PROCEEDINGS B

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THE ROYAL SOCIETY
PUBLISHING

Carry-over effects of food supplementation on recruitment and breeding performance of long-lived seabirds

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Supplementation of food to wild animals is extensively applied as a conservation tool to increase local production of young. However, in long-lived migratory animals, the carry-over effects of food supplementation early in life on the subsequent recruitment of individuals into natal populations and their lifetime reproductive success are largely unknown. We examine how experimental food supplementation early in life affects: (i) recruitment as breeders of kittiwakes *Rissa tridactyla* born in a colony on Middleton Island (Alaska) between 1996 and 2006 ($n = 1629$) that bred in the same colony through 2013 ($n = 235$); and (ii) breeding success of individuals that have completed their life cycle at the colony ($n = 56$). Birds were raised in nests that were either supplemented with food (Fed) or unsupplemented (Unfed). Fledging success was higher in Fed compared with Unfed nests. After accounting for hatching rank, growth and oceanic conditions at fledging, Fed fledglings had a lower probability of recruiting as breeders in the Middleton colony than Unfed birds. The per-nest contribution of breeders was still significantly higher for Fed nests because of their higher productivity. Lifetime reproductive success of a subset of kittiwakes that thus far had completed their life cycle was not affected by the food supplementation during development. Our results cast light on the carry-over effects of early food conditions on the vital rates of long-lived animals and support food supplementation as an effective conservation strategy for long-lived seabirds.

1. Introduction

Supplementation of food to wild animals is extensively applied as a conservation tool [1], as it often yields an immediate increase in productivity [1–3]. However, little is known about long-term carry-over effects of food supplementation during early life stages of long-lived migratory animals, mostly due to the challenge of following individuals throughout their entire life cycle [4]. One hypothesis is that food supplementation early in life has positive carry-over effects on vital rates by enhancing the quality of individuals ('silver spoon effect' [5]). On the other hand, the positive effects of food supplementation may only be short-term and/or have delayed negative consequences. For instance, food supplemented to offspring of poor quality may only result

in a temporary increase of their survival chances, followed by higher than expected mortality later in life when the food supplementation stops. In addition, the strength of the relationship between food supplementation early in life and either lifetime fitness or particular components of fitness (e.g. survival to first reproduction) of food-supplemented individuals may be further modulated by the quality of the environment after the early food-supplemented stage. A stronger correlation between individual quality and survival or other fitness components is expected in harsher environments [6], whereas in more favourable environments there might be enough resources available for all individuals, including those of low quality, to reach sexual maturity and reproduce successfully [7].

Here, we use data from a long-term experimental study of long-lived black-legged kittiwakes *Rissa tridactyla* breeding on Middleton Island (Alaska, USA) to investigate the effects of supplemental food during the nestling phase on the probability of return to breed in the colony and reproductive performance of food-supplemented birds compared with control birds. In the Middleton colony, free-living kittiwakes were raised as chicks and later reproduced in nests in which the food available to parents and chicks was experimentally manipulated ('experimental nests' hereafter): in 'Fed' nests, parents and chicks received supplemental food during the breeding season, whereas 'Unfed' nests (i.e. no supplemental food was given to either parents or chicks) served as the control group.

In seabirds, determinants of survival from fledging to adulthood and of return to the natal colony to breed are poorly understood. Cohort effects on local survival are well documented [8,9] and have been mostly associated with climatic vagaries and the effects of climate and oceanographic conditions on food availability at sea [10]. At the individual level, nestling growth rates in kittiwakes were found to be positively associated with breeding probability [11] and productivity (i.e. chicks fledged per nest) [12], thus growth rate might be used as a proxy of individual quality in kittiwakes. However, because food supplementation may substantially increase growth rates of all nestlings [12,13], this measure may be uncorrelated with individual quality when food supplementation is not taken into account. In addition, food supplementation may modulate the effects of hatching rank on growth and survival of chicks in altricial and semi-altricial species like kittiwakes. Young that hatch first in the clutch are dominant in the brood and receive a higher share of food provisioned by the parents than their siblings; this increases their growth rates and fledging success with respect to young that hatch later. Food supplementation may increase the growth rate and fledging success of late-hatching chicks, although it is unclear whether the positive effect on early life histories would persist up to reproduction.

