growth rates to answer each of our research questions (candidate model sets in Supplementary Tables S5–8). For questions 2–4, the candidate set for the first step also included crèching age, but hatch date and crèching age were correlated (Pearson correlation, $r = -0.63$), so we did consider any models that contained both.

We used R 4.0.2 (R Core Team 2020) for all analyses. We used base R for linear models and used program Mark implemented in RMark 2.2.7 (Laake 2013) for survival analysis. We used RELEASE (implemented via RMark) to estimate overdispersion of our most general model that did not contain individual covariates (Cooch and White 2019). We report estimated model coefficients and predictions along with their standard error and 95% confidence interval (CI).

RESULTS

Survival

For our first survival objective, after eliminating survival probability (ϕ) and resighting probability (p) structures with $\Delta QAIC_c \geq 5$ and uninformative parameters, we carried forward year, hatch date, T, and TT structures to the final modeling step (Supplementary Table S1). In that final step, there was good support for crèche status as a useful predictor of survival. The [ϕ (year + hatch date + T + crèche)] model had the lowest $QAIC_c$ value, and a similar model including the quadratic time effect (TT) had the next lowest $QAIC_c$, but the quadratic coefficient was uninformative ($\beta = -0.001$, 95% CI: -0.004 to 0.001). This indicates that the linear time effect (T) best represented the temporal variation in the data (Supplementary Table S2). Because we were particularly interested in contrasting survival between guard and crèche stages, based on these model selection results we added one *a posteriori* model to the candidate set with the interaction between T and crèche status: [ϕ (year + hatch date + T × crèche)]. Although this model received some support ($\Delta QAIC_c = 2.1$), the interaction term was uninformative ($\beta = 0.01$, 95% CI: -0.08 to 0.12) and the top model without the interaction re-
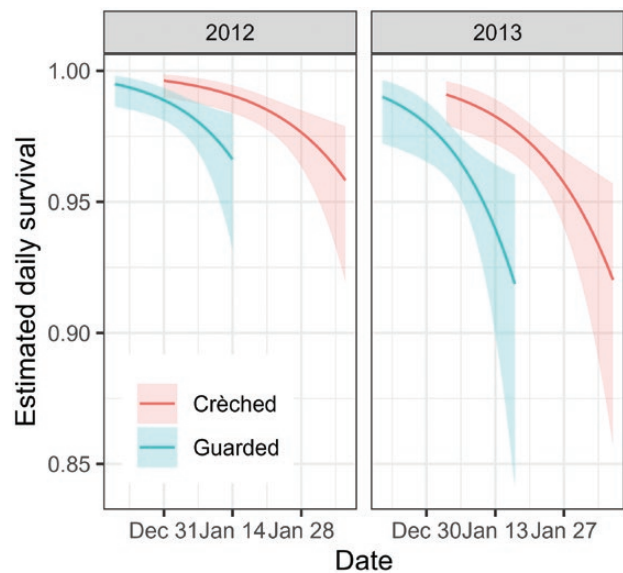

FIGURE 2. Estimates of daily survival probability from the best model evaluating survival across the entire chick-rearing period for Adélie Penguin chicks at Cape Crozier, Ross Island, Antarctica, during the Austral summers of 2012–13 and 2013–14. These estimates are for all chicks included in the study, survival estimates for the guarded period are shown from the start of the study (November 1) through the latest day chicks entered the crèche stage each year (January 14, 2013, and January 17, 2014), and crèche period estimates are shown starting with the earliest crèche day each year (December 31, 2012, and January 3, 2014) through the last day of the study (February 7 both years). The ribbons represent the 95% confidence interval around the estimates.

ceived 2.9 times more support. Therefore, we based inference on the top model with the additive linear trend [ϕ (year + hatch date + T + crèche)].

