Comparative Biochemistry and Physiology, Part A 208 (2017) 1–13

Contents lists available at ScienceDirect

Comparative Biochemistry and Physiology, Part A

journal homepage: www.elsevier.com/locate/cbpa

Feather corticosterone during non-breeding correlates with multiple measures of physiology during subsequent breeding in a migratory seabird

Graham D. Fairhurst [a,*], Louise Champoux [b], Keith A. Hobson [c], Jean-François Rail [b], Jonathan Verreault [d], Magella Guillemette [e], William A. Montevecchi [f], Pauline Brousseau [g], Catherine Soos [a,h]

[a] Department of Veterinary Pathology, University of Saskatchewan, Saskatoon, SK, S7N 5B4, Canada
[b] Environment and Climate Change Canada, Québec, QC, G1J 0C3, Canada
[c] Environment and Climate Change Canada, Saskatoon, SK, S7N 3H5, Canada
[d] Centre de recherche en toxicologie de l'environnement (TOXEN), Département des sciences biologiques, Université du Québec à Montréal, Montréal, QC, H3C 3P8, Canada
[e] Département de Biologie, Chimie et Géographie, Université du Québec à Rimouski, Rimouski, QC, G5L 3A1, Canada
[f] Memorial University of Newfoundland, NL, A1B 3X9, Canada
[g] Institut National de la Recherche Scientifique – Institut Armand-Frappier, Laval, QC, H7V 1B7, Canada
[h] Environment and Climate Change Canada, Saskatoon, SK, S7N 0X4, Canada

ARTICLE INFO

Article history:
Received 28 September 2015
Received in revised form 21 February 2017
Accepted 23 February 2017
Available online 24 February 2017

Keywords:
Carbon-13
Carry-over effects
Deepwater Horizon oil spill
Feather biomarkers
Gulf of Mexico
Hormones
Migration
Nitrogen-15
Stable isotopes
Stress physiology

ABSTRACT

Carry-over effects in migratory birds are likely mediated by physiological processes that are activated in response to environmental variation. Such processes affect body condition and/or reproductive success, and can include corticosterone (CORT) because this hormone responds to environmental stressors and influences energy balance. Few studies have considered how CORT levels during non-breeding relate to a broader physiological profile during subsequent breeding, and fewer still have considered measures other than body condition. To explore CORT's potential role in carry-over effects, we investigated the relationship between CORT and foraging ecology of northern gannets (*Morus bassanus*) during the non-breeding period, and tested for associations between these factors and variation in a suite of physiological and biochemical metrics during subsequent breeding. Northern gannets are the largest seabird top predator in the North Atlantic and were among the hardest hit by the *Deepwater Horizon* oil blowout in the Gulf of Mexico in 2010. We used light-level geolocators to confirm winter origins of individuals in our study. No interrelationships were found among levels of CORT from feathers grown during non-breeding ($CORT_f$) and variation in foraging ecology, measured by stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) from the same feathers. $CORT_f$ was correlated negatively with hematocrit and positively with triglyceride measured during subsequent incubation, and explained more variation in these variables than did body mass during incubation. These findings provide support for the hypothesis that energy management, measured using $CORT_f$, during non-breeding carries over to influence physiological measures other than body condition. Gannets that previously wintered within the Gulf of Mexico in the years following the *Deepwater Horizon* oil blowout had higher levels of $CORT_f$ compared to birds that wintered along the Atlantic coast, suggesting an increased energetic cost associated with visiting the Gulf of Mexico. Our results indicate that CORT during non-breeding is associated with a broader physiological profile during subsequent breeding than previously reported in birds.

1. Introduction

Migratory animals inhabit geographically and temporally distinct breeding and non-breeding areas during the annual cycle. Despite this separation, events during the non-breeding period can have consequences for subsequent breeding performance (i.e., carry-over effects; Crossin et al., 2012a; Harrison et al., 2011; Norris and Taylor, 2006). For example, habitat quality on the wintering grounds can induce variation in body condition among migratory songbirds, that, in turn, influences departure dates, subsequent arrival dates on breeding grounds, condition upon arrival, and reproductive success (Marra et al., 1998; Norris et al., 2004; Rockwell et al., 2012; Saino et al., 2004, 2012). Although ecological factors such as habitat quality and weather

* Corresponding author.
E-mail address: graham.fairhurst@usask.ca (G.D. Fairhurst).

http://dx.doi.org/10.1016/j.cbpa.2017.02.024
1095-6433/

are considered to be the main drivers of these carry-over effects, the underlying physiological mechanisms are poorly understood (Harrison et al., 2011).

Carry-over effects in migratory birds are likely mediated by physiological systems that respond to environmental conditions and that result in changes in body condition and/or subsequent reproductive success. Corticosterone (CORT), the major glucocorticoid in birds, is released in response to environmental stressors, has important metabolic effects, and can influence activity (e.g., foraging) and reproduction (Angelier et al., 2007b; Bonier et al., 2009, 2011; Crossin et al., 2012b; Kitaysky et al., 2010; Strack et al., 1995; Wingfield and Sapolsky, 2003). Coping with environmental conditions across life-history stages is central to individual fitness (Angelier and Wingfield, 2013; Bonier et al., 2009; Breuner et al., 2008; Krause et al., 2016b, 2016c; Wingfield and Kitaysky, 2002; Wingfield and Sapolsky, 2003), and CORT might provide a functional link between an individual's response to environmental variation (e.g., food supply) during the non-breeding period and subsequent reproductive performance (see Fairhurst et al., 2015b). Indeed, recent work with migratory waterfowl supports this hypothesis (Harms et al., 2015).