The main goal of this work was to study the long-term consequences of food supplementation and variation in early conditions in a long-lived animal species by testing the carry-over effects of food supplementation on vital rates. Specifically, we tested, after accounting for environmental conditions at sea and hatching order, whether supplemental nutrition during the neonatal stage increased, decreased or had no effect on the probability of fledged kittiwakes to return to breed in the natal colony. Then, by also taking productivity into account, we tested whether food supplementation at birth, overall, provided a positive net effect on the number of birds returning to breed in the natal colony. Finally, we tested whether food

supplementation early in life affected the lifetime reproductive success of a subset of kittiwakes (i.e. those that completed their life cycle relatively early) that were born and later bred in the colony.

2. Material and methods

(a) Methods

The black-legged kittiwake is a medium size colonial gull that breeds on vertical cliffs along coasts and islands in the Northern hemisphere. On Middleton Island (59°26′ N, 146°20′ W), Gulf of Alaska, kittiwakes nest on an abandoned United States Air Force radar tower [14]. The Middleton population declined from 166 000 birds in 1981 to fewer than 25 000 in 1999 due to an apparent food shortage and successional changes in breeding habitat following the Alaska earthquake of 1964. A large-scale supplemental feeding experiment was initiated in 1996 to test whether food was limiting the productivity of kittiwakes [14]. Today, there is very limited breeding outside the tower and other buildings nearby on Middleton Island.

Previous work showed that kittiwakes on Middleton start breeding when they are between 4 and 11 years old (average approx. 7 years old [12]). Breeders show high site fidelity and lay clutches of one to three eggs [11]. Chicks remain in the nest until they are nearly adult size. Food availability for breeding kittiwakes varies markedly from year to year [15,16] and strongly affects chick survival while in the nest [10].

The radar tower is a 12-walled polygon where artificial nest sites have been constructed on the upper walls, permitting observations and capture of breeders and their chicks from inside the building through sliding one-way windows. Since 1996, a feeding experiment has divided the experimental nests into two treatments: food-supplemented (hereafter 'Fed' group) and control (i.e. 'Unfed' group). Nests were assigned to the same treatments each year (for details of the experimental set-up, see [2,10,14]). Capelin (*Mallotus villosus*), a preferred energy-rich prey of kittiwakes in the study area [10], was used as the supplemental food for birds in Fed panels. Kittiwakes (parents and chicks) were fed three times a day from inside the tower; fish were continuously provided through a plastic tube passing through the wall at each nest site until birds were sated [14].

Nests were checked daily during the breeding season to determine content. Thus, the sighting probability of breeders is assumed to be 1. Chicks were banded for individual identification and weighed every 5 days to the nearest 0.1 g from the day of hatching until either: (i) fledging, (ii) day 40 post-hatching, or (iii) when hatching occurred in late July or August, as long as the monitoring team was on the island. Hatching rank describes the order of egg-hatching in the nest.

Single chicks were recorded as Singleton (S), while first-, second- and third-hatched chicks were recorded as A-, B- and C-chicks, respectively.

(b) Data and statistical analysis

Productivity (i.e. fledglings per nest) was measured in Fed and Unfed nests each year from 1996 to 2006. We tested for differences in mean annual productivity between Fed and Unfed nests using a paired *t*-test.

