RESEARCH ARTICLE

Finding the best predictor of reproductive performance of Leach's Storm-Petrels

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ABSTRACT

Physiological and environmental factors shape foraging strategies and energy balance. For species that breed seasonally, physiological changes in an individual can have short-term effects, but also can persist as carry-over effects from one season to the next, such as from the overwintering season to the breeding season. We tested the hypothesis that reproductive performance could be predicted by diet and energy balance during the breeding and nonbreeding seasons in a long-lived seabird, the Leach's Storm-Petrel (*Oceanodroma leucorhoa*). Specifically, we predicted that better reproductive performance would be correlated with four factors: (1) a high-lipid diet, as indexed by a high C:N ratio in stable isotope analyses; (2) a diet rich in antioxidants, as indexed by high plasma antioxidant capacity; (3) foraging at a high trophic level, as indexed by high values of $\delta^{15}N$ in stable isotope analyses, which is positively related to lipids; and (4) a positive long-term energy balance, revealed by low levels of corticosterone in feathers. Because of our interest in short-term effects vs. carry-over effects, stable isotope values were measured from two different tissue sources: erythrocytes, to test for short-term effects, and winter-grown feathers, to test for carry-over effects. We monitored reproductive performance through egg volume, chick growth, parental provisioning, and fledging success. Parents with more breeding experience were more likely to have a successful nest in 2010, but not in 2009. Individuals exhibited consistent egg volume and nonbreeding season feather $\delta^{15}N$ values across the 2 years of our study, but, overall, neither diet nor feather corticosterone predicted reproductive performance. Nonetheless, our simple, noninvasive measures of breeding performance could be applied to other species to study life-history strategies and energy balance.

Keywords: parental care, carry-over effects, breeding experience, stable isotopes, corticosterone, antioxidant capacity, seabird

Encontrando el mejor predictor de desempeño reproductivo de *Oceanodroma leucorhoa*

RESUMEN

Los factores fisiológicos y ambientales dan forma a las estrategias de forrajeo y al balance energético. Para las especies que se reproducen estacionalmente, los cambios fisiológicos en un individuo pueden tener efectos de corto plazo pero también pueden persistir como efectos de arrastre de una estación a la siguiente, tal como de la estación invernal a la estación reproductiva. Evaluamos la hipótesis de que el desempeño reproductivo podría ser predicho por la dieta y el balance energético durante las estaciones reproductivas y no reproductivas en un ave marina longeva, *Oceanodroma leucorhoa*. Específicamente, predijimos que un mejor desempeño reproductivo se correlacionaría con cuatro factores: (1) una dieta alta en lípidos, marcada por una alta relación C:N en los análisis de isótopos estables; (2) una dieta rica en antioxidantes, marcada por una alta capacidad antioxidante del plasma; (3) forrajear en un alto nivel trófico, marcado por altos valores de δ15N en los análisis de isótopos estables, lo que está positivamente relacionado a los lípidos; y (4) un balance energético positivo de largo plazo, revelado por bajos niveles de corticoesterona en las plumas. Debido a nuestro interés en los efectos de corto plazo versus los efectos de arrastre, medimos los valores de los isótopos estables en dos fuentes de tejidos diferentes: eritrocitos, para evaluar los efectos de corto plazo, y plumas de las áreas de invernada, para evaluar los efectos de arrastre. Monitoreamos el desempeño reproductivo a través del volumen del huevo, el crecimiento del pichón, el aprovisionamiento parental y el éxito de emplumamiento. Los padres con más experiencia reproductiva presentaron una mayor probabilidad de tener un nido exitoso en 2010 pero no en 2009. Los individuos mostraron valores consistentes de volumen del huevo y δ15N en las plumas de invernada a lo largo de los dos años de nuestro estudio, pero de modo global, ni la dieta ni la corticoesterona de las plumas

predijeron el desempeño reproductivo. Sin embargo, nuestras medidas simples y no invasivas de desempeño reproductivo podrían ser aplicadas a otras especies para estudiar las estrategias de las historias de vida y el balance energético.

Palabras clave: ave marina, capacidad antioxidante, corticoesterona, cuidado parental, efectos de arrastre, experiencia reproductiva, isótopos estables

INTRODUCTION

Allocation of metabolic energy from diet and endogenous resources to physiological activities shapes an individual's life-history trajectory, specifically through the amount of energy allocated to reproduction and self-maintenance (Ricklefs and Wikelski 2002). The distribution of energy to these different activities changes as the body continuously adjusts hormones and behaviors to compensate for moment-to-moment changes in its surroundings, and as its life-history stage changes (for example, from migratory behaviors to reproduction; Biro and Stamps 2010). Individual variation in energy allocation can translate to variation in reproductive performance by affecting how an individual forages, synthesizes hormones, and avoids predators (Astheimer et al. 1992, Lõhmus and Björklund 2009).

For animals that breed seasonally, the balance of energy between reproduction and self-maintenance can be influenced across two time scales: (1) immediate effects during the breeding season; and (2) delayed effects from the preceding nonbreeding season. For example, diet choice, habitat quality, and weather during the nonbreeding season affect arrival date at the breeding grounds (Marra et al. 1998), breeding body condition (Ebbinge 1989), and breeding success (Fox and Gitay 1991). In this study, we tested whether interindividual differences in diet and energy balance were correlated with reproductive performance (defined by measures of egg volume, chick growth rates, and fledging success). Due to the physiological benefits of lipids, antioxidants, and low levels of a hormone, corticosterone (CORT), we hypothesized that birds that had a high dietary trophic level, high relative amounts of dietary lipids, high dietary antioxidants, and/or low CORT would be more successful parents, as detailed below.

First, high dietary lipids are predicted to aid reproductive performance because they are energy-dense (Romano et al. 2006), which improves reproductive success in birds (Litzow et al. 2002) and is especially important for chick growth (Grémillet et al. 2008, Kwasniewski et al. 2010). The ratio of carbon to nitrogen (C:N) in a tissue sample can be used as a proxy for the relative amount of lipids in the diet (Post et al. 2007) due to the large amounts of carbon in lipids. We measured C:N in two types of tissues: winter-grown feathers, to assess diet in the nonbreeding season (e.g., Cherel et al. 2000), and erythrocytes, to assess diet during the breeding season (e.g., Ceia et al. 2012).

Second, high levels of dietary antioxidants are predicted to aid reproductive performance because of their role in quenching free radicals (Sies 1991), improving immune function (Catoni et al. 2008a), and accelerating embryonic development and chick growth (Rubolini et al. 2006). Because many antioxidants are derived from the diet (Catoni et al. 2008b), we measured plasma antioxidant capacity as a proxy for dietary antioxidant intake.

Third, foraging at a high trophic level is predicted to increase reproductive performance because high metabolic energy is found at high trophic levels (Albano et al. 2011), and because high trophic levels are associated with high lipid content (Romano et al. 2006); both factors are important for a chick's growth and energy assimilation (Grémillet et al. 2008). Trophic level is commonly estimated from the nitrogen enrichment ($\delta^{15}N$) in an animal's tissues (Fry 1988, Hobson 1993). As with our measures of dietary lipids, we tested separately for short-term effects and carry-over effects by measuring $\delta^{15}N$ in erythrocytes (Ceia et al. 2012) and winter-grown feathers (Cherel et al. 2000), respectively.