The reported influence of circulating CORT during non-breeding on subsequent reproduction is complex and might operate indirectly via body condition (e.g., Harms et al., 2015). Although morphometric indices of condition (body mass, mass-length residuals) can reflect the general physiological/nutritional state in which an individual transitions into the breeding period (Harms et al., 2015), a suite of metabolic, biochemical, and health variables (collectively "individual physiology") during breeding could influence reproductive success (Brown, 1996; Drent and Daan, 1980; Hennin et al., 2015; McNamara and Houston, 1996). However, little is known about how CORT during non-breeding relates to individual physiology during reproduction because sampling the same individuals during non-breeding and subsequent breeding is logistically difficult for many migratory bird species. To date, very few downstream physiological biomarkers have been considered in this context (e.g., Bourgeon et al., 2012). This limits our understanding of how environmental conditions can influence individual physiology and subsequent reproductive performance in migratory birds. How a physiological mechanism linking environmental variation with reproduction relates to diet during non-breeding is even less well understood, despite the fact that studies have shown the importance of external resource availability and acquisition in determining individual condition (Harrison et al., 2011; McNamara and Houston, 1996). Diet is particularly relevant because it relates to CORT (Fairhurst et al., 2015b) and body condition (Ronconi et al., 2010) during non-breeding, drives carry-over effects (Chastel et al., 1995; Kouwenberg et al., 2013; Ronconi et al., 2010; Sorensen et al., 2009), contributes to anthropogenic contaminant burdens that can affect reproduction (Borga et al., 2004; Bustnes et al., 2005; Scheuhammer et al., 2007), and affects reproduction directly (Cury et al., 2011; Kitaysky et al., 1999b, 2010).

We tested the hypothesis that interactions between diet and CORT during non-breeding carry-over to affect breeding season physiology. We investigated the relationship between CORT and stable isotopes during the non-breeding period, and explored associations with subsequent variation in individual physiology during breeding in northern gannets (*Morus bassanus*), a migratory apex seabird predator in the North Atlantic. We studied birds from the colony on Bonaventure Island in the Gulf of St. Lawrence (Canada) that winter as far south as the Gulf of Mexico (Fifield et al., 2014), where this species was among the seabirds most affected by the 2010 *Deepwater Horizon* oil spill disaster (Montevecchi et al., 2012). Previous work on individuals from this northwest Atlantic population (henceforth "gannets") revealed higher levels of the hormone prolactin during early incubation in gannets that visited the Gulf of Mexico during non-breeding (Franci et al., 2014). This finding suggested that areas used during non-breeding may influence the physiological state in which gannets transition into the breeding period. Gannets spend long periods at sea and largely inaccessible during non-breeding, but molt during this period (Mowbray, 2002; Nelson, 2010) and feathers grown then can be sampled at colonies during the subsequent breeding season. Thus, we studied gannet diet-physiology relationships retrospectively by combining measures of CORT ($CORT_f$) and ratios of stable nitrogen ($\delta^{15}N_f$) and carbon ($\delta^{13}C_f$) isotopes from feathers grown during non-breeding. $CORT_f$ values can reflect plasma levels of CORT (Fairhurst et al., 2013a; Hõrak et al., 2013) and energy management in response to a variety of environmental stressors (e.g., Fairhurst et al., 2011, 2012b; Grava et al., 2013; Harriman et al., 2014; Legagneux et al., 2013), including nutritional deficits (Fairhurst et al., 2012a; Will et al., 2014), experienced over the period of feather growth (for review, see Romero and Fairhurst, 2016). Values of $\delta^{15}N_f$ and $\delta^{13}C_f$ can describe broad patterns in diet by indicating the trophic position and location, respectively, at which an individual fed (Hobson et al., 1994; Kelly, 2000; Peterson and Fry, 1987). Values of $\delta^{13}C_f$ increase toward lower latitudes in the Northern Hemisphere and with consumption of diets derived from more inshore locations, whereas $\delta^{15}N_f$ values increase with consumption of higher trophic position prey (Cherel et al., 2000; Hobson, 1999; Hobson et al., 1994; Kelly, 2000). Gannets feed on pelagic and forage fish (e.g., Atlantic mackerel *Scomber scombrus*, herring *Clupea harengus*, capelin *Mallotus villosus*, Atlantic menhaden *Brevoortia tyrannus*; Rail et al., 2013), and although variation in $\delta^{13}C_f$ and $\delta^{15}N_f$ due to diet composition can sometimes be modest (Franci et al., 2015), use of fisheries discard (Votier et al., 2010) and differences between age classes (e.g., Votier et al., 2011) result in larger isotopic variation. Correlating $CORT_f$ with stable isotope measurements from the same feathers can provide insight into relationships between physiology and nutrient assimilation during a similar period (Fairhurst et al., 2013b, 2015b).

