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Parent age differentially influences offspring size over the course of development in Laysan albatross

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Abstract

Offspring growth and survival are predicted to be higher for older parents, due to a variety of mechanisms, such as increased breeding experience or greater investment favored by low residual reproductive value. Yet the extent to which parent age affects offspring viability is likely to vary between different aspects of growth and survival, perhaps being most pronounced at the most stressful stages of reproduction. We studied the link between parent age and nestling growth and survival in the Laysan albatross, a long-lived seabird with a mean first breeding age of 8 years. Offspring of older parents were more likely to survive to fledging. Among those that did fledge, nestlings of older parents grew more rapidly. However, parent age did not influence the eventual asymptotic size that nestlings reached before fledging: fast-growing nestlings of older parents reached 90% of asymptotic size roughly 1 week sooner, but slow-growing nestlings of younger parents eventually caught up in size before fledging. Older parents bred *c.* 2 days earlier than younger parents, but hatch date did not explain observed variation in offspring success. The extent to which parent age accounted for variation in size of individual nestlings was not constant but peaked near the midpoint of development. This could reflect a time period when demands on parents reveal age-based differences in parental quality. Overall, growth and survival of offspring increased with parent age in this species, even though the late age of first breeding potentially provides a 7-year period for birds to hone their foraging skills or for selection to eliminate low-quality individuals.

Introduction

Growth and survival of offspring are influenced by genetic and environmental factors, including the quality of parental care (Clutton-Brock, 1991). In species with parental care, older individuals may provide more or better care (e.g. more food or food of higher quality), improving the growth and survival of offspring (Stearns, 1992). This may be particularly true for long-lived animals, such as seabirds or large mammals (Forslund & Pärt, 1995; Cameron *et al*., 2000), but a relationship between parent age and quality of parental care has also been seen in insects, other short-lived animals that provide care to offspring (Mappes & Kaitala, 1994) and animals that provision eggs that are subsequently untended (Paitz *et al*., 2007).

Several mechanisms could underlie an increase in breeding performance with age. First, older parents might be better quality individuals, having survived to an advanced age (Mauck, Huntington & Grubb, 2004). Second, they might breed on better sites or at a better time of the year (Smith & Moore, 2005). Third, they could have more breeding experience as individuals or pairs (Cézilly & Nager, 1996). Fourth, they might have become better foragers with age (Daunt *et al*., 2007). Fifth, they could be selected to invest more in offspring because of lower residual reproductive value (Ericsson *et al*., 2001). In addition, the relationship between parent age and reproductive success can be affected by reproductive senescence, with very old individuals exhibiting physiological deterioration that reduces their reproductive output (Nussey *et al*., 2006).

The influence of parent age on offspring performance could vary with ecological circumstances (Saether, 1990). Specifically, differences between old and young parents might be most apparent in the presence of ecological stressors (Bunce, Ward & Norman, 2005), similar to the manifestation of inbreeding depression under poor ecological conditions (Keller *et al*., 2002). Thus, heightened effects of parent age on offspring success may occur during periods of food shortage, when differences in foraging ability of old and young parents would become more critical.

The effect of parent age on offspring performance may also be mediated by the pattern of offspring development. Although better provisioning of offspring could lead to improved offspring growth, components of growth may be differentially influenced by variation in parental care. For animals with determinant growth, the growth of body parts often follows a sigmoidal curve (Starck & Ricklefs, 1998); in that case, variation could be seen in either the rate of growth, the final asymptotic size, or both. If provisioning is temporally variable, some animals could slow their growth during food shortages and later either resume a normal rate of growth or undergo a rapid burst of 'catch-up' growth (Metcalfe & Monaghan, 2001). If the duration of parental care is flexible, slow-growing individuals might reach an asymptotic size that is equivalent to fast-growing individuals.

Both growth rate and asymptotic size can be under directional selection via their impact on subsequent survival (Gebhardt-Henrich & Richner, 1998), but much of the variation in these traits may be due to environmental effects including parental care. Studies of wild birds have found moderate heritability for adult size and asymptotic nestling size, but low or no heritability for growth rate (van Noordwijk & Marks, 1998). Consequently, the effects of parent age should be stronger on nestling growth rate than on asymptotic size of nestlings.