Fourth, we predicted that strong reproductive performance would be correlated with a positive energy balance, as indexed by low levels of CORT (e.g., Crossin et al. 2013, Bourgeon et al. 2014). CORT is a hormone that enables animals to mobilize energy (Sapolsky et al. 2000). Although continuously present at fluctuating baseline concentrations, large amounts of CORT are synthesized and released when an individual encounters a stressful situation, such as disease (Owen et al. 2012) or low prey availability (Kitaysky et al. 2007). High CORT titers over a long timeframe can have negative consequences for an individual, including poor body condition (Kitaysky et al. 1999) and low reproductive success (Buck et al. 2007). To obtain a measure of CORT that reflected energy balance over a period of 1–2 weeks, we measured CORT in feathers, providing an integrated measure of CORT during the prebreeding period of feather growth (Bortolotti et al. 2008).

We tested these predictions with multiple measures of reproductive performance in a long-lived seabird, Leach's Storm-Petrel (*Oceanodroma leucorhoa*; Figure 1). This species is a surface feeder that forages on phytoplankton, zooplankton, and small fish—organisms that vary in lipid (Neighbors and Nafpaktitis 1982, Schukat et al. 2013) and

FIGURE 1. Leach's Storm-Petrel chick, aged 60 days, at Bowdoin Scientific Station on Kent Island, New Brunswick, Canada, September 2010. Photo credit: Morgan E. Gilmour

antioxidant (Andersson et al. 2003, Nie et al. 2011) content. We monitored the reproductive performance of Leach's Storm-Petrels by measuring egg volume, chick growth, parental provisioning, and fledging success. On a subset of birds, we measured interannual variation of diet and reproductive performance to determine whether individuals were consistent in foraging behavior and energy allocation over two breeding seasons.

METHODS

Study Area
We studied Leach's Storm-Petrels at Bowdoin Scientific Station on Kent Island, New Brunswick, Canada (44.58°N, 66.81°W), in July 2009 and June–October 2010.

Study Species
Leach's Storm-Petrels are nocturnal at the breeding colony in order to avoid predation by gulls (Gross 1935, Huntington et al. 1996). They lay one egg in a burrow nest and both sexes share the work of the 43-day incubation period and 66-day chick-rearing period (Huntington et al. 1996). To minimize the risk of abandonment, we sampled adults at least 14 days after an egg was found in their burrow (Blackmer et al. 2004, R. A. Mauck personal observation).

Blood and Feather Sampling
We sampled incubating birds by venipuncture, collecting 120 μL of blood into heparinized capillary tubes. Blood for sex determination (in 2009 and 2010) was stored in lysis buffer. Blood for stable isotope and antioxidant analyses (in 2010) was divided into cells and plasma: less than 4 hr after sampling, we separated blood by centrifuging at 1,400× *g*

for 5.5 min; we then froze the components at −20°C until laboratory analyses (4–8 mo later). To measure feather CORT, we plucked 13 feathers from the nape of each bird, which comprised feathers that were molted in mid–late winter; 3 feathers were pooled for stable isotope analysis and 10 feathers were pooled for the feather CORT assay. This sampling scheme ensured that these feathers were grown around the same time because the molt of Leach's Storm-Petrel body feathers occurs during the nonbreeding season and in a predictable spatial sequence across the body (Ainley et al. 1976, Spear and Ainley 2007, C. Huntington personal communication). Leach's Storm-Petrel feathers grow 1.5–2.0 mm per day (Ainley et al. 1976, Mauck et al. 2011); the feathers we used were 20.80 ± 0.06 mm in length, so each feather likely took 10.5–21.0 days to grow, meaning that our feather-based measures of CORT or stable isotopes were integrative over this 10- to 21-day time period. Feathers were stored in envelopes at room temperature for up to 4 mo before laboratory analyses.

Reproductive Performance Monitoring
We used calipers to measure the length and width of all eggs to the nearest 0.1 mm to calculate egg volume (volume = 0.51 * Length * B^2, where B is breadth, which is the maximum diameter of the egg; Hoyt 1979). Leach's Storm-Petrels lay one egg per clutch (Huntington et al. 1996). The egg volumes of 17 females were measured in both 2009 and 2010; additionally, the egg volumes of 60 other females were measured in either 2009 or 2010. The coefficient of variation of egg volume measurements was 0.06 in 2009 and 0.11 in 2010. In 2010, we also monitored the daily growth of 22 chicks: after hatching, we measured mass and flattened wing length daily between 08:00 and 10:00 until fledging, using an electronic balance accurate to 0.1 g (Ohaus Scout Pro, Parsippany, New Jersey, USA) and a wing ruler accurate to the nearest 0.5 mm.

We considered parents "successful" if they fledged a chick, and "failed" if they did not fledge a chick. Nesting failure at our study site is generally related to parental reproductive performance (for example, parents incubate the egg for too short a time, then abandon the unhatched egg; Zangmeister et al. 2009) or sometimes to extremely wet weather; nest predation is rare (but see Gross 1935). To obtain a finer scale of reproductive performance, we created a multicategory measure for parents sampled in 2010: categories on an 8-point scale distinguished the amount of time elapsed before failure within the "failed" group, and the categories of the "successful" group incorporated peak chick mass (Table 1A). Dates of failure were determined through daily nest checks: we placed twigs at burrow entrances, and every morning we checked to see whether the twigs had been moved during the previous night; moved twigs indicated that a bird had

TABLE 1. (**A**) Eight-point scale of categories of reproductive performance of Leach's Storm-Petrels on Kent Island, New Brunswick, Canada, in 2010; (**B**) Nonparametric correlations of measures of diet and energy balance with 8-point scale of reproductive performance; * indicates that P is significant at $\alpha = 0.05$. CORT = corticosterone. We included variables that were correlated with sample mass ($\delta^{15}N$ erythrocytes) as "sample mass-adjusted" in analyses. For variables that were sampled throughout a season (erythrocyte stable isotopes, plasma antioxidant capacities), we analyzed the residuals of a regression of each variable on sample date; these values are presented as "date-adjusted."

A

Category	Definition	No. adults in category
1	Failed in early incubation (13 days from laying date)	20
2	Failed in mid incubation (27 days from laying date)	10
3	Failed in late incubation (39 or 40 days from laying date)	15
4	Failed during chick rearing (65 to 116 days from laying date)	6
5	Peak chick mass 65–74 g; chick fledged	6
6	Peak chick mass 75–84 g; chick fledged	16
7	Peak chick mass 85–94 g; chick fledged	12
8	Peak chick mass $\geq$95 g; chick fledged	4

B

Measure of breeding–nonbreeding ecology	Spearman's r_s	P
Nonbreeding season feather $\delta^{15}N$ (‰)	−0.11	0.30
Breeding season erythrocyte $\delta^{15}N$ (‰)	−0.11	0.29
Breeding season erythrocyte $\delta^{15}N$ (‰), date-adjusted	0.01	0.25
Nonbreeding season feather CORT (pg CORT mm^{-1})	−0.13	0.25
Breeding season plasma antioxidant capacity (μmol HClO mL^{-1})	0.07	0.77
Parents' breeding experience (yr)	0.43	<0.001*
Nonbreeding season feather C:N	0.02	0.82
Breeding season erythrocyte C:N	−0.14	0.21
Breeding season erythrocyte C:N, date-adjusted	−0.07	0.49
Breeding season erythrocyte $\delta^{15}N$, sample mass-adjusted	0.03	0.79

entered or exited the burrow (Blackmer et al. 2004, Zangmeister et al. 2009). These data enabled us to determine how many days had elapsed since the last burrow visit by the adults, and thus enabled us to place failed nests into the categories described in Table 1A.