We predicted that $CORT_f$ and $\delta^{15}N_f$ would covary negatively if gannets benefitted energetically from feeding at higher trophic levels during non-breeding (Fairhurst et al., 2015b; Hedd and Montevecchi, 2006), but would covary positively if there was a cost to feeding at higher trophic positions (e.g., metabolic demands of increased foraging effort; Kouwenberg et al., 2013). The location of prey during non-breeding may be an important determinant of body condition in gannets (Fifield et al., 2014). Thus, we correlated $CORT_f$ with $\delta^{13}C_f$ to explore a possible energetic consequence of spatial variation in winter foraging, which is poorly understood (Cherel et al., 2006). To gain a better understanding of how feeding ecology varied across seasons, we additionally compared $\delta^{13}C$ and $\delta^{15}N$ from feathers to values from red blood cells (RBC) and plasma collected during the subsequent breeding period (reflecting diet within a month and within a week, respectively, of blood sampling; Hobson and Clark, 1993). Assuming that lower $CORT_f$ values would indicate birds in better physiological condition (Harms et al., 2015; and see Lattin et al., 2016), we expected that $CORT_f$ values would be reflected in scores from a suite of metabolic and serological biomarkers from blood collected during breeding. Because the birds in our sample were outfitted with light-level geolocators, we were able to determine if measures of ecophysiology during non-breeding (i.e., $CORT_f$, $\delta^{13}C_f$, and $\delta^{15}N_f$) differed between birds that had previously wintered in the Gulf of Mexico following the *Deepwater Horizon* disaster and those that had not.

2. Methods

2.1. Fieldwork

Fieldwork was conducted in the colony on Bonaventure Island (48° 30′ 08″ N, 64° 10′ 07″W) in l'Île-Bonaventure-et-du-Rocher-Percé National Park (QC, Canada). The majority of gannets in this population return to the colony in late April and lay a single egg in late May, with incubation lasting approximately 44 days. Gannets exhibit bi-parental incubation, and the duration of parental foraging trips remains fairly constant throughout incubation (~28 h; S. Garthe, pers. comm.).

Similarly, levels of baseline plasma CORT also remain constant throughout incubation (Franci et al., 2014).

In June and July of 2013, adult gannets with a band and/or a geolocator (see below) were identified using binoculars and captured during early incubation (3–5 June; $n = 12$) or late incubation (8–12 July; $n = 25$) using a noose-pole. Two greater (secondary) covert feathers (one from each wing) were cut from each bird with clean scissors below the base of the feather vane and placed in a paper envelope for CORT and stable isotope analyses (below). Molt in gannets is poorly understood (Howell, 2010) so there is uncertainty regarding the geographical location of covert feather molt. However, years of experience studying this population have revealed an apparent lack of wing molt during breeding (J.-F. Rail and M. Guillemette, pers. obs.), and these observations are supported by published evidence that gannets usually suspend wing molt during breeding (Ginn and Melville, 1983; Howell, 2010; Mowbray, 2002; Stauss et al., 2012). Thus, we are confident that the covert feathers we sampled were grown during the non-breeding period.

Additionally, for the 25 birds captured during late incubation only, individuals were weighed using a spring balance and, immediately (<10 min) following capture, 10–15 mL blood was collected from the brachial vein using a 23-gauge butterfly needle fitted to a 5 mL syringe and transferred into 5 mL Vacutainers (BD Diagnostics, Franklin Lakes, USA) coated with lithium heparin and kept on ice. Upon the completion of fieldwork each day, capillary tubes were filled with blood and centrifuged for 5 min at 3800 rpm (1790 $\times g$) and hematocrit was measured. One vacutainer was centrifuged for 5 min at 3900 rpm (1720 $\times g$) and aliquots of plasma were transferred to Nunc cryovials (Nalge Nunc International, Roskilde, Denmark) and stored in liquid nitrogen for biochemical and serological biomarker analyses. Aliquots of whole blood were transferred to Nunc cryovials for sex determination from DNA by PCR (Griffiths et al., 1998) and stable isotope analyses. Plasma samples were immediately frozen at −10 °C then stored at −40 °C until subsequent analyses. Birds were sampled under appropriate permits from the Canadian Wildlife Service and the Environment and Climate Change Canada Animal Care Committee.

To sum up, during the incubation period of 2013 we captured 37 gannets and collected feathers that were grown in the previous non-breeding season (2012−2013). We also weighed and collected blood from 25 of these birds, so our serum biochemistry and RBC and plasma stable isotope data (below) are from a subset of birds for which we have feather data from the non-breeding period (i.e., $CORT_f$ and feather stable isotopes; see below for more details).

2.2. Identification of non-breeding locations

Of the 37 birds we sampled in 2013, we were able to determine or infer non-breeding locations for 28 birds, based on telemetry data collected using procedures detailed in Franci et al. (2014). Briefly, in September 2010, 2011, and 2012, we captured, respectively, 11, 8, and 9 adult gannets at the colony prior to departure for migration using a long noose-pole, and attached a 2.5 g light-level geolocator (<0.1% the gannets' body mass; MK15, British Antarctic Survey, Cambridge, United Kingdom) to the leg band of each bird. Geolocators weighing 4–5% of body mass did not influence $CORT_f$ in small aerial insectivores (Fairhurst et al., 2015a), so we assume that data from small geolocators attached to gannets were unbiased with regard to device-induced physiological stress. Light level data were recovered from geolocators when birds were recaptured at the colony the year following tracking (i.e., breeding seasons of 2011, 2012, 2013) and were analyzed using TransEdit2 in the BASTrack software (version 18; British Antarctic Survey). Delineation of wintering sites in the Gulf of Mexico (i.e., marine area west of the tip of Florida, USA) or on the Atlantic Coast (i.e., encompassing the south-eastern tip of Florida to the Gulf of Maine, USA) was accomplished by kernel density estimation (Bächler et al., 2010) using Geospatial Modelling Environment software (Version 0.6.0.0) in ArcGIS 10 (Esri, France). Location data from gannets instrumented in 2010 and 2011 are taken from previously published work (Franci et al., 2014), whereas location data from gannets instrumented in fall 2012 have not been published elsewhere.