Oceanographic conditions largely determine food availability for seabirds and they need to be taken into account when investigating the individual- or cohort-level determinants of survival. Following [10], we used a summer (June–August) average Pacific Decadal Oscillation (PDO) index (http://jisao.washington.edu/pdo/PDO.latest) at fledging year as a measure of oceanographic conditions for kittiwakes during nestling and immediate post-fledging stages. The PDO index identifies 'warm' and 'cool'

conditions in the northeastern Pacific, according to its sign ([−] for cold phases). 'Warmer' oceanic conditions (as reflected by a positive PDO index) have been associated with lower food availability in the region [10]. We tested whether productivity of Fed and Unfed nests was correlated with the PDO index.
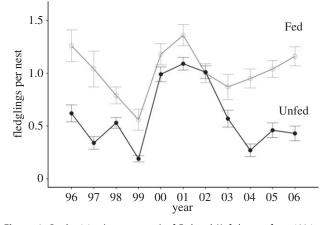
Our dataset at the individual level includes information for 1629 kittiwakes (hereafter 'complete dataset') that fledged during 1996–2006, and reproduced (laid eggs at least once, 'breeders' hereafter) at the tower from 1997 through to 2013 ($n = 235$). The choice of 2006 as last year of birth of kittiwakes to be included in the analyses was based on the distribution of age at recruitment for Fed and Unfed birds [12]. For each individual, we recorded: hatching rank H_R (as determined by the hatching order: A-chick, B-chick, C-chick and S-singleton), year of birth Y_b, and feeding treatment (Fed/Unfed) at the nestling stage T_N. A subset of the complete dataset (hereafter 'reduced dataset', $n = 1177$) included measurements of body mass for each chick from day 5 to day 20 post-hatching (5 day intervals).

Growth rate of body mass is approximately linear in kittiwake chicks between day 5 and day 20 post-hatch [11,12,17]. We used daily growth during the linear phase G_m (between day 5 and day 20, from approx. 75 to 300 g) to characterize growth rate. We estimated G_m separately for each chick by fitting a linear model with age as a predictor of mass. We also checked for consistency of results when G_m was calculated as: (mass at day 20 − mass at day 5)/15. To test for potential delayed deleterious effects of compensatory growth following periods of slow growth [18], we also computed G_{max} as $\max(G_5)$, where G_5 is the set of growth measures for each 5-day interval, and G_{min} as $\min(G_5)$. We used ordinary least-square regression analysis to model the relationship between growth G_m and H_R, Y_b, T_N and the PDO index, including their two-way interactions.

Sex was found to be an important determinant of growth and recruitment in the kittiwake [11,17]. Kittiwake males grow on average faster and reach a greater peak mass than females [12,19]. In our study, sex was known only for the majority of birds that bred in the colony, while only a few chicks that did not return to breed were sexed. A random forest classifier [20] with the PDO index, T_N, H_R, Y_b, G_m, G_{max} and G_{min} provided a poor sex classification of chicks of known sex (see the electronic supplementary material, table S1), thus we were not able to determine the sex of birds that did not return to breed or include the sex of chicks as a predictor in our models.

We computed the year-specific recruited as breeder(R)-to-fledged(F) ratio (hereafter 'R/F') for each birth year from 1996 to 2006 for Fed and Unfed nests separately. We applied a χ^2 test of equality of proportions to the complete dataset to test: (i) whether fledglings from Unfed nests were more or less likely than fledglings from Fed nests to breed in the Middleton tower colony than expected by chance alone, and (ii) whether the sex ratio of breeders (overall and for Fed/Unfed separately) was significantly different from 50:50. We tested with analysis of covariance (ANCOVA) whether environmental conditions at fledging (as reflected in the PDO index [10]) had an effect on R/F. As R/F is a ratio, we also applied the ANCOVA using logit-transformed R/F as response variable [21]. We then tested with a linear model whether the annual differences in R/F between Fed and Unfed birds was associated with the PDO index.

Using the reduced dataset, we applied logistic regression to model the relationship between the breeding status of fledglings that were born between 1996 and 2006 ('1' for fledglings that recruited as breeders and '0' for those that did not breed) with H_R, G_m, G_{max}, G_{min} and PDO index at the time of fledging, including their two-way interactions, as predictors. We also used t-tests at a more fine-grained scale to test whether within feeding treatment and hatching rank there were significant differences in mean G_m between fledglings that later bred in the tower colony and fledglings that did not.