In that model the coefficient for the linear time effect was negative ($\beta = -0.07$, SE = 0.02, 95% CI: -0.12 to -0.02), indicating a decline in survival probability through the season both before and after crèching. However, the coefficient for crèche status in this model indicated a higher survival probability for crèched than guarded chicks (crèched $\beta = 1.25$, SE = 0.47, 95% CI: 0.25–2.25). Thus, entering the crèche stage increased each chick's chance of survival relative to remaining guarded, but the bump in survival was not sufficient to reverse the overall negative trend in survival as the chick-rearing period progressed (Figure 2). Furthermore, the difference between guard vs. crèche survival and the overall survival decline were largest in 2013, the year of apparently limited food availability. For example, on the median day that chicks entered the crèche in 2012 (January 8), the daily survival probability of a crèched chick was 0.994 (SE = 0.003; 95% CI: 0.986–.997), whereas, for a guarded chick, it was 0.980 (SE = 0.006; 95% CI: 0.962–0.989), a difference of 0.014. In contrast, on the median crèche day in 2013 (January 9) the daily survival probability was 0.987 (SE = 0.005; 95% CI: 0.973–0.994) for crèched and 0.957 (SE = 0.010; 95% CI: 0.931–0.973) for guarded chicks, a difference of 0.026.

The initial stages of covariate selection to evaluate how well the age and size at which chicks entered the crèche predicted survival during the crèche stage resulted in similar model structures to those identified as important for our first survival objective (Supplementary Table S3). When we added individual covariates for crèching age and size to the
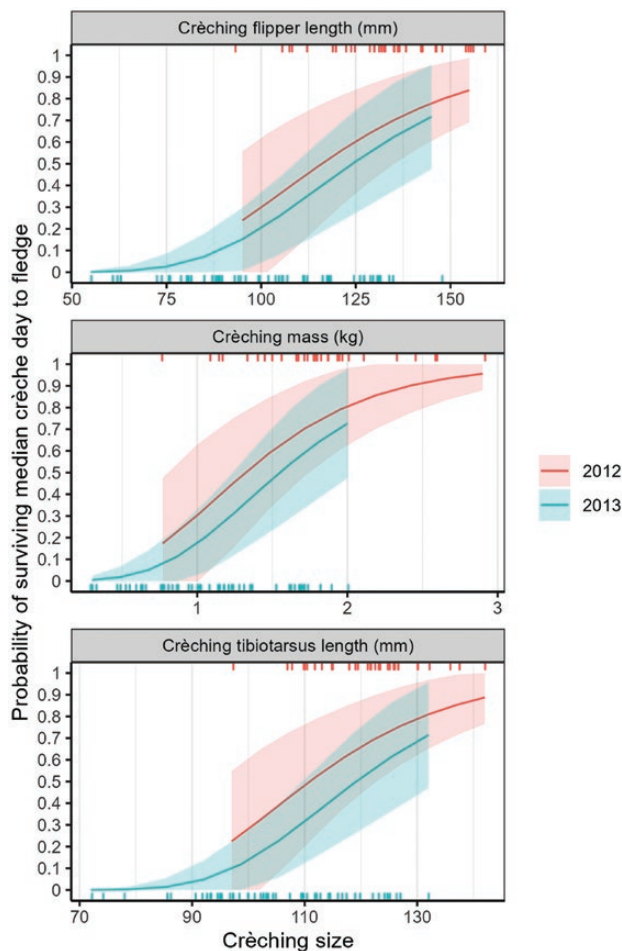
FIGURE 3. Estimates of the probability of survival from mean crèching day to fledging as a function of size at crèching for Adélie Penguin chicks at Cape Crozier, Ross Island, Antarctica, during the Austral summers of 2012–2013 and 2013–2014. Survival estimates are from best-supported models for flipper, mass, and tibiotarsus size at crèching; 95% confidence intervals were calculated using the delta method. Because this calculation is done on the scale of the response variable (i.e., back transformed from link scale), values outside the 0–1 limits are not mathematically possible so these values were clipped to the 0–1 limits prior to plotting. These estimates were based on a subset of chicks that lived long enough to enter the crèche stage and estimates were calculated across the range of size values that those chicks entered the crèche at (ticks along upper and lower x-axes). Estimates were calculated from the mean crèching date (January 8) through the end of the study period (February 7).

competitive base models (Supplementary Table S3C), several models within 5 ΔQAIC$_c$ included crèching size, but crèching age was not supported as a predictor of survival during the crèche period (Supplementary Table S4). The coefficients for crèching size in all these models were positive (Table 2). Thus, there was good evidence that larger crèching chicks had higher daily survival rates (Figure 3), but there appeared to be no survival benefit to crèching at an older age.