Eleven gannets were tracked during the non-breeding period of 2010–2011, 8 were tracked during non-breeding of 2011–2012, and 9 were tracked during non-breeding of 2012–2013, though all were recaptured and sampled for feathers during breeding in 2013 (see Fieldwork, above). Thus, 19 birds in our sample were tracked in years prior to when feathers were grown for this study, but gannets wintering in North America show very strong fidelity to non-breeding areas (median distance between wintering areas in two consecutive years = 87 km; Fifield et al., 2014), so we inferred their non-breeding areas based on areas they used in the year they were tracked.

2.3. $CORT_f$ analyses

We used a methanol-based procedure (Bortolotti et al., 2008) to extract CORT from feathers in one batch. Following removal of the calamus from each feather, the remaining sample was cut into small pieces (<5 mm^2) and 10 mL of methanol (HPLC grade, VWR International, Mississauga, ON, Canada) was added. Samples were then sonicated in a water bath at room temperature for 30 min, followed by overnight incubation at 50 °C in a water bath. Methanol was separated from feather material using vacuum filtration, and the feather pieces were kept for stable isotope analyses (below). The methanol extract was placed in a 50 °C water bath and allowed to evaporate in a fume hood. Once dry, extracts were reconstituted in a small volume of phosphate buffered saline (PBS; 0.05 M, pH 7.6) and kept at −20 °C until analyzed by radioimmunoassay (RIA). We assessed the efficiency of the extraction procedure by including three feather samples spiked with approximately 5000 CPM of ^{3}H–labeled corticosterone (see Appendix S1 in Bortolotti et al. (2008) for details). On average, 95% of the radioactivity was recovered in the reconstituted samples.

Measurements of CORT were determined by RIA as in previous studies (Bortolotti et al., 2008; Fairhurst et al., 2013a, 2015b; Wayland et al., 2002) and were performed on duplicates of reconstituted methanol extracts in two assays using a commercial antiserum (Sigma-Aldrich, St. Louis, MO, USA; product# C8784). Serial dilutions of sample extracts were parallel to the standard curve, indicating no interference with the antibody. Assay variation was computed using three (duplicated) aliquots of the same standard CORT solution in each assay. Average intra-assay coefficient of variation (CV) was 6.23% (standard deviation (SD) = 0.69) and inter-assay CV was 7.00%. The average detection limit of our assays was 16.20 pg CORT (SD = 6.58) and all values were above detection limits. Data values are expressed as pg CORT per mm of feather, which gives a valid estimate of CORT per unit time of feather growth (Bortolotti, 2010; Jenni-Eiermann et al., 2015). $CORT_f$ assays were performed at the University of Saskatchewan, SK, Canada.

2.4. Stable isotope analyses

Following CORT extraction, feather pieces were subsequently analyzed at the National Hydrology Research Center of Environment Canada in Saskatoon, Canada. Feathers were first cleaned by soaking in a 2:1 chloroform:methanol solvent mixture and multiple rinsing before drying overnight in a fume hood. Between 0.5 and 1.0 mg of feather material were used for $\delta^{13}C$ and $\delta^{15}N$ analyses, which were combusted online using a EuroVector 3000 (EuroVector, Milan, Italy) elemental analyzer. The resulting CO_2 and N_2 was separated by gas chromatography (GC) coupled to a Nu Horizon (Nu Instruments, Wrexham, UK) triple-collector isotope-ratio mass-spectrometer via an open split, and compared to pure CO_2 and N_2 reference gasses respectively. Stable isotope ratios were expressed in delta (δ) notation, as deviation in parts per thousand (‰) from reference standards Vienna Pee Dee Belemnite carbonate (VPDB) for $\delta^{13}C$ and AIR for $\delta^{15}N$. Using previously calibrated internal

laboratory standards (powdered Bowhead Whale Baleen [BWB-2] keratin and gelatin), within-run precision was ±0.15‰ for $\delta^{13}C$ and ±0.25‰ for $\delta^{15}N$ ($n = 5$).

Blood $\delta^{13}C$ and $\delta^{15}N$ analyses were run at the Centre de recherche en géochimie et géodynamique (GEOTOP), Université du Québec à Montréal (Montréal, QC, Canada), as described in Caron-Beaudoin et al. (2013). Aliquots of homogenized blood cell samples were freeze-dried (Freezone 12; Labconco, Kansas City, MO, USA) and ground into a homogenous powder, while plasma was dried at room temperature (~22 °C). Aliquots of water-free plasma and blood cells were loaded into tin cups and weighed (1.000 ± 0.001 mg). Isotopic measurements were performed in duplicates using a continuous flow isotope ratio mass spectrometer (Micromass Isoprime, Cheadle, UK) coupled to an elemental analyzer (Elementar Vario MicroCube; Hanau, Germany). Results were expressed in delta notation (δ) relative to an international standard (VPDB and AIR) in per mil (‰). Raw data were normalized on the respective scales using three previously calibrated internal reference materials (leucine, urea and shark tissues). Analytical precision were within 0.1‰ for $\delta^{13}C$ and 0.2‰ for $\delta^{15}N$.