On a subset of adults (9 pairs), we measured burrow attendance with a Passive Integrated Transponder (PIT) system (Model TX1400ST, BioMark, Boise, Idaho, USA; Zangmeister et al. 2009), consisting of PIT tags on adults, an antenna encircling the burrow entrance, and a reader/datalogger. Glass-encapsulated radio-frequency identification (RFID) PIT tags weighing 0.102 g ($\sim$0.2–0.3% of adult mass) were attached to Darvic leg bands (Avinet, Dryden, New York, USA). These tags and attachment methods have been used successfully in the past in this colony of Leach's Storm-Petrels, with very few ill effects on the birds (R. A. Mauck personal observation). The readers/dataloggers were turned on at night (21:30 to 06:00), operated at 10% antenna power, and constantly recorded PIT tags that passed through the antenna. Burrows were monitored for an average ($\pm$ SE) of 62.0 $\pm$ 7.5 nights (range of nights monitored: 36–96 nights; $n = 9$ burrows). Using these data, we quantified individual parental provisioning by calculating: (1) the percentage that each mate contributed to the

pair's total number of burrow visits during chick rearing; and (2) the percentage that each mate contributed to the pair's total food mass brought to the chick. A parent's contribution to the chick's net change in mass was determined by combining records of the parents' visits to the burrow (using PIT tag data) with the chick's 24-hr net mass gain as determined by measurements the next morning. However, on some nights (59 of 321 nights = 18% of nights when at least one parent visited the burrow) both parents visited the burrow, and it was impossible to determine the amount of food delivered to the chick by each parent; in those cases, we included that night in each parent's total burrow visits, but excluded meal mass from calculations of percent contribution by the two mates.

Stable Isotope Analysis

Feathers were washed in a 2:1 chloroform:methanol solution for 24 hr to remove lipids and then allowed to dry. We cut the feathers into small fragments with stainless steel scissors, avoiding the calamus, rachis, and aftershaft, and packed the feather pieces into a tin capsule. Enough sample material was yielded by 2–3 feathers to reach a target mass of 0.20 to 0.76 mg (2009 feather samples) or 0.30 to 1.20 mg (2010 feather samples) for subsequent

analysis. The variance of the feather sample masses in 2009 was 1.9% and in 2010 was 4.2%. The variance for the blood sample masses in 2010 was 5.9%.

Avian red blood cells represent integrated diet ~1 mo prior to sampling (Hobson and Clark 1993, Hahn et al. 2012), making them an ideal tissue with which to assess early-breeding-season diet (we sampled blood between June and July; breeding begins in May). Packed red blood cells were dried in tin capsules in an oven at 55°C for up to 120 hr. Our samples of 4–5 μL of red blood cells yielded a dry mass of 0.50 to 1.50 mg for subsequent analysis.

Blood and feather samples were sent to the Stable Isotope Facility at the University of California–Davis for natural abundance analysis of $\delta^{13}C$ and $\delta^{15}N$. Samples were analyzed using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon, Cheshire, UK). Stable isotope ratios are expressed in delta notation (δ) as parts per thousand (‰) relative to international standards V-PDB (Vienna PeeDee Belemnite) for carbon and air for nitrogen, using the equation:

$$\delta X = \left[(R_{sample}/R_{standard}) - 1\right],$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. In-house laboratory standards were used as secondary isotope reference materials in our analyses (SD range within runs, mean ± SD among all runs): nylon ($\delta^{13}C$: 0.03–0.07, −27.81 ± 0.04‰; $\delta^{15}N$: 0.07–0.13, −9.77 ± 0.11‰), glutamic acid, enriched ($\delta^{13}C$: 0.003–0.150, 43.74 ± 0.13‰; $\delta^{15}N$: 0.15–0.20, 45.31 ± 0.18‰), bovine liver ($\delta^{13}C$: 0.13–0.04, −21.69 ± 0.07‰; $\delta^{15}N$: 0.07–0.20, 7.72 ± 0.17‰), and glutamic acid ($\delta^{13}C$: 0.06–0.12, −28.85 ± 0.12‰; $\delta^{15}N$: 0.14–0.41, −4.26 ± 0.39‰).

Due to mass-dependent differences in isotope ratios that can occur due to differences in gas pressures in a mass spectrometer during stable isotope analyses, the masses of sample material for isotopic analyses should be within ±5% of the target mass (Bond and Hobson 2012). Because sample masses among feathers and among erythrocytes in our study varied (2009 feather sample mass [mean ± SE]: 0.35 ± 0.01 mg, range: 0.2–0.8 mg; 2010 feather sample mass [mean ± SE]: 0.66 ± 0.02 mg, range: 0.2–1.3 mg; 2010 erythrocyte sample mass [mean ± SE]: 0.85 ± 0.02 mg, range: 0.4–1.5 mg), we ran a regression of each isotope variable with sample mass to assess whether variations in our sample masses could have affected our results. Only one sample type, erythrocytes, was negatively correlated with isotope values (breeding erythrocyte $\delta^{15}N = 12.97 - 0.57 *$ sample mass; adjusted $r^2 = 0.05$, $F_{1,119} = 6.64$, $P < 0.01$); thus, for this variable, we saved the residuals and included those values in our analyses (noted as "erythrocyte $\delta^{15}N$, sample mass-adjusted").

Feather CORT Analysis

We removed the calamus and aftershaft from 10 feathers from each bird and then measured the lengths of each feather. We minced the feathers into pieces <5 mm^2 using stainless steel scissors over an analytical balance to standardize all samples to within 0.2 mg of each other, in order to reduce intersample variation (Lattin et al. 2011). To extract CORT from the minced feathers, we followed the methods of Bortolotti et al. (2008). After extraction, samples were subjected to radioimmunoassay to determine CORT concentrations (Wingfield et al. 1992). We assayed samples in duplicate using antibody C 8784 (Sigma Aldrich, Saint Louis, Missouri, USA). To determine individual recoveries, we spiked samples with a small amount of radiolabeled CORT and corrected the assay values for individual recoveries following extraction. A parallel relationship between feather extracts and the CORT standard curve was shown by Bortolotti et al. (2008) using the same antibody, suggesting that feather extracts do not contain any substances that could interfere with this assay. Inter- and intra-assay coefficients of variation were determined by running two types of standards in each assay: (1) a sample containing a known concentration of CORT, and (2) a feather standard of a homogenous mixture of several Leach's Storm-Petrel feathers (Lattin et al. 2011) pulverized using a ball mill (model 4200, Kleco, Visalia, California, USA). Interassay variation was 14% and intra-assay variation was 1%.

Previous work (Bortolotti et al. 2008, 2009, Lattin et al. 2011) has found significant positive relationships between feather CORT and feather length and between feather CORT and feather mass. Measurements of feather CORT per mm of feather were strongly correlated with measurements of feather CORT per mg of feather in our samples (Spearman's $r_s = 0.98$, $P < 0.001$, $n = 109$). Measuring CORT per unit of length may be more relevant, due to the way that a feather grows (Bortolotti et al. 2008), and therefore we report pg CORT mm^{-1}. The natural log (base e) was used to normalize the distribution of feather CORT, and these values were used in regression analyses.

Antioxidant Assay

We determined the antioxidant capacities of a subset of birds in 2010 ($n = 34$ birds) with the OXY-Adsorbent test (Diacron International, Grosseto, Italy; Haussmann et al. 2012), assaying samples in duplicate. The assay was scored with a spectrophotometric measure of absorbance at 490 nm using the formula:

$$\text{Antioxidant capacity} = [(\text{Abs blank} - \text{Abs sample})/$$
$$(\text{Abs blank} - \text{Abs standard})]$$
$$\times 350,$$

where "Abs" is the absorbance reading of the blank, standard, and samples (Diacron International). An intra-assay coefficient of variation was determined by running standards in the assay; intra-assay variation was 7%.

Only values for individuals who had returned from a foraging trip the previous night were used in statistical analyses (we used 23 of 34 birds) because antioxidant capacity decreases during fasting (Milinkovic-Tur et al. 2009).