Growth Rate and Crèche Timing
The effect of year and hatch date received the most support for predicting age at crèching (Supplementary Table S5). The models with mass, flipper, and tibiotarsus growth rates had ΔAIC$_c$ values ≤3 but these growth coefficients were unin-

formative (95% CI broadly overlapping 0; Table 3). Thus, based on the coefficients from the best model only, chicks entered the crèche stage about 0.5 days younger for each day later in the season that they hatched and they crèched about 1.9 days younger in 2013 than in 2012 (Table 3).

For mass, flipper length, and tibiotarsus length at crèching, the model with the additive year, crèching age, and growth rate effects had the lowest AIC$_c$ values for each morphological character (Supplementary Tables S6–8). For crèching mass, the model with the above structure and the additive sex effect was also supported (ΔAIC$_c$ = 1.01), but the sex coefficient was uninformative, so we do not use this model for inference. For all 3 morphological characters, chicks that both grew faster and crèched older were the ones that crèched larger (Table 4).

DISCUSSION
In what appears to be the first study to evaluate Adélie Penguin chick survival while accounting for imperfect resighting, we found that although the transition to crèche stage was associated with an increase in daily survival probability, daily survival probability nevertheless declined throughout the entire chick-rearing period. The sharpest declines occurred in the crèche stage during the last 10–15 days before fledging. Additionally, we found that chicks had a higher probability of surviving to fledge if they were larger at crèche onset, but we found no such relationship with the age at which chicks joined a crèche. Finally, we found that Adélie Penguin chicks entered the crèche stage older when they hatched earlier in the season, and we found that they entered the crèche stage larger when they had entered the crèche both older and after experiencing faster growth.

These results support our first prediction that larger crèching chicks would survive to fledge at higher rates. Likely mechanisms for this are that larger chicks can better ward off attacks by skuas and they may be less susceptible to adverse weather (Davis 1982, Young 1994, Ainley 2002). We also predicted that older crèching chicks would survive better, but this was not supported by our data, indicating crèching size is more important than crèching age for chick survival. Our results did not support our second prediction that parents were making tradeoffs between chick provisioning and chick defense. Rather, because *both* crèching age and growth rates together were good predictors of crèching size, some parents appeared to maximize chick growth rates while at the same time retaining one parent at the nest for chick defense despite the short breeding season. Therefore, these parents at least partially avoided tradeoffs between growth and defense, supporting previous findings (Ballard et al. 2010, Lescroël et al. 2010).

We found that growth rate was a good predictor of crèching size, and that crèching size was a good predictor of survival to fledging. Provisioning rate was previously shown to be a good predictor of chick growth rate (Chapman et al. 2011, Jennings et al. 2021). Especially under challenging environmental conditions, only a small proportion of breeding adults contribute to that year's cohort of new chicks (Lescroël et al. 2009, 2010), and in challenging years provisioning with more energy-dense fish was associated with faster growth rates (Ainley et al. 2018, Jennings et al. 2021). Considering our results in the context of these past studies, we suggest a mechanistic pathway for high-quality parents to

TABLE 2. Estimated model coefficients and 95% confidence intervals (95% CIs) for competitive models evaluating the effect of crèching size on subsequent daily survival probability of Adélie Penguin chicks at Cape Crozier, Ross Island, Antarctica, during the Austral summers of 2012–13 and 2013–2014. Size measurements estimated at crèching were mass (g), flipper length (mm), and tibiotarsus length (mm). Also shown for each model is the difference in Akaike Information Criterion values corrected for overdispersion and small sample size (QAIC$_c$) between the current model and the one with the lowest QAICc (ΔQAIC$_c$). See Table 1 for description of model variables.

	Estimated coefficients (95% CI)			
Model structure	Year	Time (TT or ln$T$)	Crèching size (flipper, mass, or tibio)	ΔQAIC$_c$
Yr [a] + T + Crèching flipper	−0.29 (−1.20; 0.62)	−0.11 (−0.16; −0.07)	0.036 (0.017; 0.054)	0.00
Yr [a] + T + Crèching mass	−0.40 (−1.30; 0.50)	−0.11 (−0.15; −0.06)	0.002 (0.001; 0.003)	0.34
Yr [a] + T + Crèching tibio	−0.47 (−1.34; 0.40)	−0.11 (−0.16; −0.07)	0.057 (0.026; 0.088)	0.91
Yr [a] + ln$T$ + Crèching flipper	−0.29 (−1.23; 0.64)	−1.93 (−2.85; −1.01)	0.034 (0.016; 0.053)	0.96
Yr [a] + ln$T$ + Crèching mass	−0.39 (−1.31; 0.54)	−1.89 (−2.80; −0.98)	0.002 (0.001; 0.003)	1.10
Yr [a] + ln$T$ + Crèching tibio	−0.46 (−1.36; 0.44)	−1.94 (−2.87; −1.01)	0.055 (0.024; 0.086)	1.80

[a]Indicates coefficients with confidence limits overlapping zero.