2.5. Metabolic and serological variables

Serum biochemical analyses were performed by the diagnostic service of Faculté de médecine vétérinaire, Université de Montréal, using an Autoanalyzer Unicel Dxc 600 (Beckman Coulter, Inc., Pasadena, CA, USA). The following 11 metabolic variables were determined for each sample: glucose, triglycerides, cholesterol, uric acid, alkaline phosphatase, alanine aminotransferase, gamma-glutamyl transpeptidase, lactate dehydrogenase, aspartate aminotransferase, creatine kinase, and total protein. Heterophil:lymphocyte (H:L) ratios were also calculated, using methods previously reported by Brousseau-Fournier et al. (2014). The viability of white blood cells was determined by flow cytometry using propidiumiodide (PI; Sigma Chemical Co., St. Louis, MO, USA), an exclusion dye that binds to the nucleic acid of dead cells which become strongly fluorescent. Briefly, 1 μL of a 1 mg mL^{-1} stock solution of PI was added to each cell suspension and flow cytometric acquisition of these suspensions was performed. Fluorescence emission was collected at 670 nm. The results are expressed in percentage of viable cells. To monitor phagocytosis, a volume of 100 μL of peripheral blood was mixed with yellow-green latex FluoSpheres (Molecular Probes Inc., Eugene, OR, USA) at a ratio of 1:100 (leukocytes:beads) in Eppendorf tubes. After an incubation of 1 h at 40 °C, the cells were washed once with PBS, recovered by centrifugation at 150 ×*g* at room temperature and resuspended in 200 μL of PBS and flow cytometric acquisition was performed. Fluorescence emission was collected at 533/30 nm. Results are expressed in percent of phagocytic cells containing one or more beads and 3 beads or more. Flow cytometry acquisition A BD Accuri™ C6 (Becton Dickinson, San Jose, CA, USA) providing an excitation at 488 nm was used. Heterophils were defined based on their forward and right angle scatter properties. A total of 10,000 events were acquired for each sample. The data were then analyzed, once displayed as two-parameter complexity and cell size, in the process of gating and as fluorescence (FL1 and FL3) frequency distribution histogram. Data collection and analysis were performed with the BD Accuri™ C6 software.

2.6. Statistical analyses

2.6.1. Ecophysiology during non-breeding

Sex differences in $CORT_f$, $\delta^{13}C_f$, and $\delta^{15}N_f$ were first tested using separate general linear models (GLMs; SAS v. 9.2). A GLM including $\delta^{15}N_f$ as the response variable and $\delta^{13}C_f$, sex, and the $\delta^{13}C_f \times$ sex interaction as predictors was used to study the potential influence of sex-specific foraging areas (i.e., $\delta^{13}C_f \times$ sex interaction) on the trophic position at which gannets fed (i.e., $\delta^{15}N_f$). Next, the effect of diet on CORT was investigated using a GLM with $CORT_f$ as the response variable and $\delta^{13}C_f$ and $\delta^{15}N_f$ as predictors. Given a lack of sex effects on $CORT_f$ (see Results), sex was not considered in this model.

2.6.2. Seasonal differences in foraging ecology

Comparisons of $\delta^{13}C$ and $\delta^{15}N$ among sample types (feathers, RBCs, and plasma) were used to gain insight into how diet changed through time from non-breeding (feathers) to within a month (RBCs) and within a week (plasma; Hobson and Clark, 1993) prior to blood sampling during late incubation. Two mixed effects models were used, including either $\delta^{13}C$ or $\delta^{15}N$ values as the response variable, and sample type, sex, and a sample type × sex interaction as predictors. Because feathers and blood samples were taken from the same individuals and reflect three time periods, individual identity was used as a random term to account for repeated sampling. Denominator degrees of freedom were estimated using the Kenward-Rodger method. Non-significant interactions were removed from models, models were re-run, and significant main effects were explored with post-hoc tests using Tukey adjusted *P*-values. Because they reflect different measures at different time points, stable isotope data for these models were corrected for discrimination differences among tissues (i.e., normalized to the diet) using discrimination factors derived from great skuas (*Catharacta skua*; Bearhop et al., 2002): 1.1‰ and 2.8‰ for $\Delta^{13}C$ and $\Delta^{15}N$ respectively in blood, and 2.1‰and 4.6‰ for $\Delta^{13}C$ and $\Delta^{15}N$ respectively in feathers, as in previous studies of gannets in our study area (Franci et al., 2015) and the Northeastern subpopulation (Votier et al., 2010).

2.6.3. Relationships between ecophysiology during non-breeding and individual physiology during breeding

We explored how the variation in each breeding season response variable was explained by ecophysiology during non-breeding. Body mass, hematocrit, each of the 11 metabolic variables, and H:L ratios were modeled as separate responses using GLMs. To achieve normality, values for triglyceride, uric acid, and creatine kinase were log-transformed. For each response variable, we considered a set of 14 *a priori* models that included: a full model with $CORT_f$, $\delta^{13}C_f$, $\delta^{15}N_f$, sex, and a $CORT_f \times$ sex interaction; eight models with various combinations of these predictors, all of which included $CORT_f$; a model with only $\delta^{13}C_f$ and $\delta^{15}N_f$; models with each predictor alone; and an intercept-only (i.e., "null model") (Appendix 1). For all model sets (except body mass), we also included a model that fit body mass as the sole predictor, as this could be an important determinant of breeding season physiology. This allowed us to identify a potential effect of body mass on breeding season physiology and, more importantly, provided a means of determining if a measure of current body condition was a better predictor than measures of past (non-breeding) ecophysiology.

We used an information–theoretic approach (Akaike's information criterion adjusted for small sample size; AICc) to rank models in each set (Burnham and Anderson, 2002). The model with the smallest AICc value was considered the best-supported (Burnham and Anderson, 2002), but was eliminated in favor of a less complex version that was within 2 AICc units (ΔAICc <2; Arnold, 2010). For each model set we report the best-supported model (in relation to the null) and the β ± SE for each term in that model.