Molecular Sex Determination

Because Leach's Storm-Petrels are sexually monomorphic, we used molecular sex determination (Griffiths et al. 1996). Whole blood (2009 samples) or red blood cells (2010 samples) were digested with lysis buffer and proteinase K, DNA was isolated by ethanol precipitation, and sex-specific markers were amplified and visualized with a modified version of the Griffiths et al. (1996) PCR protocol (J. Zangmeister and M. F. Haussmann personal communication). The sexes of 50 sampled birds were determined in this manner; the sex of 49 birds had been determined previously; and the sex of 7 birds sampled in 2009 could not be determined because blood was not obtained from these birds. The sexes of mates of known-sex birds were inferred by assuming heterosexual pairings (47 birds); genetic sex determination of both members of 50 pairs of Leach's Storm-Petrels in 2006 and 66 pairs in 2010 showed no cases of same-sex pairings (R. A. Mauck and D. C. Dearborn personal observations).

Statistical Analyses

We used univariate and multivariate analyses to test whether interseasonal measures of diet (stable isotopes and antioxidant capacities) and energy balance (feather CORT) affected reproductive performance in Leach's Storm-Petrels. First, we measured chick growth statistically in two ways: (1) the time that the chick reached the end of structural development, defined by T (Mauck and Ricklefs 2005), which signals a phase of anorexia in the chick in preparation for fledging and reflects parental provisioning; and (2) because T is a measure of time to reach asymptotic size, and does not address chick size directly, we used peak chick mass as a measure of size and parental effort (Mauck and Ricklefs 2005). Next, we analyzed whether the diet and energy balance of parents predicted reproductive effort in five ways, in order to use the most appropriate analyses for the dataset: (1) we used Spearman rank correlations to determine whether the diet and energy balance of females predicted egg volume; (2) we used ANOVAs to assess whether measures of diet and energy balance of parents predicted the parents' contributions to chick T, total burrow visits, net change in chick mass per burrow visit, and peak chick mass; (3) we used a Mann-Whitney-Wilcoxon test to assess difference in measures of diet and

energy balance between "successful" and "failed" parents; (4) we used Spearman rank correlations to compare the 8-point scale of reproductive effort with measures of parental diet and energy balance; and (5) we conducted multivariate analyses to evaluate the interaction of diet, energy balance, and breeding experience variables on reproductive success. The univariate analyses had the advantage of using all of the data (because the different variables had different sample sizes), while the multivariate approach had the benefit of considering multiple variables simultaneously. For the multivariate analysis, we predicted that birds that had high $\delta^{15}N$, high C:N, high plasma antioxidant capacities, and/or low feather CORT would exhibit better reproductive performance. We evaluated all possible models in multiple regressions, and then we employed two analyses to calculate the best predictor models of the reproductive performance of Leach's Storm-Petrels: (1) Akaike's Information Criterion corrected for small sample sizes (AIC_c); and (2) model averaging. We used differences in AIC_c ($\Delta AIC_c = AIC_{c,model i} - AIC_{c,min}$) to rank candidate models, and we considered the top models to be those in which $\Delta AIC_c < 2$ (Burnham and Anderson 2002). We calculated the relative likelihood (Akaike weight, w_i) of each model with the formula: $e^{((AIC_{c,min} - AIC_{c,model i})/2)}$. Model averaging provided parameter and error estimates of predictor variables from weighted averages of these parameters across multiple models. All models were considered, regardless of whether an individual had data for all variables that we measured; for example, plasma antioxidant capacity was only measured in 23 of 121 Leach's Storm-Petrels in 2010. A large SE indicated that confidence in that variable was low.

Because survival and reproductive success increase with age in this population of Leach's Storm-Petrels (Mauck et al. 2012), we also included parent age as a factor in analyses. Leach's Storm-Petrels have been monitored on Kent Island for over 60 years; many breeding birds are banded, and demographic information is available. Most birds in the Kent Island colony are 6.4 ± 2.9 yr at age of first breeding ($n = 53$; Mauck et al. 2012). We combined this with banding data to estimate the "breeding experience" of parents in the study. We used the breeding experience of each individual only once per analysis per study year.

Because the components of blood turn over at different rates (Hobson and Clark 1993, Hahn et al. 2012), it is important to consider sampling date when comparing blood-based data among individuals that were sampled at different times during the breeding season. Therefore, in addition to using erythrocyte-based isotopes and plasma-based antioxidant capacities in our analyses, we ran a regression of each blood-based variable with sample date. For the variables that were statistically significantly correlated with sample date (breeding erythrocyte $\delta^{15}N =$

TABLE 2. Nonparametric correlations of egg volume (mm^3) with measures of diet and energy balance in Leach's Storm-Petrels on Kent Island, New Brunswick, Canada, in 2009 and 2010; * = P is significant at $\alpha = 0.05$. Dashed lines indicate that those data were not sampled in 2009. NB = nonbreeding season, B = breeding season, CORT = corticosterone. For variables that were sampled throughout a season (erythrocyte stable isotopes, plasma antioxidant capacities), we analyzed the residuals of a regression of each variable on sample date; these values are presented as "date-adjusted." We included variables that were correlated with sample mass (δ^{15}N erythrocytes) as "sample mass-adjusted" in analyses.

Measure of diet–energy balance	Egg volume 2009			Egg volume 2010		
	Spearman's r_s	P	n	Spearman's r_s	P	n
NB feather δ^{15}N (‰)	0.14	0.43	35	0.10	0.46	59
NB feather CORT (pg CORT mm^{-1})	—	—	—	0.19	0.18	52
B erythrocyte δ^{15}N (‰)	—	—	—	−0.07	0.58	59
B erythrocyte δ^{15}N (‰), date-adjusted	—	—	—	−0.10	0.44	59
Breeding experience (yr)	0.09	0.60	35	−0.08	0.58	56
NB feather C:N	0.20	0.25	35	0.00	0.98	59
B erythrocyte C:N	—	—	—	−0.08	0.54	59
B erythrocyte C:N, date-adjusted	—	—	—	−0.07	0.60	59
B erythrocyte δ^{15}N, sample mass-adjusted	—	—	—	0.09	0.49	59

−69011.50 + 0.03 * blood sample date; adjusted $r^2 = 0.20$, $F_{1,119} = 26.7$, $P < 0.001$; C:N= −3766.556 + 0.002 * blood sample date; adjusted $r^2 = 0.03$, $F_{1,119} = 4.71$, $P = 0.03$), we saved the residuals and reran the analyses (included as "date-adjusted" parameters of erythrocyte δ^{15}N, C:N).

We conducted post-hoc calculations of confidence intervals (CI) for the effect sizes observed in our study (Steidl and Thomas 2001). We calculated CI for the differences of the means of successful and failed parents' measures of diet, energy balance, and breeding experience with the program Exploratory Software for Confidence Intervals (ESCI; Cumming 2012). We used a sequential Bonferroni correction of alpha for both study years: in 2009, alpha was adjusted for the 4 comparisons of diet and energy balance between successful and failed parents, 0.05/4 = 0.0125; and in 2010, alpha was adjusted for 9 comparisons, 0.05/9 = 0.0056 (Rice 1989). If a comparison is statistically significant, the CI should not span zero, but the CI should also represent values that are biologically meaningful (e.g., a difference of 1.0‰ in δ^{15}N is not large enough to be considered a difference in trophic level because trophic levels are generally considered to be 3–4‰ apart; Hobson and Welch 1992).

All statistical analyses were performed in SPSS 18 and SPSS 20 (IBM, Chicago, Illinois, USA) and JMP 9.0.0 (SAS, Cary, North Carolina, USA). All means are presented ± standard deviation.