TABLE 3. Estimated model coefficients and 95% confidence intervals (95% CIs) for competitive models evaluating factors associated with the age at which Adélie Penguin chicks entered the crèche stage at Cape Crozier, Ross Island, Antarctica, during the Austral summers of 2012–2013 and 2013–2014.

	Estimated coefficients (95% CI)				
Model structure	Year	Hatch date	Growth rate	ΔAIC$_c$	Adj. R^2
Yr + Hatch date	−1.91 (−3.05; −0.78)	−0.50 (−0.63; −0.37)		0.00	0.46
Yr + Hatch date + Mass [a]	−2.25 (−3.57; −0.94)	−0.53 (−0.67; −0.39)	−0.01 (−0.03; 0.01)	1.18	0.46
Yr + Hatch date + Flipper [a]	−2.11 (−3.32; −0.90)	−0.52 (−0.65; −0.38)	−0.27 (−0.80; 0.27)	1.25	0.46
Yr + Hatch date + Tibio [a]	−1.92 (−3.07; −0.78)	−0.50 (−0.63; −0.37)	−0.13 (−0.91; 0.64)	2.14	0.45

[a]Indicates coefficients with confidence limits overlapping zero.

TABLE 4. Estimated model coefficients and 95% confidence intervals (95% CIs) for competitive models evaluating factors associated with the size at which Adélie Penguin chicks entered the crèche stage at Cape Crozier, Ross Island, Antarctica, during the Austral summers of 2012–13 and 2013–14. Models in this table represent the best-supported model from three separate candidate model sets. Also shown for each model is the difference in Akaike Information Criterion values corrected for small sample size (AIC$_c$) between the current model and the one with the lowest AIC$_c$ (ΔAIC$_c$), and the adjusted R^2 (Adj. R^2). See Table 1 for description of model structure variables.

	Estimated coefficients (95% CI)				
Model structure	Year	Growth rate	Crèching age	ΔAIC$_c$	Adj. R^2
Crèching mass					
Yr + Crèching age + Mass	−241.46 (−386.20; −96.72)	9.43 (7.28; 11.59)	60.19 (41.61; 78.76)	0.00	0.76
Crèching flipper length					
Yr + Crèching age + Flipper	−17.27 (−23.94; −10.60)	6.53 (3.73; 9.33)	4.03 (3.14; 4.93)	0.00	0.71
Crèching tibiotarsus length					
Yr + Crèching age + Tibio	−10.11 (−14.53; −5.70)	3.09 (0.25; 5.93)	2.45 (1.82; 3.07)	0.00	0.58

achieve higher chick survival. The parents that could achieve earlier hatch date, faster chick growth, and older-crèching age were those that could maximize chick crèching size and subsequent survival to fledging. Parents that can achieve an earlier hatch date are likely those who are more proficient at foraging (before and during the breeding season), navigation, locomotion, or other factors that allow them to arrive at the colony and lay eggs earlier in the spring (Ballard et al. 2010, Lescroël et al. 2019, Kappes et al. 2021). These factors are also likely required to achieve fast chick growth and long guard period together. It should also be noted, however, that

an earlier hatch date may force parents to extend the crèche onset because the per nest predation risk may be too high if just the relatively few early nests also crèche early (Ims 1990).

Life history tradeoffs are expected to be more pronounced when limiting resources are less available (Stearns 1989). We observed that chicks at Cape Crozier entered the crèche younger and smaller in 2013 (a year of apparent food limitation) than in 2012. These results are interesting when compared to chick provisioning, guarding, and growth at a smaller colony nearby. At Cape Royds (2 orders of magnitude

fewer nests), parental foraging trips are short and it appears food is much less limited due to less competition among foraging penguins (Ainley et al. 2015, Saenz et al. 2020). There, parents guard throughout the chick-rearing period (no crèches formed; D.G.A. personal observation), chick growth rates are higher (Whitehead et al. 2015), and chicks fledge heavier than those at Crozier (Ainley et al. 2018). Considering these observations in the context of prior theory, it seems that when food is relatively plentiful Adélie Penguin parents are not faced with tradeoffs between chick growth rates and survival probabilities, but when food is limited parents chose provisioning rate (or their own food needs) over chick survival.