Here, we test whether adult age influences offspring growth rate, asymptotic size, or survival to independence in the Laysan albatross *Phoebastria immutabilis*, a long-lived seabird. We also test whether the influence of parent age on offspring size is constant over the course of offspring development or, alternatively, is stronger at particular developmental stages; finding the latter pattern might help illuminate mechanisms underlying any differences in success of old and young parents.

Materials and methods

Study population

Laysan albatross breed colonially, primarily in the Hawaiian archipelago, and are classified as Vulnerable by International Union for the Conservation of Nature (IUCN, 2006). They forage pelagically on squid and the eggs of flying fish (Whittow, 1993), traveling as far as Alaska to forage during chick rearing (Fernández *et al.*, 2001). They lay a single 285 g egg year^{-1}. Incubation lasts 64 days and the chick is fed up to 6 months, with males and females contributing roughly equally to parental care (Whittow, 1993). At the start of incubation, adult mass is 3.2 kg for males and 2.6 kg for females (Whittow, 1993).

Nestling growth and survival were monitored in a population of *c.* 1000 breeding pairs on Tern Island (23°45′N, 166°17′W), a predator-free island in the Hawaiian archipelago. Albatross in this population lay eggs in late November and early December. Because of banding efforts begun by the Smithsonian's Pacific Ocean Biological Survey Program in the 1960s and continued by the US Fish and Wildlife Service in the late 1970s, some birds in the population have known ages (banded as nestlings) and some have known minimum ages (banded as adults).

Measurements and data analysis

In the 1997–1998 breeding season, the breeding attempts of 123 Laysan albatross pairs, ranging in age from 7 to at least 32 years, were recorded. Of the 246 birds, 78 were initially banded as adults of unrecorded breeding status, and therefore only a minimum age was known. Although mean age at first breeding is 8–9 years (Fisher, 1975), most individuals reach adult plumage their first year of life (Whittow, 1993). As a proxy for true age, birds banded as adults were entered in our analyses using 1 year plus years since banding date. The oldest birds in our sample (and the oldest banded birds in the colony) are almost entirely those banded as adults, because that was the initial focus of banding in the 1960s and 1970s. Consequently, among our 123 breeding pairs the median age of known-age birds is 11 years, whereas the median minimum age of those birds banded as adults is 22 years. Furthermore, 95% of sampled birds over the age of 18 years are individuals for which only the minimum age is known. Although including minimum-age birds in our analyses introduces imprecision about age (thereby compromising statistical power, particularly for tests of senescence), this seemed less problematic than the bias that would result from excluding those birds, as such a sample would eliminate nearly all of the oldest half of the breeding population.

The ages of pair members were positively correlated (intra-class correlation coefficient = 0.789, $P < 0.001$, $n = 72$ known-age pairs; age range: 7–32 years) but not identical, and the sex of birds was not known. Thus, our analyses test whether offspring growth and survival were influenced by the mean of the age estimates for the two parents (henceforth referred to simply as 'parent age'). Qualitatively similar results were obtained in analyses based on age of younger parent or age of older parent.

We measured body mass, tarsus length, culmen length and bill depth of nestlings on the day after hatching and then every 2 weeks until they fledged or died. To analyze structural growth, first we used a Gompertz equation to calculate growth rate and asymptotic size for tarsus length, culmen length and bill depth (Weimerskirch, Barbraud & Lys, 2000):

$$\text{size} = A\mathrm{e}^{\mathrm{e}(-\mathrm{K}(\mathrm{t}-\mathrm{t_i}))^3}$$

where A is asymptotic size, K is growth rate, t is age and t_i is the age at which the inflection point is reached. For each individual nestling, Gompertz equations were fitted iteratively based on least squares, using nonlinear regression in SPSS. Linear regression was then used to test whether parent age influenced nestling growth; these analyses used a particular growth parameter (e.g. asymptotic size of tarsus) as a dependent variable, with parent age and hatch date evaluated as candidate predictor variables with stepwise model selection. Nestling mass could not be analyzed, because mass exhibited too much within-nestling variation to accurately fit a Gompertz growth curve. This is presumably a consequence of large intervals between feedings by parents, such that a chick's mass at our biweekly