RESULTS

Reproductive Performance

Parental breeding experience was positively correlated with our 8-point scale of reproductive performance (Table 1B). Egg volume (Table 2), the completion of nestling structural growth, T (adjusted $r^2 = 0.17$, $F_{8,5} = 1.34$, $P = 0.39$), and peak chick mass (adjusted $r^2 = -0.04$, $F_{8,5} = 0.94$,

$P = 0.56$) were not predicted by parental nonbreeding season feather or breeding season erythrocyte δ^{15}N, date-adjusted erythrocyte δ^{15}N, sample mass-adjusted δ^{15}N, nonbreeding season feather or breeding season erythrocyte C:N, date-adjusted erythrocyte C:N, feather CORT, or breeding experience. Egg volumes of females sampled in both years were correlated (Figure 2A). The completion of nestling structural growth, T, ranged from 57.0 to 69.4 days, and peak mass of chicks ranged from 65.70 to 98.40 g. The breeding experience of parents ranged from 6 to 15 yr.

Leach's Storm-Petrel parents provided food to their chicks that enabled a net change in mass that ranged from 0.10 to 11.90 g per burrow visit (Figure 3A). Neither the percentage of burrow visits made by each parent nor the proportion of net change in chick mass were predicted by parental nonbreeding season feather or breeding season erythrocyte δ^{15}N, date-adjusted erythrocyte δ^{15}N, sample mass-adjusted δ^{15}N, nonbreeding season feather or breeding season erythrocyte C:N, date-adjusted erythrocyte C:N, feather CORT, sex, or breeding experience (% of net change in chick mass: adjusted $r^2 = -0.59$, $F_{9,8} = 0.30$, $P = 0.96$; % of burrow visits by each parent: adjusted $r^2 = 0.15$, $F_{9,8} = 1.32$, $P = 0.35$). However, males made significantly more burrow visits than females (Figure 3B), but did not provision chicks with a larger amount of food than females to enable a larger net change in chick mass (Figure 3A).

There were no differences in parental nonbreeding season feather or breeding season erythrocyte δ^{15}N, date-adjusted erythrocyte δ^{15}N, sample mass-adjusted δ^{15}N, nonbreeding season feather or breeding season erythrocyte C:N, date-adjusted erythrocyte C:N, plasma antioxidant capacity, or feather CORT between birds that had successful vs. failed nests in 2009 or 2010, although in 2010 parents with more breeding experience were more
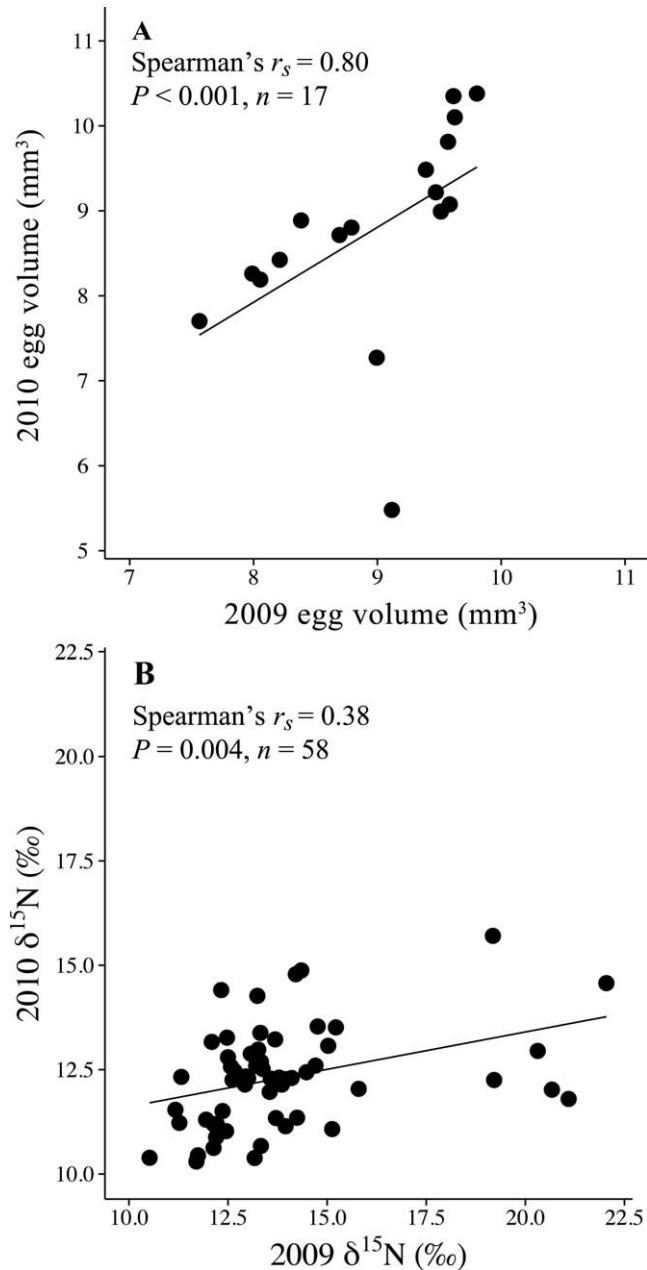
FIGURE 2. (**A**) Egg volumes (mm^3) of Leach's Storm-Petrels breeding on Kent Island in 2009 and 2010 were consistent within individuals between years (Spearman's $r_s = 0.80$, $P < 0.001$, $n = 17$); (**B**) $\delta^{15}N$ (‰) values of feathers of nonbreeding Leach's Storm-Petrels sampled in 2009 and 2010 were consistent within individuals between years (Spearman's $r_s = 0.38$, $P = 0.004$, $n = 58$).

likely to fledge a chick than less experienced parents (Table 3), and this relationship was still significant under a sequential Bonferroni correction. The breeding experience of parents in 2010 also remained a significant predictor between successful and failed birds if males and females were analyzed separately (females: Spearman's $r_s = -0.31$, P

$= 0.02$, $n = 55$; males: Spearman's $r_s = -0.27$, $P = 0.05$, $n = 53$), but there were no differences between successful and failed birds in 2009 if males and females were analyzed separately (females: Spearman's $r_s = -0.007$, $P = 0.97$, $n = 36$; males: Spearman's $r_s = -0.260$, $P = 0.15$, $n = 43$). The upper and lower confidence limits of parents' breeding experience between successful and failed parents were small in 2009, but did not span zero in 2010 (Table 4). The CI of measures of diet and energy balance of parents spanned a range of differences in values between successful and failed parents that generally were not biologically meaningful (Table 4). The CI of breeding season plasma antioxidant capacity spanned zero, as did other nonsignificant variables (Table 4), but in the case of breeding season plasma antioxidant capacity the range of the CI was large enough to encompass values that would be of biological interest; for example, Rubolini et al. (2006) found significant differences in plasma antioxidant capacities between 2 groups of only ~30 μmol HClO mL^{-1}. Thus, the test of breeding season plasma antioxidant capacity is equivocal.