Figure 1. Productivity (mean ± s.e.) of Fed and Unfed nests from 1996 to 2006. The smallest differences in productivity between Fed and Unfed nests were observed from 2000 through to 2003, a period when natural food availability was high.

We did not discriminate among models with difference in the Akaike information criterion (ΔAIC) < 3 from the best model [22], for either the growth or breeding models. In the case of multiple models with ΔAIC < 3, we proceeded with model averaging without shrinking model parameters. We report the relative importance of the explanatory variables, computed as a sum of the Akaike weights of all models in which a parameter of interest appeared.

We obtained statistics on breeders per Fed or Unfed nest (i.e. including in the analysis the number of fledglings produced in a nest) using a Monte Carlo procedure, as described in the electronic supplementary material, S1. Briefly, we obtained distributions of number of breeders per nest for Fed and Unfed nests and then used parametric (t-test) and non-parametric (Mann–Whitney U-test) tests to assess whether there were significant differences in the expected number of breeders per nest between Fed and Unfed nests.
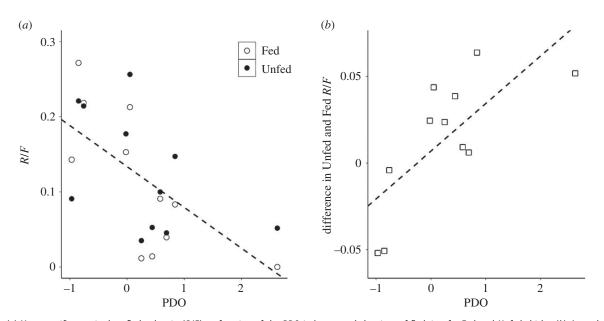
To test whether nutritional conditions at the neonatal stage affected lifetime reproductive success of breeders, we applied a Poisson regression model with nutritional conditions at birth and at breeding along with their interaction as predictors. For this analysis, we included kittiwakes that had completed their life cycle (i.e. they died or have disappeared from the colony) through 2014. We assumed that birds which did not return to breed for three consecutive years were either dead or permanently migrated to other colonies (previously, only 4% of birds missing for 3 years were subsequently found breeding again in the colony).

All analyses were run in R v. 3.01 [23] and are fully reproducible (code and data available at http://dx.doi.org/10.6084/m9.figshare.1003898). Statistical significance was assumed at the 0.05 level.

3. Results

(a) Productivity

During 1996–2006, the number of fledglings per nest was significantly higher in Fed than in Unfed nests (mean difference ± s.d.: 0.43 ± 0.25 fledglings per nest; paired t-test, $p < 0.01$) (figure 1). The annual productivity estimates of Fed and Unfed nests were positively correlated (Pearson's $r = 0.61$, $p = 0.047$). Neither Fed nor Unfed annual productivity was correlated with the PDO index (Fed, $r = 0.05$, $p = 0.88$; Unfed, $r = -0.41$, $p = 0.21$).

Figure 2. (a) Year-specific recruited-to-fledged ratio (R/F) as function of the PDO index around the time of fledging for Fed and Unfed chicks. (b) Annual difference in R/F between Fed and Unfed birds as a function of the PDO index at fledging.