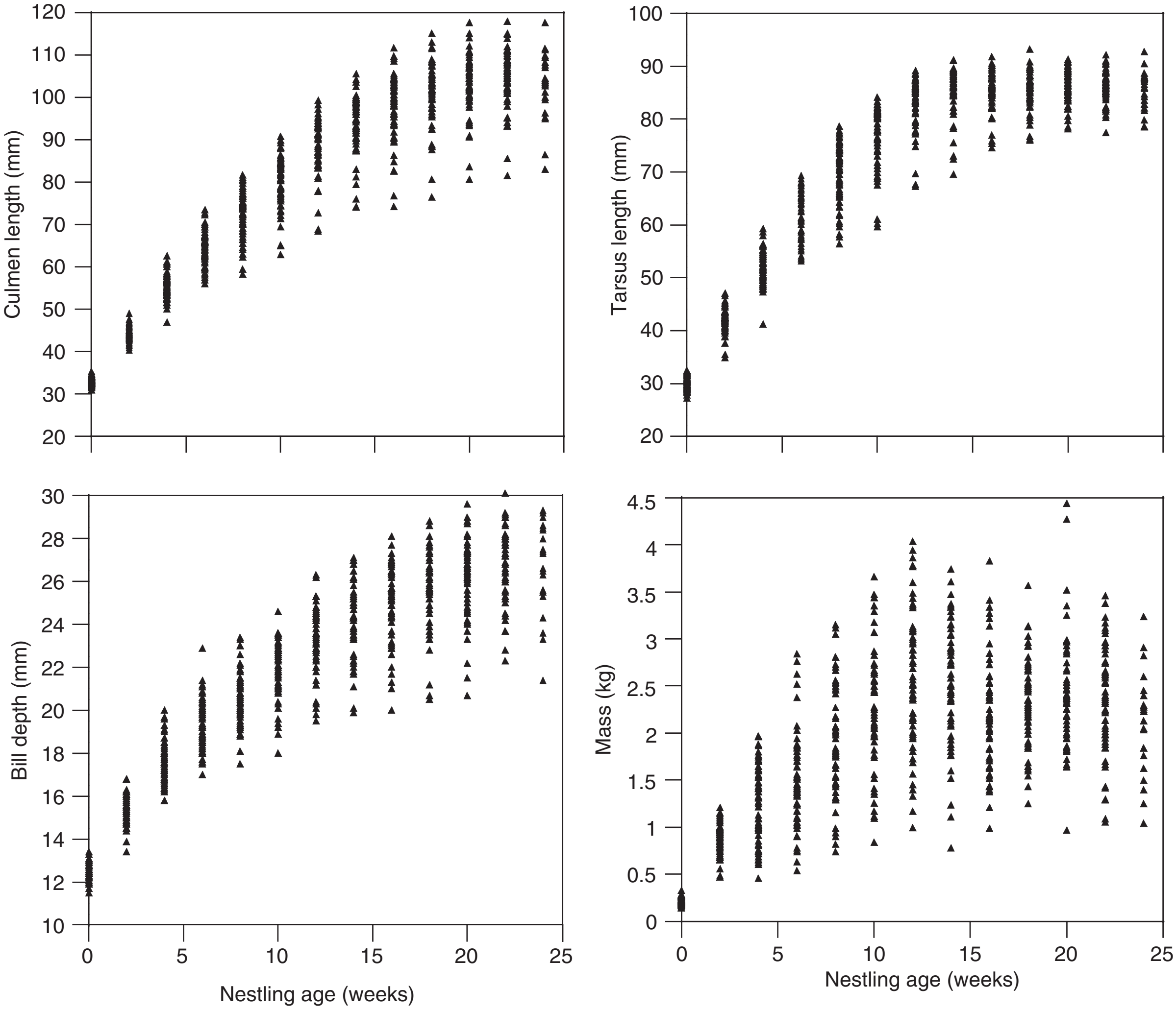

Figure 1 Bi-weekly measurements of 59 albatross nestlings that survived from hatching to fledging.

measurement was strongly influenced by number of days since last feeding.

Second, we used a generalized linear model (GLM) to test whether the influence of parent age on nestling size varied with stage of nestling development. For each component of structural size, we used restricted maximum likelihood to fit a model with nestling size as the dependent variable, individual nestling as a random predictor variable and continuous predictor variables of nestling age, nestling age squared, parent age and the interaction between parent age and the two nestling age variables. Significant interactions would indicate that the effect of parent age on nestling size was not constant across the period of nestling development.