Diet and Energy Balance

Leach's Storm-Petrels demonstrated interseasonal and interindividual variation of isotopic values in 2009 and 2010 (Figure 4). Birds sampled in both 2009 and 2010 had consistent nonbreeding season feather $\delta^{15}N$ (Spearman's $r_s = 0.38$, $P = 0.004$, $n = 58$; Figure 2B) and C:N between years, although nonbreeding season feather $\delta^{15}N$ in 2010 was significantly lower than in 2009 (Wilcoxon $z = -5.101$, $P < 0.001$, $n = 58$). Breeding experience was not correlated with nonbreeding season feather $\delta^{15}N$ (2009: Spearman's $r_s = 0.13$, $P = 0.27$, $n = 79$; 2010: Spearman's $r_s = -0.09$, $P = 0.35$, $n = 112$), breeding season erythrocyte $\delta^{15}N$ (Spearman's $r_s = -0.09$, $P = 0.33$, $n = 112$), nonbreeding season feather C:N (2009: Spearman's $r_s = 0.05$, $P = 0.66$, $n = 79$; 2010: Spearman's $r_s = -0.14$, $P = 0.14$, $n = 112$), or breeding season erythrocyte C:N (Spearman's $r_s = -0.07$, $P = 0.47$, $n = 112$) in either year. However, nonbreeding season feather $\delta^{15}N$ of 2009 and 2010 birds that were only sampled in either 2009 or 2010 was not different ($\delta^{15}N$: Mann-Whitney-Wilcoxon $W = 2868.50$, $P = 0.32$, $n = 94$). In 2009, the range of nonbreeding season feather $\delta^{15}N$ values was 10.52‰ to 22.04‰ ($n = 89$), and the range of nonbreeding season feather $\delta^{13}C$ was −19.14‰ to −15.84‰ ($n = 89$). In 2010, the range of nonbreeding season feather $\delta^{15}N$ values was 10.27‰ to 15.70‰ ($n = 121$); the range of nonbreeding season feather $\delta^{13}C$ was −18.45‰ to −15.33‰ ($n = 121$); the range of breeding season erythrocyte $\delta^{15}N$ was 10.79‰ to 14.21‰ ($n = 121$); and the range of breeding season erythrocyte $\delta^{13}C$ was −20.47‰ to −18.64‰ ($n = 121$). The C:N ratio of nonbreeding season feathers in 2009 ranged from 3.13 to
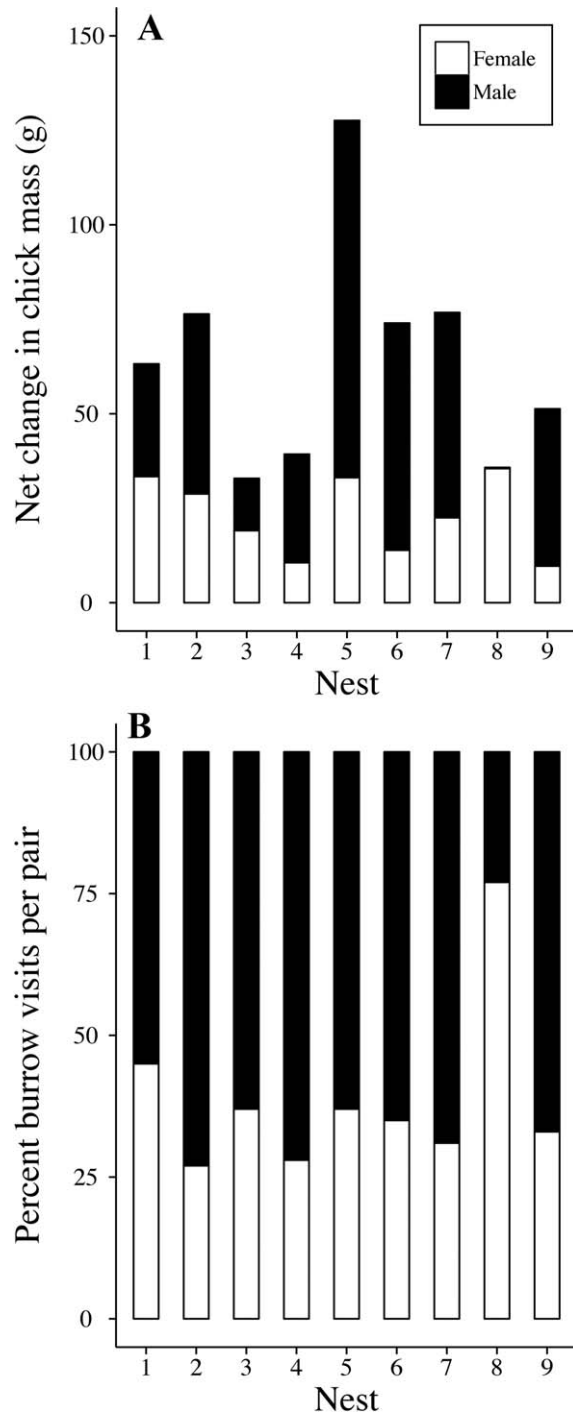
FIGURE 3. (**A**) The amounts of food provisioned to Leach's Storm-Petrel chicks that enabled a net change in chick mass were not different between male and female parents (Mann-Whitney $U = 21.0$, $P = 0.09$, $n = 18$); (**B**) Male Leach's Storm-Petrel parents visited the nest significantly more often than female parents (Mann-Whitney $U = 17.0$, $P = 0.04$, $n = 18$). Females visited the nest 12.9 ± 1.5 times; males visited the nest 22.8 ± 4.3 times.

3.78 and in 2010 ranged from 3.14 to 3.50; the range of breeding season erythrocyte C:N was 3.10 to 3.49 in 2010.

The mean plasma antioxidant capacity in 2010 was 224.50 ± 104.40 µmol HClO mL^{-1} (range: 0.00–342.40 µmol HClO mL^{-1}, $n = 23$, coefficient of variation = 46.5%). The mean CORT of nonbreeding season feathers in 2010 was 0.16 ± 0.06 pg CORT mm^{-1} (range: 0.06–0.39 pg CORT mm^{-1}, $n = 109$, coefficient of variation = 37%).

Model Selection for Diet, Energy Balance, and Reproductive Performance

There was no clear diet or energy balance predictor of reproductive performance by Leach's Storm-Petrel parents in either 2009 or 2010 (Tables 5, 6). Overall, the breeding experience of parents was the most common and important variable in positively explaining variation in reproductive performance.

DISCUSSION

Leach's Storm-Petrels exhibited consistency in diet and reproductive performance in 2009 and 2010. Specifically, nonbreeding season feather δ^{15}N and egg volume were positively correlated within individuals, suggesting that these birds may have used similar foraging strategies throughout the seasons, and might be consistent in maintaining a certain degree of energy balance from year to year. Generally, however, our proxies for diet (stable isotopes, plasma antioxidant capacities) and energy balance (feather CORT) did not predict reproductive performance. Nonbreeding season feather δ^{15}N weakly predicted reproductive success, and the breeding experience of parents more strongly positively predicted reproductive success in 2010.

Fifty-eight Leach's Storm-Petrels sampled in two successive years had consistent nonbreeding season feather δ^{15}N, demonstrating that they fed consistently at the same trophic level relative to other sampled birds. Consistent foraging behaviors could benefit long-lived seabirds in several ways, e.g., by providing access to predictable seasonal oceanographic patterns that yield primary productivity (Pinet et al. 2012), and through avoidance of intraspecific competition (Wiley et al. 2012). Consistency in nonbreeding season feather δ^{15}N was not correlated with breeding experience in this study, although consistency in foraging may be a measure of individual quality because basal metabolic rate, another measure of diet and subsequent energy balance, was correlated with positive reproductive performance and physiological quality of males in this population of Leach's Storm-Petrels (Mauck et al. 2004, Blackmer et al. 2005).

In addition to demonstrating between-year consistency in stable isotope values, female Leach's Storm-Petrels

TABLE 3. Comparisons of measures of diet and energy balance and breeding experience with "successful" and "failed" Leach's Storm-Petrel parents on Kent Island, New Brunswick, Canada, in 2009 and 2010. IQR = interquartile range; n = number of individuals in Successful and Failed groups; test-stat = test statistic of nonparametric (Mann-Whitney-Wilcoxon) test conducted between successful and failed parents; * = P is significant at $\alpha = 0.05$; NB = nonbreeding season, B = breeding season, CORT = corticosterone. For variables that were sampled throughout a season (erythrocyte stable isotopes, plasma antioxidant capacities), we analyzed the residuals of a regression of each variable on sample date; these values are presented as "date-adjusted." We included variables that were correlated with sample mass (δ^{15}N erythrocytes) as "sample mass-adjusted" in analyses.