(b) Chick growth in the nest

In the reduced dataset (i.e. including only chicks with a complete record of growth during the nestling phase), average daily increase in body mass G_m in the nest was $11.38 \pm 1.74 \, \mathrm{g \, d}^{-1}$ (mean $\pm$ s.d.). G_{max} and G_{min} were not significantly correlated (Pearson's $r = 0.05$, $p = 0.1$). The averaged model for G_m during the linear phase included the PDO index, feeding treatment and hatching order as explanatory variables, including interactions among those predictors (electronic supplementary material, tables S2 and S3). A positive PDO index (i.e. warmer oceanographic conditions) negatively affected G_m, with the negative effect being stronger for Unfed chicks (electronic supplementary material, table S3). Unfed chicks had only a slightly slower mean growth rate from day 5 to day 20 than Fed chicks (G_m, Fed = $11.44 \, \mathrm{g \, d}^{-1} \pm 1.67$; Unfed = $11.33 \, \mathrm{g \, d}^{-1} \pm 1.81$). Year-specific mean growth of A-chicks in Unfed nests correlated positively with productivity of Unfed nests in the same year (Pearson's $r = 0.69$, $p < 0.05$), while mean growth of B-chicks was not significantly correlated with productivity (Pearson's $r = 0.49$, $p = 0.12$). Mean growth of Fed chicks was uncorrelated with productivity in Fed nests, for either A- (Pearson's $r = 0.11$, $p = 0.75$) or B-chicks ($r = 0.24$, $p = 0.47$). We obtained the same results when G_m was calculated as (mass at day 20 − mass at day 5)/15 (see online code and data).

In synthesis for this section of Results, we found that A-chicks grew faster than B-chicks in both Fed and Unfed nests, and warmer oceanographic conditions decreased chick growth and affected more strongly Unfed chicks.

(c) Recruitment as breeders

From 1996 to 2006, 1629 chicks successfully fledged from the experimental nests (Unfed = 937, Fed = 692); up to 2013, 235 of those (Unfed = 152, Fed = 83) returned to breed in the tower. Sex ratio of breeders ($M = 167$, $F = 52$, unknown sex = 12) was male-biased (χ^2-test, $\chi_1^2 = 59.34$, $p < 0.01$), but the same sex ratio was observed within feeding treatments (χ^2-test, $\chi_1^2 = 0$, $p = 1$). R/F within hatching ranks (A- and B-chicks, and singletons) was not significantly
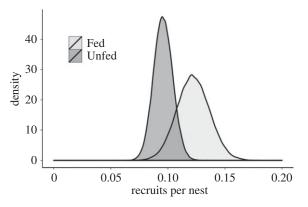
different between fledged and breeders in either treatment (Unfed: χ^2-test, $\chi_2^2 = 0.98$, $p = 0.61$; Fed: χ^2-test, $\chi_2^2 = 1.35$, $p = 0.51$).

Using the complete dataset (1629 chicks), Unfed fledglings were more likely to breed in the tower than Fed fledglings (mean and 95% CI: Fed = 0.12 [0.10–0.15]; Unfed = 0.16 [0.14–0.19]; χ^2-test, $\chi_1^2 = 5.43$, $p = 0.02$). Within each hatching rank, there was a 4% lower probability of returning to breed for Fed birds. The ANCOVA model indicated that R/F decreased with an increasing PDO index at birth year (i.e. with warmer oceanographic conditions) in both feeding treatments, while the interaction between feeding treatment and the PDO index was not statistically significant. Annual differences between R/F of Unfed and Fed birds increased with an increase in the PDO index (electronic supplementary material, table S4; figure 2).
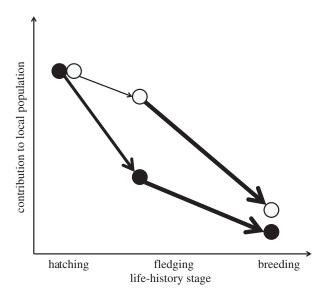
We found that Unfed fledglings had a greater probability of returning to breed than Fed fledglings also when using the reduced dataset (electronic supplementary material, table S5). The averaged logistic model (electronic supplementary material, table S6) indicates that a positive PDO index around fledging time decreased the probability of returning to breed for fledglings in both treatments, but the negative effect of warmer oceanographic conditions was stronger for Fed fledglings. For both feeding treatments, fledglings growing faster during the nestling phase had a higher probability of breeding in the colony. Within feeding treatment at birth and hatching rank, t-tests indicated that fledglings which later recruited as breeders to the tower grew significantly faster than fledglings that did not recruit as breeders, the only exception being Unfed B-chicks, for which we found no significant difference in growth rates between fledglings that did or did not recruit (t-test, $p = 0.18$).