To graphically show how the influence of parent age on nestling size varies over development, we used each separate set of raw biweekly measurements (i.e. at week 0, week 2 and so on to week 22) to calculate r^2 from regressions of nestling size on parent age, using only chicks that eventually fledged.

We used logistic regression to test whether parent age and hatch date influenced the probability of hatching success, fledging success and reproductive success.

To assess whether our findings are robust to uncertainty about the age of birds banded as adults, we ran an alternative set of analyses using two definitive age categories. We used 18 years as a cut point for mean age of parents, putting in one class all pairs with mean age ≥ 18 years (regardless of whether banded as nestlings or as adults) and into the other class all pairs with mean age <18 years and with both birds of true known age. This ensured that all birds were correctly classified, and it reduced the sample only slightly: of 123 pairs, it eliminated 19 pairs with mean age <18 years and at least one bird banded as an adult (i.e. having the potential to be older than the 18-year cutoff). The advantage of this approach is that it retains old birds in the dataset while eliminating ambiguity about age assignment; the disadvantage is the reduced power of categorical analyses.

Results

Nestlings of older parents exhibited faster growth and greater likelihood of surviving to fledge, but the long period of parental care allowed nestlings of younger parents to eventually reach the same pre-fledging size.

Of 123 nests monitored, 99 chicks hatched. Mass at hatching did not vary with parent age, whether analyzing all chicks (linear regression: $b = 0.55 \pm 0.73$ SE, $t = 0.750$, d.f. = 97, $P = 0.455$, $r^2 = 0.006$) or only those that survived to fledge (linear regression: $b = 0.42 \pm 1.0$, $t = 0.416$, d.f. = 58, $P = 0.679$, $r^2 = 0.003$). Among chicks that survived to fledge ($n = 59$), variance in culmen length and bill depth generally appeared to increase with age (Fig. 1); variance in tarsus length and mass increased until late in development and then decreased somewhat before fledging (Fig. 1).

Offspring of older parents had higher Gompertz-fitted growth rates for tarsus length (linear regression: $b = 0.00226 \pm 0.00092$, $t = 2.465$, d.f. = 58, $P = 0.017$, $r^2 = 0.096$; Fig. 2) and culmen length ($b = 0.00128 \pm 0.00053$, $t = 2.427$, d.f. = 58, $P = 0.018$, $r^2 = 0.094$) but not for bill depth ($b = 0.00082 \pm 0.00067$, $t = 1.213$, d.f. = 58, $P = 0.230$, $r^2 = 0.025$). Despite effects of parent age on growth rate, Gompertz-fitted asymptotic size did not vary with parent age for any of the structures measured: tarsus length (linear regression: $b = 0.015 \pm 0.086$, $t = 0.181$, d.f. = 58, $P = 0.857$), culmen length ($b = 0.082 \pm 0.067$, $t = 1.05$, d.f. = 58, $P = 0.299$) or bill depth ($b = 0.067 \pm 0.063$, $t = 1.061$, d.f. = 58, $P = 0.293$). Nestlings of older adults (mean pair age ≥ 18 years) reached 90% of Gompertz-estimated asymptotic tarsus length and culmen length significantly earlier than nestlings of younger adults (<18 years): the difference in nestling age at this growth milestone was 1.1 weeks for tarsus length (unequal variance t-test: $t = 2.13$, d.f. = 55.3, $P = 0.037$), 1.6 weeks for culmen length (t-test: $t = 2.01$, d.f. = 57, $P = 0.049$) and 0.95 weeks for bill depth ($t = 1.06$, d.f. = 57, $P = 0.294$).

The influence of parent age on nestling size varied in strength over the course of nestling development. Parent age significantly interacted with nestling age and nestling age squared in GLM of tarsus length (Z-scores: 0.043 ± 0.011 SE, $t = 3.73$, $P = 0.0002$, $n = 731$ measurements of tarsus, and -0.00185 ± 0.00049, $t = -3.76$, $P = 0.002$, $n = 731$), culmen length (Z-scores: 0.067 ± 0.013, $t = 5.11$, $P < 0.0001$, $n = 731$ measurements of culmen, and -0.0021 ± 0.00055, $t = -3.86$, $P = 0.001$, $n = 731$) and bill depth (Z-scores: 0.011 ± 0.0034, $t = 3.22$, $P = 0.0013$, $n = 731$ measurements of bill depth, and -0.00030 ± 0.00014, $t = -2.12$, $P = 0.034$, $n = 731$). The signs of the Z-scores describe a parabolic shape for the influence of parent age across nestling development, with the strongest effect near the middle of development (Fig. 3).