	Successful		Failed			
Measure of breeding–nonbreeding ecology	Median ± IQR	n	Median ± IQR	n	Test-stat	P
2009						
NB feather δ^{15}N (‰)	13.19 ± 1.14	30	13.07 ± 1.69	34	$z = -0.31$	0.76
Egg volume (mm^3)	9.12 ± 0.82	15	9.12 ± 1.00	17	$z = -0.56$	0.57
Parents' breeding experience (yr)	11.00 ± 3.00	30	10.50 ± 3.00	34	$z = 1.11$	0.27
NB feather C:N	3.44 ± 0.26	30	3.37 ± 0.16	34	$z = 1.80$	0.07
2010						
NB feather δ^{15}N (‰)	12.32 ± 1.75	38	12.30 ± 1.31	79	$z = -0.62$	0.53
Egg volume (mm^3)	9.13 ± 1.17	19	9.23 ± 0.97	39	$z = -0.75$	0.94
B erythrocyte δ^{15}N (‰)	12.54 ± 0.82	38	12.57 ± 0.78	79	$z = -0.12$	0.89
B erythrocyte δ^{15}N (‰), date-adjusted	0.07 ± 0.63	38	−0.04 ± 0.89	79	$z = 0.49$	0.63
NB feather CORT (pg CORT mm^{-1})	−0.16 ± 0.06	37	0.16 ± 0.06	69	$z = 0.18$	0.86
B plasma antioxidant capacity (μmol HClO mL^{-1})	266.70 ± 283.60	11	241.10 ± 83.10	12	$z = 0.77$	0.44
Parents' breeding experience (yr)	12.00 ± 3.00	30	10.00 ± 5.00	63	$z = 3.28$	0.001*
NB feather C:N	3.25 ± 0.14	38	3.25 ± 0.18	79	$z = -0.38$	0.70
B erythrocyte C:N	3.23 ± 0.13	38	3.22 ± 0.09	79	$z = -0.62$	0.54
B erythrocyte C:N, date-adjusted	−0.00 ± 0.08	38	−0.01 ± 0.10	79	$z = -0.39$	0.69
B erythrocyte δ^{15}N, sample mass-adjusted	0.04 ± 1.11	38	−0.07 ± 1.01	78	$z = 0.45$	0.65

showed a strong correlation in egg volume between years, a trait that has been observed in other seabirds (Coulson and Porter 1985, Cobley et al. 1998). Egg volume represents a female's ability to allocate nutrient reserves to form the egg. Leach's Storm-Petrel egg volume is ~22% of adult body mass, and includes a large yolk necessary for embryo development during a long incubation period (Montevecchi et al. 1983). To form eggs, Leach's Storm-Petrels use a combination of endogenous reserves obtained during the prebreeding period and locally obtained nutrients (Bond and Diamond 2010). Female physiology (Christians 2002, Ortego et al. 2007) may provide a mechanism through which females maintain consistent foraging strategies during both the nonbreeding and breeding seasons. However, egg volumes were not correlated with our measures of diet or energy balance.

There were no differences in measures of diet and energy balance from either the breeding or nonbreeding seasons between parents whose nests succeeded or failed. More experienced Leach's Storm-Petrel parents were more likely to have successful nests in 2010; Mauck et al. (2012) also observed a positive relationship between breeding experience and reproductive success. Because survival and reproductive success increase with age, this result is perhaps not surprising; however, the relationship was not significant in 2009, and parental breeding experience did not correlate with δ^{15}N or egg volume, which were consistent within individuals between years.

The δ^{15}N values in our blood and feather samples were consistent with previous work (Gross 1935, Huntington et al. 1996) which showed that Leach's Storm-Petrels from Kent Island forage at trophic levels that include zooplank-

TABLE 4. Confidence intervals (CI) of measures of diet and energy balance of successful and failed Leach's Storm-Petrel parents on Kent Island, New Brunswick, Canada, in 2009 and 2010. If a comparison is statistically significant, the CI should not span zero, but the CI should also represent values that are biologically meaningful. NB = nonbreeding season, B = breeding season, CORT = corticosterone. Dashed lines indicate that those data were not sampled in 2009.

| Factor	Confidence interval 2009	Confidence interval 2010
Parents' breeding experience (yr)	−0.64 to 2.04	0.56 to 3.44
NB feather δ^{15}N (‰)	−1.06 to 1.57	−0.55 to 0.80
NB feather C:N	−0.16 to 0.02	−0.04 to 0.05
Egg volume (mm^3)	−0.69 to 0.39	−0.71 to 0.78
NB feather CORT (pg CORT mm^{-1})	—	0.03 to 0.04
B erythrocyte δ^{15}N (‰)	—	−0.31 to 0.35
B erythrocyte C:N	—	−0.03 to 0.05
B plasma antioxidant capacity (μmol HClO mL^{-1})	—	−128.80 to 160.59
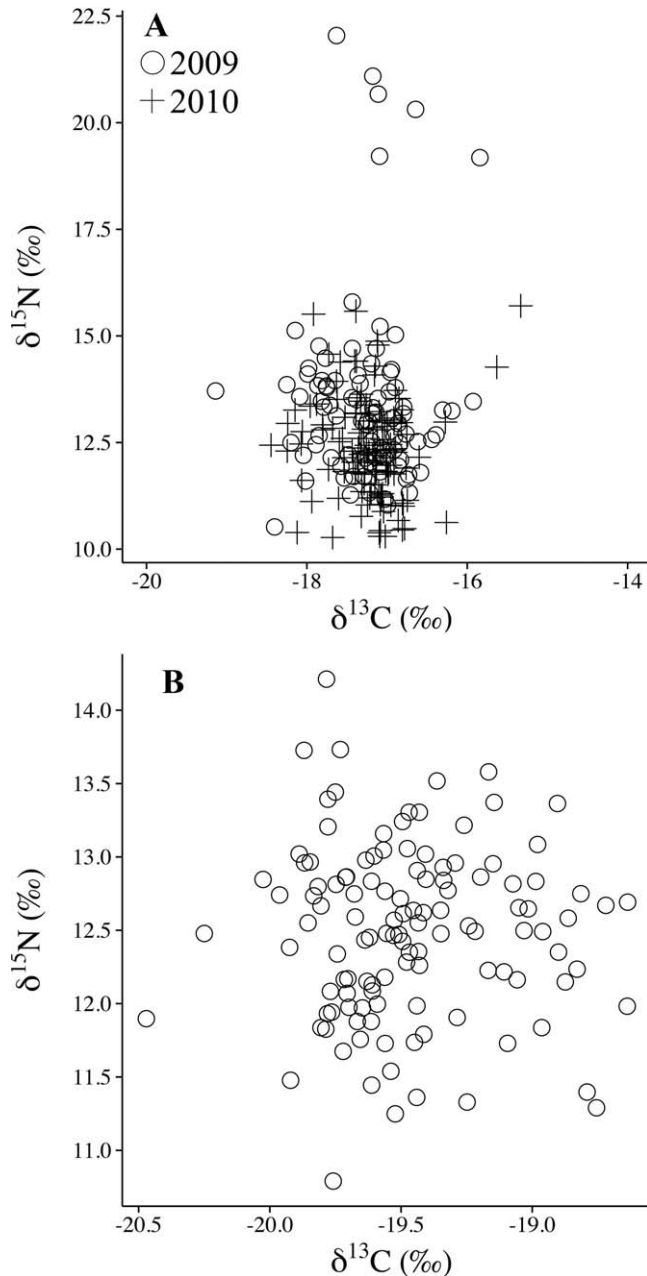
FIGURE 4. Scatterplots of $\delta^{15}N$ (‰) and $\delta^{13}C$ (‰) values of Leach's Storm-Petrel (**A**) feathers of nonbreeders in 2009 (circles) and 2010 (plus signs) and (**B**) breeding season erythrocytes in 2010 (circles).