(d) Net effect of food supplementation on recruitment

The results of the Monte Carlo simulations indicated that Fed nests are expected to produce more breeders per nest per year than Unfed nests (figure 3), i.e. all t tests and Mann-Whitney U-tests found significant differences in the expected number and distribution of breeders per nest: 0.122 [0.11–0.13]

Figure 3. Distribution of breeders per nest from 1996 to 2013 obtained with Monte Carlo simulations (10^5 replicates). Over the 10^5 replicates, for Fed birds, mean $\pm$ s.d. $= 0.122 \pm 0.014$ breeders per nest. For Unfed birds, 0.096 ± 0.008 breeders per nest.

Figure 4. Schematic of results for the effect of food supplementation on contribution of Fed (grey circles) and Unfed (black circles) nests to local population (i.e. relative number of chicks reaching that stage): the experimental food supplement affected the timing (life-history stage) and strength (indicated in thickness of connecting lines) of viability selection in long-lived kittiwakes.

(mean over 11 years [95% CI]) recruits per Fed nest, and 0.096 [0.09–0.10] breeders per Unfed nest (figure 4).

(e) Lifetime reproductive success

Fifty-six kittiwakes that bred in the Middleton colony were assumed to have completed their life cycle (i.e. they were not resighted during at least three consecutive years; mean and 95% CI of age at last re-sighting: 11[6–16] years old). Of those, 21 were born in Fed nests (10 then bred in Fed nests) and 35 were born in Unfed nests (27 bred in Unfed nests). One individual, which was born in a Fed nest, bred in an Unfed nest during the first reproduction and then bred in a Fed nest during the second (and last) reproduction, was excluded from the analysis. The Poisson regression model did not find any significant contribution of food supplementation during development for lifetime reproductive performance of the kittiwakes that completed their life cycle. However, kittiwakes breeding in Fed nests produced significantly more fledglings throughout their lifetime than kittiwakes breeding in Unfed nests (electronic supplementary material, table S7).

4. Discussion

The results of our unique experimental study suggest that supplemental food provided early in life to kittiwake chicks may only temporarily increase their survival chances. Although no clear carry-over effects to lifetime reproductive success were observed in a subset of kittiwakes that completed their life cycle early, the higher per-nest number of breeders that grew as chicks in Fed nests supports the hypothesis of a positive net effect of food supplementation on number of recruits per nest. We address these findings along with their implications for our understanding of the effects of food supplementation and variation in early conditions on life histories of individuals and on the conservation of long-lived seabirds.

(a) Productivity and growth during development

Food-supplemented parents produced more fledglings, thus confirming findings of previous experiments on birds and other vertebrates [24,25]. We found that yearly variation in productivity in Fed and Unfed nests were strongly correlated. Food-supplemented parents also continue feeding on natural prey [14,26] and local foraging conditions mediate the reproductive effort of both food-supplemented and control parents. Availability and quality of food play a major role in determining seabird productivity and colony dynamics, and largely explained the substantial variation in productivity that was observed on Middleton Island from 1996 to 2006 in both food-supplemented and control nests [10]. The substantial year-to-year variation in productivity of food-supplemented nests may indicate that food supplementation is not sufficient to entirely offset the natural decrease in productivity owing to low food abundance or poor food quality [27].

Following a late 1970s regime shift to warmer conditions in the North Pacific [28], many kittiwake colonies experienced frequent breeding failures owing to insufficient food for reproduction [29]. At Middleton, and probably over a larger region of the North Pacific, reversions to cooler conditions between 2000 and 2003 and after 2008 brought the re-emergence of important schooling fishes (particularly capelin) and substantially improved production of young by kittiwakes [10]. A recent meta-analysis found that food supplementation may not produce any obvious effect on production of young when food abundance in the environment is high [24]. Accordingly, the temporary return to cooler oceanographic conditions might explain why from 2000 through to 2003 we observed the smallest difference in yearly productivity between food-supplemented and control nests.