Fledging success of nestlings was higher for older parents (logistic regression: Wald $\chi^2 = 4.71$, d.f. = 1, $n = 99$, $P = 0.030$, Nagelkerke $R^2 = 0.068$). Forty of 99 (40.4%) chicks died before fledging; 22 of these chicks died by their eighth week, and a total of 14 chicks died after an unusual period of weight loss and a plateau in structural size, suggestive of starvation. Other chicks appeared to die from thermal stress while unattended during periods of either heavy, cold rain or high temperatures with low wind speeds.

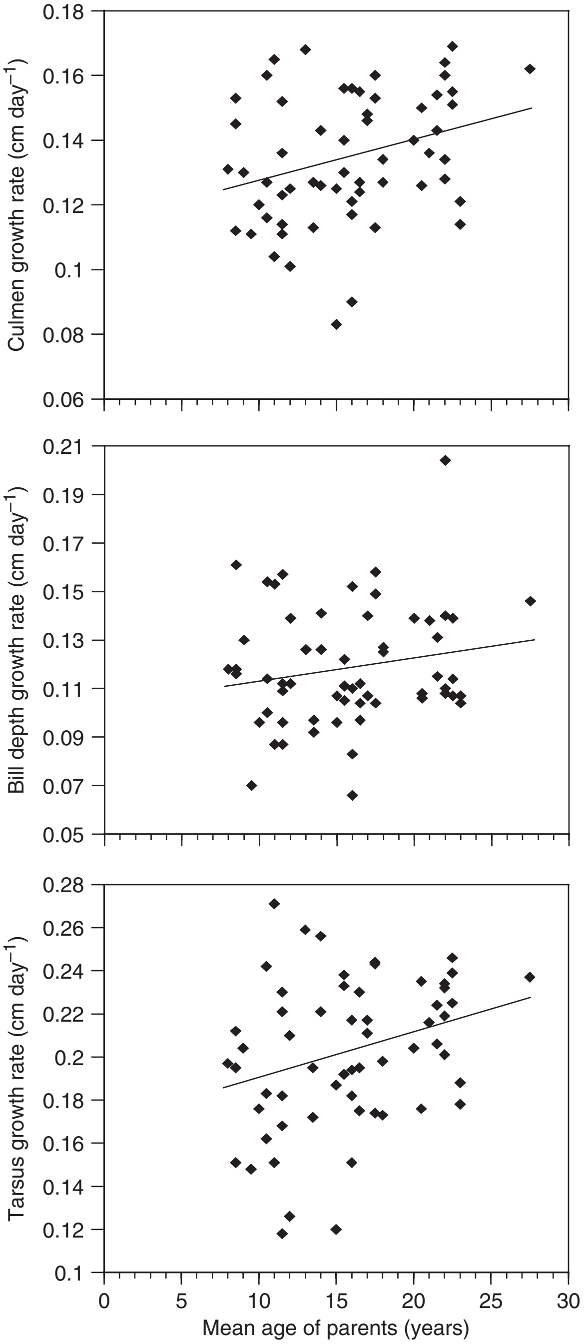

Figure 2 Growth rates of 59 albatross chicks that survived to fledging, shown in relation to mean age of the two parents.