2.6.4. Non-breeding ecophysiology in relation to wintering in the Gulf of Mexico

Differences in $CORT_f$, $\delta^{13}C_f$, and $\delta^{15}N_f$ were assessed between gannets that had wintered in the Gulf of Mexico and those that had not using separate GLMs for each response variable. These analyses included all birds in our dataset for which the location of a non-breeding area was known from tracking in one of the past three non-breeding periods ($n = 28$). For comparison, models were also run using only those gannets that were tracked throughout the period when feathers were grown (2012–2013; $n = 9$), recognizing that the power of these latter analyses would be weakened considerably by small sample sizes.

3. Results

3.1. Ecophysiology during non-breeding

Neither $CORT_f$ ($F_{1,35} = 0.77$, $P = 0.39$), $\delta^{13}C_f$ ($F_{1,34} = 0.50$, $P = 0.49$), nor $\delta^{15}N_f$ ($F_{1,34} = 0.02$, $P = 0.90$) differed between the sexes. $\delta^{15}N_f$ was not significantly related to $\delta^{13}C_f$ ($F_{1,33} = 1.62$, $P = 0.21$), sex ($F_{1,33} = 0.00$, $P = 0.98$), or their interaction ($F_{1,32} = 0.63$, $P = 0.43$). $CORT_f$ was not related to $\delta^{13}C_f$ ($F_{1,33} = 1.65$, $P = 0.21$) or $\delta^{15}N_f$ ($F_{1,33} = 0.00$, $P = 0.97$).

3.2. Seasonal differences in foraging ecology

There was no overall effect of sex on $\delta^{13}C$ ($F_{1,23.1} = 0.00$, $P = 0.97$; sex × sample type interaction: $F_{2,45.4} = 0.43$, $P = 0.65$) or $\delta^{15}N$ ($F_{1,23.2} = 0.01$, $P = 0.94$; sex × sample type interaction: $F_{2,45.1} = 1.03$, $P = 0.36$) from all sample types. Values of $\delta^{13}C$ differed among sample types ($F_{2,47.7} = 19.76$, $P < 0.0001$; Fig. 1a) and a post-hoc test confirmed that $\delta^{13}C_f > \delta^{13}C_{RBC} > \delta^{13}C_p$ (all $P_{adj} < 0.0001$). Values of $\delta^{15}N$ also differed among sample type ($F_{2,47.4} = 5.10$, $P = 0.008$; Fig. 1b) and a post-hoc test revealed that $\delta^{15}N_f$ was significantly lower than $\delta^{15}N_p$ ($t_{1,47.2} = -3.24$, $P_{adj} = 0.006$) but did not differ from $\delta^{15}N_{RBC}$ ($t_{1,47.2} = -2.12$, $P_{adj} < 0.10$), and $\delta^{15}N_{RBC}$ and $\delta^{15}N_p$ were similar ($t_{1,47.2} = 1.16$, $P_{adj} = 0.48$). Varying the discrimination factors by ±5% for $\delta^{13}C_f$ and $\delta^{15}N_f$ had no effect on models of the former and a negligible effect on models of the latter, but did not change the interpretation of any models.

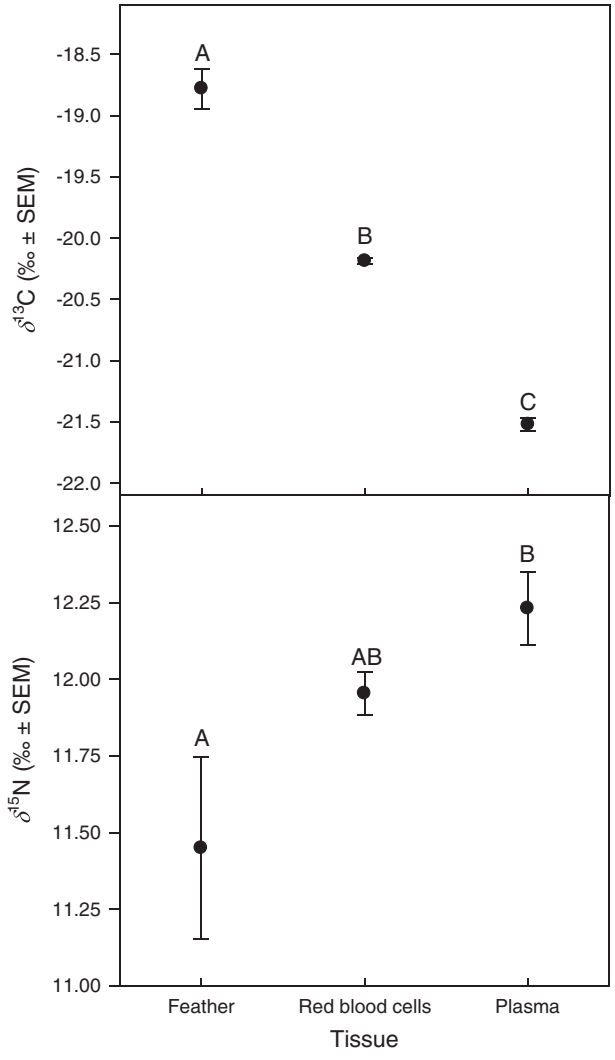

Fig. 1. Ratios of stable isotopes of carbon ($\delta^{13}C$; top) and nitrogen ($\delta^{15}N$; bottom) from northern gannets differ significantly among tissues formed during non-breeding (feather) and early (red blood cells) and late (plasma) during incubation in the subsequent breeding period. Groups with different letters differed at $P < 0.0001$ (top) and $P < 0.01$ (bottom). Data have been corrected for discrimination between diet and tissue (see Methods section for additional details).