As expected, we found that food-supplemented chicks grew on average slightly faster than control chicks, and A-chicks grew faster than B-chicks. We also found a negative effect of PDO summer index on growth of chicks, especially in the control group. A stronger effect in Unfed chicks was expected, as the unlimited food provided to parents and chicks in Fed nests buffered the negative effects of warmer oceanographic conditions. Growth of Unfed chicks was faster than that of kittiwakes living in other northeastern Pacific colonies [12], which suggests that either foraging conditions were substantially better at Middleton compared with other colonies or stronger selection was exerted on low-quality chicks.

(b) Return to the colony

We found that a lower proportion of Fed fledglings later recruited as breeders in the Middleton colony compared with Unfed fledglings. Two processes may explain the observed pattern: (i) food-supplementation postponed viability selection, and the effect was stronger when local foraging conditions were relatively poor, and/or; (ii) a higher proportion of food-supplemented individuals reproduced elsewhere.

It has been suggested that high-quality individuals may have a higher probability of breeding in non-natal colonies, possibly at distant locations [30]. Although we cannot exclude the possibility of higher dispersal to other colonies of food-supplemented than control birds, it is unlikely that differential emigration explains the observed higher proportion of breeders from control nests. First, our results showed an increased probability of returning to breed in the tower colony between faster growing and probably higher quality chicks in both the food-supplemented and control groups. Although the sex ratio of breeders was male-biased, we did not find any substantial difference in growth between males and females in the subset of known-sex chicks (see Material and methods). Thus, it is unlikely that the higher probability of breeding in faster growing birds was driven by the male-biased recruitment. In addition, over four recent years, we found that sex ratios at fledging were not male-biased or different between Fed and Unfed nests (Fed, male to female ratio: 0.47 ± 0.03, $n = 219$; Unfed: 0.47 ± 0.04, $n = 176$). Thus, although we lack data for sex of the majority of fledglings from 1996 to 2006, we can rule out the possibility that male-biased sex ratio at breeding was a result of female-biased mortality at the nestling stage. Nevertheless, further investigations are needed to determine whether sex-biased probability of returning to breed in the colony was a result of higher post-fledging mortality or higher dispersal of females [31].

Second, prospecting kittiwakes are more likely to breed in highly productive colonies [32]. Tower-breeding kittiwakes on Middleton may have the highest productivity of any colony in the Northeastern Pacific, and previous work has shown high, fine-scale site fidelity of young kittiwakes returning there to nest [12]. Specifically, two thirds of kittiwakes that grew as chicks in Fed or Unfed nests later bred in Fed and Unfed sites, respectively, and most breeders settled on the same wall panel where they were born [12]. Third, cohort effects on the survival of seabird juveniles are well known and usually attributed to climatic effects on food quality and quantity. Accordingly, we found that the recruitment rate of cohorts decreased with an increasing PDO summer index (i.e. poorer oceanographic conditions) in birth year for both feeding treatments.

Our results thus support the hypothesis that food supplementation early in life increased only temporarily (i.e. during the nestling stage) the survival chances of poorer quality offspring. One of the potential mechanisms may be selective brood reduction via sibling aggression in control nests [33]. In kittiwakes, even subtle decreases in environmental conditions often lead to brood reduction via elimination of junior chicks, as the support of low-quality chicks when environmental conditions are not optimal would probably compromise the fitness of higher quality chicks [34]. In support of this hypothesis, we observed that mean growth of Unfed A-chicks was positively correlated with productivity, whereas growth of B-chicks was not. As mean growth of neither food-supplemented A- nor B-chicks was correlated with productivity, this result, along with the observed lower productivity in control nests and no difference in growth of control B-chicks that later recruited as breeders or not, suggests that stronger viability selection was operating on B-chicks in Unfed nests, i.e. B-chicks either fledged in near-optimal conditions or died prior to fledging.