Hatching success was not influenced by parent age (logistic regression: Wald $\chi^2 = 0.03$, d.f. = 1, $n = 123$, $P = 0.866$, Nagelkerke $R^2 = 0.000$), but the influence of

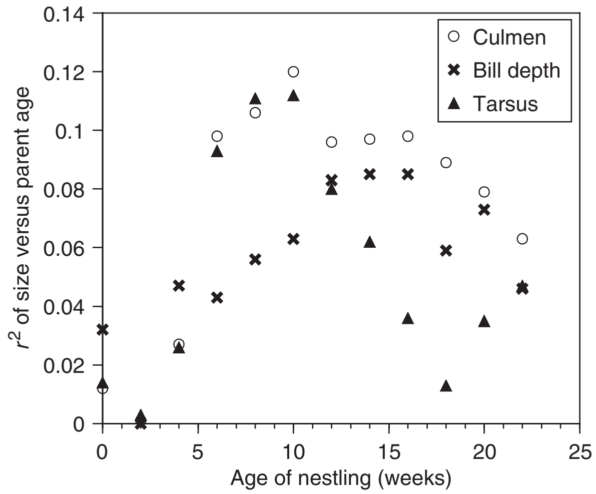

Figure 3 Generalized linear models of nestling sizes showed significant interactions between nestling age and parent age, indicating that the strength of the effect of parent age varied over the course of nestling development. To visualize that variation, size of nestling was regressed on mean age of parents for each set of bi-weekly measurements of all nestlings. This graph shows the coefficient of determination (r^2) between nestling size and parent age, from each of those regressions. Over the course of nestling development, the extent to which parent age affects nestling size changes. Data shown here are from only those nestlings that eventually fledged.

parent age on fledging success was strong enough that parent age had an influence on the probability of an offspring surviving from egg laying through fledging (logistic regression: Wald $\chi^2 = 3.92$, d.f. = 1, $P = 0.048$, $n = 123$, Nagelkerke $R^2 = 0.044$).

Older parents bred earlier in the season, whether considering all nests that hatched (linear regression of hatch date vs. parent age: $t = -3.417$, d.f. = 98, $P = 0.001$, $r^2 = 0.107$) or only those nestlings that survived to fledge ($t = -2.091$, d.f. = 58, $P = 0.041$, $r^2 = 0.071$). Mean hatch date for older parents (≥ 18 years) was 1.8 days earlier than for younger parents (< 18 years). In the analyses of the influence of parent age on hatching success or fledging success (via logistic regression) or on nestling growth parameters (via linear regressions), stepwise model building rejected hatch date as a predictor variable (all $P > 0.1$). Thus, although older parents bred earlier than younger parents, hatch date did not contribute additionally to explaining variation in offspring success.

Alternative analyses based on definitive age categories of adults were generally supportive of the findings described above. The two age classes of parents did not differ significantly in offspring survival, but the values were in the predicted direction for both fledging success (72.0% for old parents vs. 54.4% for young parents; $\chi^2 = 2.24$, d.f. = 1, $P = 0.134$, $n = 82$ nests) and overall reproductive success (54.5% for old parents vs. 43.7% for young parents; $\chi^2 = 1.07$, d.f. = 1, $P = 0.301$, $n = 104$ nests). Older parents had offspring that grew more quickly in tarsus length (t-test: $t = 2.07$, d.f. = 47, $P = 0.044$) and culmen length ($t = 2.73$, d.f. = 47, $P = 0.009$); the difference in growth rate for bill depth was not significant but was in the predicted direction ($t = 1.97$, d.f. = 47, $P = 0.055$). Parent age was not related to asymptotic size of tarsus length (t-test: $t = 0.91$, d.f. = 47, $P = 0.368$), culmen length ($t = 0.74$, d.f. = 47, $P = 0.464$) or bill depth ($t = 0.52$, d.f. = 47, $P = 0.603$).

Discussion

Older Laysan albatross parents outperformed younger parents in nestling growth, fledging success and overall reproductive success, as with other long-lived seabird species (Sydeman *et al.*, 1991; Daunt *et al.*, 1999; Berrow, Humpidge & Croxall, 2000; Weimerskirch *et al.*, 2000; Hipfner & Gaston, 2002). Eggs of older parents hatched *c.* 2 days earlier than younger parents, but hatch date did not influence nestling growth or survival. Although an experiment would better disentangle the correlated predictor variables, our data suggest that the effect of parent age on nestling performance may be due to differences in parenting behavior, rather than a consequence of breeding date.

The influence of parent age on offspring development was interesting in two ways. First, older parents produced young that grew more rapidly, but parent age did not influence asymptotic size: if slow-growing chicks of young parents survived to fledge, they eventually reached the same asymptotic size as the rapidly growing chicks of older parents. This pattern occurs in wandering albatross (Berrow *et al.*, 2000), but other studies have shown varied patterns, including no effect of parent age on growth of surviving nestlings (Daunt *et al.*, 1999), and effects on growth that persist through size at fledging (Weimerskirch *et al.*, 2000).