3.3. Relationships between ecophysiology during non-breeding and individual physiology during breeding

Among the 14 metabolic and serological response variables measured during late incubation, hematocrit, triglyceride, and glucose were best explained by a model that included only the effect of $CORT_f$ (Table 1). These models revealed a negative relationship with hematocrit and positive relationships with levels of triglyceride and glucose (Table 1; Fig. 2). However, for glucose, this model was only 1.8 AICc points less than the null model, indicating that $CORT_f$ explained very little (if any) variation in this variable. For cholesterol, the model containing only $\delta^{15}N_f$ was the best-supported, but this model was only 0.6 AICc points less than the null model, suggesting that it explained very little variation. Although the model that included only $\delta^{13}C_f$ was the best-supported for aspartate aminotransferase and lactate dehydrogenase, in the latter case the model was rejected in favor of the null model, which was 1.1 AICc points greater. The model with body mass as the only predictor was the best-supported for alkaline phosphatase, alanine aminotransferase, and creatine kinase. For uric acid, gamma-glutamyl transpeptidase, total protein, and H:L ratio, the null model was the best-supported. Finally, the best supported model explaining variation in body mass contained only sex (females heavier than males; mean ± SE: 3253 ± 80 g vs. 2983 ± 64 g; Table 1) but, other than this expected effect (Mowbray, 2002), neither sex nor its interaction with $CORT_f$ was a significant term in any model explaining breeding season physiology. Rankings for all models are in Appendix 1.

3.4. Non-breeding ecophysiology in relation to wintering in the Gulf of Mexico

Gannets that spent the wintering period in the Gulf of Mexico during 2010–2011 or 2011–2012 ($n = 5$) had higher $CORT_f$ (mean ± SE: 77.0 ± 7.8 pg/mm vs. 61.9 ± 2.5 pg/mm; $F_{1,26} = 5.71$, $P = 0.02$; Fig. 3a), lower $\delta^{13}C_f$ values (mean ± SE: −17.6 ± 0.6‰ vs. -16.5 ± 0.1‰; $F_{1,25} = 8.97$, $P = 0.006$; Fig. 3b), and higher $\delta^{15}N_f$ values (mean ± SE: 17.1 ± 0.3‰ vs. 15.9 ± 0.2‰; $F_{1,25} = 6.17$, $P = 0.02$; Fig. 3c) during the 2012–2013 non-breeding period than gannets that wintered along the Atlantic coast ($n = 23$). The direction of these three relationships were maintained when analyses were restricted to only those gannets tracked throughout the 2012–2013 wintering period ($n = 9$), and differences in $CORT_f$ approached significance ($F_{1,7} = 4.91$, $P = 0.06$), but differences in $\delta^{13}C_f$ ($F_{1,7} = 0.58$, $P = 0.47$) and $\delta^{15}N_f$ ($F_{1,7} = 2.73$, $P = 0.14$) were not significant, likely due to reduced power from small sample sizes.

4. Discussion

Our results provide several insights into carry-over effects in a migratory seabird. Contrary to our predictions, there were no interrelationships among $CORT_f$, $\delta^{13}C_f$, and $\delta^{15}N_f$ during non-breeding. Gannet diet outside the breeding period is poorly known (Mowbray, 2002), but a lack of relationships may indicate that the nutritional value of prey items, or the energetic costs of acquiring prey, did not vary enough during the feather growth period to influence $CORT_f$ (e.g., Fairhurst et al., 2013a, 2015b). We did not sample prey so cannot confirm this, but our stable isotope data supports this interpretation. After adjusting for differences in discrimination between diet and gannet tissues, $\delta^{15}N$ values from non-breeding and subsequent breeding period (from feathers, RBCs, and plasma) were similar (within 1‰) and comparable

Table 1
Best supported models explaining variation in each of 14 physiological response variables measured in northern gannets during breeding in 2013 in terms of non-breeding feather-based measures of corticosterone ($CORT_f$), stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), and sex. Model selection was based on rankings of AICc scores from candidate model sets (see text for an explanation and Appendix 1 for model rankings).

Response variable	model terms	β	SE	95% confidence limits		χ^2	*P*-value
Body mass	Sex	−270.09	96.73	−59.68	−80.49	7.8	0.005
Hematocrit	$CORT_f$	−0.12	0.04	−0.21	−0.04	7.84	0.005
Glucose	Null	15.28	0.28	14.73	15.84	2915.2	<.0001
Triglyceride[a]	$CORT_f$	0.007	0.002	0.003	0.01	11.32	0.0008
Cholesterol	Null	7.09	0.19	6.72	7.46	1391.21	<.0001
Uric acid[a]	Null	2.85	0.06	2.75	2.96	2696.24	<.0001
Alkaline phosphatase	Body mass	0.30	0.09	0.12	0.48	10.28	0.001
Alanine aminotransferase	Body mass	0.02	0.01	0.01	0.04	6.94	0.008
Gamma-glutamyl transpeptidase	Null	20.23	1.73	16.83	23.62	136.39	<.0001
Lactate dehydrogenase	Null	149.45	13.12	123.75	175.16	129.83	<.0001
Aspartate aminotransferase	$\delta^{13}c$	−52.77	21.91	−95.72	−9.82	5.8	0.02
Creatine kinase[a]	Body mass	0.0004	0.0001	0.0002	0.0006	16.64	<.0001
TOTAL protein	Null	39.94	1.18	37.62	42.26	1140.1	<.0001
H:L ratio	Null	0.20	0.01	0.17	0.23	182.86	<.0001

[a] Values were log-transformed to achieve normality.