In the case of higher mortality of B-chicks during the nesting stage in Unfed nests, the highest difference in probability of returning to breed in the colony between Fed and Unfed birds is expected for B-chicks of all the social ranks. However, we found approximately 4% lower recruitment rates in each social rank of Fed birds compared with controls. As Unfed B-chicks born in only 5 out of 11 years later bred in the colony, longer time series would be necessary to confirm that viability selection on B-chicks during the nesting stage was stronger in control than food-supplemented nests.

A stronger correlation between individual quality and fitness is expected in poor environments. For instance, Reed et al. [6] found that the negative effects of low genetic quality of individuals on population growth rates in two species of spiders were mediated by nutritional stress. Genetic effects owing to inbreeding were strongest in environments that allowed low capture rates of prey and induced high levels of competition among spiders. Similarly, we found that the difference in recruited to fledged ratios between Unfed and Fed birds increased with warmer conditions (a higher PDO index) around the time of fledging. This result has two main implications. First, it suggests that inter-cohort differences in the probability of breeding were largely determined by oceanographic conditions at independence, which is a critical period in the life of seabirds [35]. Second, it supports the hypothesis that the post-fledging survival of low-quality food-supplemented kittiwakes was lower when foraging conditions at independence were poor. This might also be a consequence of a mismatch between growth in the nest and (low) quality of birds, i.e. the effects of poor foraging conditions after fledging may be more severe for low-quality birds that were growing too fast in the nest due to food supplementation (e.g. increased risk of starvation) or faced other physiological costs of fast growth [36].

(c) Reproductive success

We found that the food supplementation during development did not explain a substantial part of the variation in number of fledglings per nest for kittiwakes that completed their life cycle up to the year 2014. This result may suggest a similar quality of individuals breeding in the colony, or stochastic factors heavily influencing the lifetime reproductive success of kittiwakes [37]. However, we emphasize that thus far we were able to examine the reproductive performance of only a subset of individuals that quickly completed their life cycles (mean age at last re-sighting was approx. 11 years old, which is substantially less than expected maximum age of approx. 25 years old in the wild) owing to early death or emigration to other colonies. Thus, whether early feeding conditions affected lifetime fitness of kittiwakes that had a longer reproductive life or adopted slower histories (e.g. less energy allocated to reproduction, higher age at reproduction) remains to be tested.

Controlled studies on the long-term or intergenerational consequences for birds of poor early foraging conditions are

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rare [4,38]. Zanette *et al.* [4] conducted a food supplementation experiment on song sparrows *Melospiza melodia* and tested whether male quality (using song repertoire size as a proxy of quality) differed between the adult sons of food-supplemented and control parents. Surprisingly, Fed parents produced sons with smaller adult song repertoires, who may thus be expected to contribute fewer offspring to the next generation. In natural conditions, it has been found that food limitations early in life associated with the El Niño Southern Oscillation (ENSO) had long-term consequences on life-history strategies of blue-footed boobies *Sula nebouxii* [38]. Birds that experienced warm oceanographic conditions at birth were underweight at fledging, recruited earlier and bred less frequently. However, breeding success and longevity of birds that were born in warm ENSO years were not different from those of birds that were born in cool ENSO years [38].

(d) Implications for conservation

Despite a lower probability of recruiting as breeder in the local population for kittiwakes that had been food-supplemented as chicks, the per-nest number of produced breeders was higher for food-supplemented than for control nests. Although we currently lack data to determine the lifetime reproductive success of the majority of experimental birds that are still breeding in the colony, the results of this work suggest that food supplementation may have long-term positive effects on the kittiwake colony of Middleton Island. While long-term effects of food supplementation to food-limited seabirds may face logistical and financial constraints, food supplementation might be among the few conservation measures that, at least in the short-term, can help endangered species or populations persist when facing a strong decline in productivity.

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