Nestlings of older parents reached 90% of asymptotic size *c.* 1 week earlier than nestlings of younger parents. The slower growth of nestlings of young parents might have no cost – that is, all's well that ends well. Alternatively, these nestlings might later pay a cost for having matured more slowly. For example, slow growth due to small or low-quality meals is linked to higher chronic levels of corticosterone and reduced cognitive function in seabirds (Kitaysky *et al.*, 2003, 2006). Thus, nestlings that attain a similar final size may still vary in quality or in likelihood of post-fledging survival, as a function of their pre-fledging growth process.

The second notable finding was that the influence of parent age on nestling size varied over the course of nestling development (Fig. 3). Specifically, parent age had a weak positive relationship with nestling size shortly after hatching, a stronger positive relationship midway through development and a weak positive relationship near fledging. In one sense, this is a consequence of the growth pattern: if nestlings of old and young parents hatch at a similar size then grow at different rates, but the duration of the nestling period allows all chicks to reach a similar asymptote before fledging, the influence of parent age on nestling size will be strongest in the middle of development. This explanation does not address the biology of the pattern, however. One possibility is that the middle stage of nestling development could coincide with heightened demands on the parents – perhaps due to a combination of larger nestling size, faster growth and smaller parental reserves, or perhaps due to changing oceanic conditions. Such stressors could induce a stronger relationship between parent age and reproductive performance (Bunce *et al*., 2005). A second possibility is a temporal change in the foraging behavior of breeders in this population, documented in the same year as our study: at *c*. 3 weeks post-hatch, parents shifted from making exclusively short-distance foraging trips to making a mix of short trips and long trips, a behavior which continued until fledging (Fernández *et al*., 2001). The new use of distant foraging sites could increase the importance of parents' experience at traveling and locating food resources. This long-trip hypothesis leaves unanswered the question of why the influence of parent age on nestling size becomes weak again, as nestlings near fledging.

Overall, we found rather small effect sizes for the influence of parent age on nestling growth rate and nestling survival. A weak influence of parent age might be expected for albatross and other long-lived species because of the delay between fledging and first breeding. Laysan albatross breed for the first time at an average age of 8–9 years (Fisher, 1975), potentially providing 7 years for birds to hone their foraging skills (Daunt *et al*., 2007) or for selection to eliminate poor foragers (Mauck *et al*., 2004). Either process could yield young breeders that are similar in quality or foraging ability to older, more experienced breeders. However, this is not consistent with our findings of a gradual increase in success with age or with previous studies on this species showing that parents have low success in their first breeding attempt (Fisher, 1975; Whittow, 1993).

A second possibility is that environmental factors may have a strong effect on nestling growth or survival, reducing the relative importance of parent age. Some albatross nestlings on Tern Island die from apparent weather-induced thermal stresses (USFWS, unpubl. data). Nestlings that survive these events could pay temporary growth costs, and variation between nest sites in summer sun or winter flooding could create between-nestling variation in growth rate. Because of extreme natal site fidelity (Fisher, 1976), variation in nest environment may be unrelated to parent age, in which case nest-site effects could reduce the relative importance of parent age. However, high-quality birds could choose better nest sites and also live longer (Espie *et al*., 2004), thereby creating a positive correlation between parent age and nest-site quality.

A third factor that could reduce the relative importance of parent age is the potential for nestlings to suffer from ingesting plastics. Adult Laysan albatross often mistake floating plastic objects (bottle caps, manufacturing pellets, etc.) for food, eating them and then regurgitating them to offspring at the breeding colony (Blight & Burger, 1997). These objects can reduce the digestive ability of nestlings and may inhibit growth (Auman *et al*., 1997). If adults' tendency to ingest plastic were random or were related to factors other than adult age, a decrease in the extent to which between-nestling variation in growth is explained by parent age could occur.

In summary, we found a positive relationship between parent age and nestling survival and growth rate in Laysan albatross, even though the delayed age at first breeding potentially provides a 7-year period for birds to hone their foraging skills or for selection to eliminate low-quality individuals.

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