ton, small squid, and small fishes. These $\delta^{15}N$ values also agree with $\delta^{15}N$ values from a more recent study of potential prey items such as krill and small fishes in the Bay of Fundy (Ronconi et al. 2010). Within this range, though, individuals likely differed from one another in trophic level of foraging and, consequently, in lipid and antioxidant intake; for example, copepods contain more carotenoids than fish that are found at higher trophic levels (Andersson et al. 2003, Nie et al. 2011). These

variations in parental diet could be expected to translate into variation in chick growth rates (Romano et al. 2006, Hipfner et al. 2010). Regardless of the variation that we observed in parental diet, energy balance, and chick growth, however, T and peak chick mass were not predicted by measures of parental diet, energy balance, or breeding experience. Indeed, the Leach's Storm-Petrel parents that had the smallest antioxidant capacities (0.0 and 3.2 μmol HClO mL^{-1}) were mates, and successfully fledged a chick; yet a pair that had some of the largest antioxidant capacities (291.1 and 282.9 μmol HClO mL^{-1}) abandoned their newly hatched chick. In addition to this observation and our large CI for plasma antioxidant capacity, another study also observed a negative correlation between antioxidant capacity and hatching success in Leach's Storm-Petrels (Cohen et al. 2009). However, it is possible that dietary antioxidants do not reflect reproductive effort in Leach's Storm-Petrels because they are quickly used in physiological processes for self-maintenance. Alternatively, the temporal scale of our blood-based measures of diet may simply have reflected local temporal and environmental conditions that Leach's Storm-Petrels encountered while foraging during incubation, rather than conditions during the chick-provisioning period.

A parent's ability to find food for itself and its chick several hundred kilometers from the breeding colony requires balancing energy allocation between self-maintenance and reproduction; therefore, seabird parents alternate short foraging trips to provision the chick with longer self-foraging trips (Weimerskirch et al. 1997, Fernández et al. 2001). Leach's Storm-Petrel parents typically fed their chicks every 2–3 nights, indicating that parents continuously traveled between the foraging grounds and the breeding colony, although males made significantly more burrow visits than females. Indeed, male Leach's Storm-Petrel parents typically allocate greater energy reserves to reproduction than females (Blackmer et al. 2005, Mauck et al. 2011). However, Leach's Storm-Petrel parents provided enough food to their chicks for a mean net change in mass of 4.05 ± 0.24 g per visit, and there were no relationships between percentages of burrow visits or food provisioned to chicks and our measures of parental diet or energy balance. As mentioned above, though, our measures of "breeding season" diet were from birds sampled during incubation; these samples may not accurately represent parental energy acquisition during chick rearing. It is also possible that sampled feathers grown during mid–late winter did not accurately capture the diet or physiology of the entire "nonbreeding" period; baseline and stress-induced CORT concentrations can change seasonally, especially between molting and breeding (Romero 2002).

Several studies have demonstrated that reproductive performance can be influenced by environmental factors as well as by individual physiology throughout the

TABLE 5. Results of AIC$_c$ (Akaike's Information Criterion corrected for small sample sizes) model selection for interseasonal measures of Leach's Storm-Petrel diet and energy balance, with δ^{15}N, C:N, CORT (corticosterone), and breeding experience as predictors and with reproductive effort as the response variable, in 2009 and 2010 on Kent Island, New Brunswick, Canada. Models are ranked by Akaike weights (w_i) and only models with ΔAIC$_c$ < 2 (difference in AIC$_c$ value from the top model) are shown. K is the number of model parameters, and $-2\ln L$ is the log-likelihood function. NB = nonbreeding season, B = breeding season. For variables that were sampled throughout a season (erythrocyte stable isotopes, plasma antioxidant capacities), we analyzed the residuals of a regression of each variable on sample date; these values are presented as "date-adjusted."

Model	K	$-2\ln L$	ΔAIC$_c$ [a]	w_i
2009				
NB feather C:N	1	97.72	0.00	1.00
Breeding experience + NB feather C:N	2	100.98	1.26	0.53
NB feather δ^{15}N + NB feather C:N	2	101.37	1.65	0.44
2010				
Breeding experience	1	32.41	0.00	1.00
B erythrocyte C:N, date-adjusted	1	33.47	1.06	0.59
CORT [b]	1	33.81	1.40	0.50
B erythrocyte C:N	1	33.83	1.42	0.49
NB feather C:N	1	34.31	1.90	0.39
B erythrocyte δ^{15}N, date-adjusted	1	34.35	1.94	0.38
Breeding experience + B erythrocyte C:N, date-adjusted	2	34.83	0.42	0.81
Breeding experience + B erythrocyte C:N	2	35.39	0.98	0.61
Breeding experience + CORT [b]	2	36.07	1.66	0.44

[a] Minimum AIC$_c$ in 2009 = 95.72 and in 2010 = 30.41.
[b] ln(CORT) (pg CORT mm^{-1}) was used in analyses.

TABLE 6. Results of model averaging for interseasonal measures of Leach's Storm-Petrel diet and energy balance, with δ^{15}N, C:N, CORT (corticosterone), and breeding experience as predictors and with reproductive effort as the response variable, in 2009 and 2010 on Kent Island, New Brunswick, Canada. NB = nonbreeding season, B = breeding season. For variables that were sampled throughout a season (erythrocyte stable isotopes, plasma antioxidant capacities), we analyzed the residuals of a regression of each variable on sample date; these values are presented as "date-adjusted." We included variables that were correlated with sample mass (δ^{15}N erythrocytes) as "sample mass-adjusted" in analyses.

Parameter	Estimate	Standard error
2009		
Breeding experience	−0.01	0.02
NB feather δ^{15}N	0.01	0.02
NB feather C:N	0.65	0.39
2010		
Breeding experience	−0.03	0.03
B erythrocyte δ^{15}N	0.08	0.19
NB feather δ^{15}N	−0.01	0.05
B plasma antioxidant capacity	−0.00	0.00
B erythrocyte δ^{15}N, date-adjusted	−0.08	0.21
NB feather CORT [a]	0.05	0.13
NB feather C:N	0.33	0.95
B erythrocyte C:N	0.90	3.59
B erythrocyte C:N, date-adjusted	−2.11	3.51
B erythrocyte δ^{15}N, sample mass-adjusted	−0.00	0.07

[a] ln(CORT) (pg CORT mm^{-1}) was used in analyses.

breeding and nonbreeding seasons (Yerkes et al. 2008, Inger et al. 2010, Crossin et al. 2013). In this population of Leach's Storm-Petrels, we found evidence for consistent foraging strategies and egg volumes within individuals between 2 years, but our measures of diet and reproductive performance were not useful as short-term predictors of reproductive performance. Therefore, other factors, such as breeding experience, may be more powerful predictors of breeding effort (Mauck et al. 2012). Additionally, a longitudinal study combining diet, energy balance, and reproductive effort with concurrent oceanographic data could provide valuable information about this species' ability to adapt to environmental trends and changes. Although we did not find short-term predictors of reproductive performance, these simple, noninvasive measures of diet and energy balance could easily be tested in other species and study systems to investigate predictors of reproductive performance in other migratory bird species.

ACKNOWLEDGMENTS

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