We also observed year-based differences in chick survival that were not explained by the predictor variables we considered: For chicks with similar growth rates and crèching sizes, the probability of surviving to fledge was substantially lower in 2013. Thus, it appears there were additional factors related to chick survival that we did not measure in this study. As noted above, prey type and feeding rate are important predictors of growth rates (Chapman et al. 2011, Jennings et al. 2021). But it could also be that reduced provisioning impacted survival in ways beyond direct effects on growth rate. For example, infrequent feeding may require chicks to trade-off between growth and endothermy (Wegrzyn 2013), thus impacting resilience to weather. Or food-limited chicks may have experienced chronically elevated blood corticosterone (Lyons and Roby 2011), possibly increasing susceptibility to disease. Conversely, the amount of food delivered to chicks increases when the crèche stage begins and both parents begin foraging simultaneously (Salihoglu et al. 2001), and this increased feeding rate could have positive survival effects beyond those acting directly through growth rate (Chapman et al. 2011). This may help explain why we observed an increase in survival upon crèching.

We observed a decline in daily survival probability throughout the crèche stage, contrary to what has previously been reported (Taylor 1962, Davis 1982, Davis and Mccaffrey 1986), although these authors worked at much smaller colonies having less intraspecific competition (see below). In fact, Taylor (1962) worked at tiny Cape Royds where crèche formation, as noted above, is minimal owing to continued guarding by parents. On the other hand, our study, as far as we know, is the first to estimate Adélie Penguin chick survival while accounting for imperfect resighting, and because crèched chicks are highly mobile this methodological difference could account for the different results. It is unlikely that predation or weather was responsible for these differences because chicks generally become less susceptible to those risks as they grow larger (especially beyond 800 g) and become more mobile (Davis 1982, Young 1994). Alternatively, as has also been suggested for colonial seabirds generally (Ashmole 1971, Jovani et al. 2016, Weber et al. 2021), the large number of penguins currently nesting at Cape Crozier likely deplete prey increasingly farther from the colony as the nesting season progressed (Ballance et al. 2009, Ainley et al. 2015, Ballard et al. 2019), likely leading to a decline in feeding rates (Ballard et al. 2010) and possibly chick survival. In contrast, during the 1970s, the Cape Crozier colony was about half as large as during the present study (100,000–150,000 vs. 250,000–275,000; Ainley 2002, Lyver et al. 2014) and there was no observed loss of crèched chicks from experienced breeders and only minor losses among young breeders (Ainley and Schlatter 1972, Ainley et al. 1983).

Our results build on previous work by showing how chick survival varies with crèching size, and we show that some apparently high-quality individuals seem able to maximize both chick growth and guarding, thus providing a mechanism to increase their fitness. Our results contribute to our understanding of how parental behavior and environmental conditions interact to determine chick outcomes and parental reproductive success. However, our results also indicate that additional factors are acting on chick survival, especially during the crèche stage, and that these may be indirectly related to provisioning or may be related to other environmental factors. Additional study of these factors will increase our ability to predict how Adélie Penguin populations will respond to changing habitats and climate change. Future long-term work relating parental survival to offspring reproductive success will aid understanding of how seabird parents adjust investment in the growth and survival of current vs. future broods.

Supplementary material

Supplementary material is available at *Ornithology* online.

Ethics statement

All penguin chick capture, handling, and data collection performed during this study were approved under Antarctic Conservation Act permit (2011-002 to H.T. Harvey and Associates) from the National Science Foundation Office of Polar Programs and with oversight by Oregon State University's Institutional Animal Care and Use Committee.

Conflict of interest statement

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. DGA is employed by a commercial company, H.T. Harvey and Associates, but otherwise, there are no conflicts of interest.

Author contributions

All authors conceived and designed the research. S.J. and G.B. performed the experiments. S.J., in consultation with K.M.D., analyzed the data. All authors wrote the paper.

Data availability

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