to $\delta^{15}N$ values reported for gannet prey during previous breeding seasons (Franci et al., 2015). Changes in $\delta^{13}C$ values from non-breeding to early and late incubation are consistent with gannets foraging in relatively low latitude coastal areas during non-breeding and shifting to higher latitudes for breeding (Fifield et al., 2014; Hobson, 1999; Hobson et al., 1994; Kelly, 2000; Montevecchi et al., 2012), where $\delta^{13}C$ values likely reflected seasonal availability in preferred prey (e.g., Franci et al., 2015; Garthe et al., 2007). Thus, gannets likely fed on trophically-similar prey as they moved their foraging areas throughout the year, which is in agreement with their characterization as specializing on high quality prey (Garthe et al., 2014; Montevecchi et al., 2009). Recent work suggests that gannets are not sexually segregated throughout their winter range (Fifield et al., 2014) and, accordingly, we did not detect sex differences in measures of non-breeding ecophysiology. Thus, to the extent that $\delta^{15}N$ and $\delta^{13}C$ from feathers can provide insight into gannet foraging ecology during non-breeding, it appears that diet was of consistently high quality for both sexes and therefore not a strong determinant of CORT levels in the year of our study.

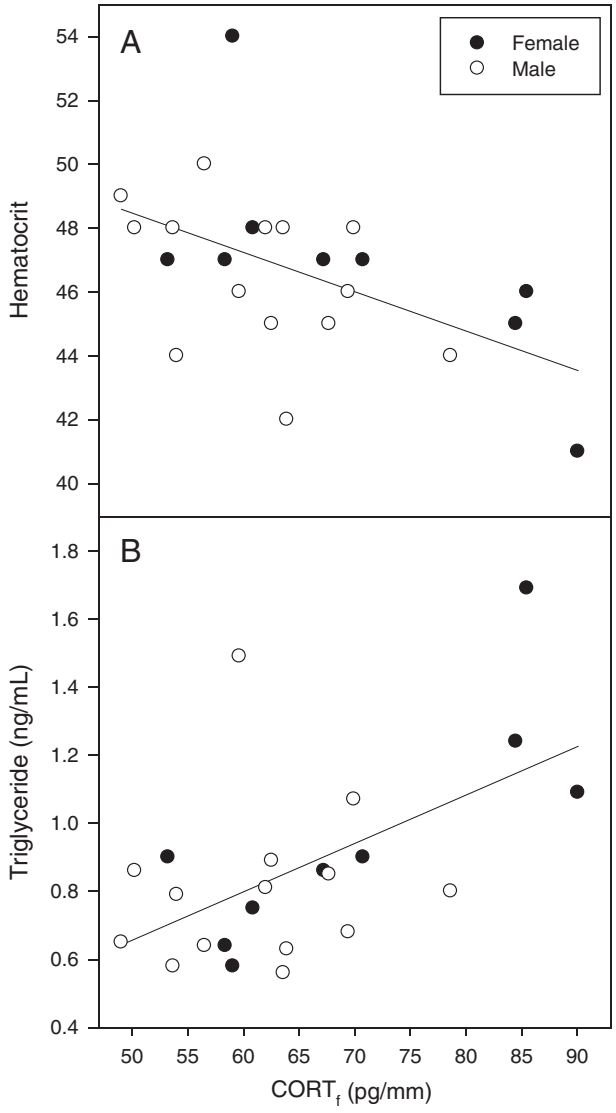

Fig. 2. Relationships between levels of corticosterone ($CORT_f$) from northern gannet feathers grown during non-breeding and (A) hematocrit and (B) levels of triglyceride measured from plasma collected during incubation in the subsequent breeding period.

Although this interpretation of the $CORT_f$ and stable isotope data seems reasonable, three issues warrant further investigation. First, we may have sampled gannets during a spring (i.e., pre-breeding) of particularly good prey availability. Long-term studies that include years of known poor prey abundance are needed to reveal the full range of possible diet-physiology relationships (Kitaysky et al., 1999b, 2007). Second, and relatedly, we did not measure the quantity of prey consumed during molt. For example, a food shortage could have influenced $CORT_f$ without being reflected in $\delta^{15}N_f$ values, and it is possible that individual physiological state during molting could have influenced isotope values (e.g., Cherel et al., 2005). Quantifying gannet diet and physiology directly during non-breeding (e.g., while in the Gulf of Mexico) could provide a better understanding of how diet quality and quantity interact to affect both $CORT_f$ and stable isotope values. Finally, we were not able to account for geographic variation in baseline $\delta^{15}N$ values, which could have introduced additional variation into our data (e.g., Jennings and Warr, 2003). Future studies should aim to estimate $\delta^{15}N$ at the base of food webs in areas used regularly during non-breeding, and continued year-round tracking of gannets from Bonaventure Island will help identify such areas (e.g., Fifield et al., 2014).

$CORT_f$ from non-breeding was, as predicted, related to measures of individual physiology in the subsequent breeding period. Gannets with higher $CORT_f$ had lower hematocrit scores and higher plasma levels of triglyceride during incubation, providing some support for the hypothesis that energy management during non-breeding (estimated using $CORT_f$) can carry-over to influence more than just body condition. Moreover, variation in hematocrit and triglyceride during incubation were better explained by $CORT_f$ from non-breeding than by body mass during incubation.

In birds, lower hematocrit is associated with poorer condition (Bókony et al., 2012; Howlett et al., 2002; Korschgen, 1977; Sakaluk et al., 2014; Sánchez-Guzmán et al., 2004; Svensson and Merilä, 1996)

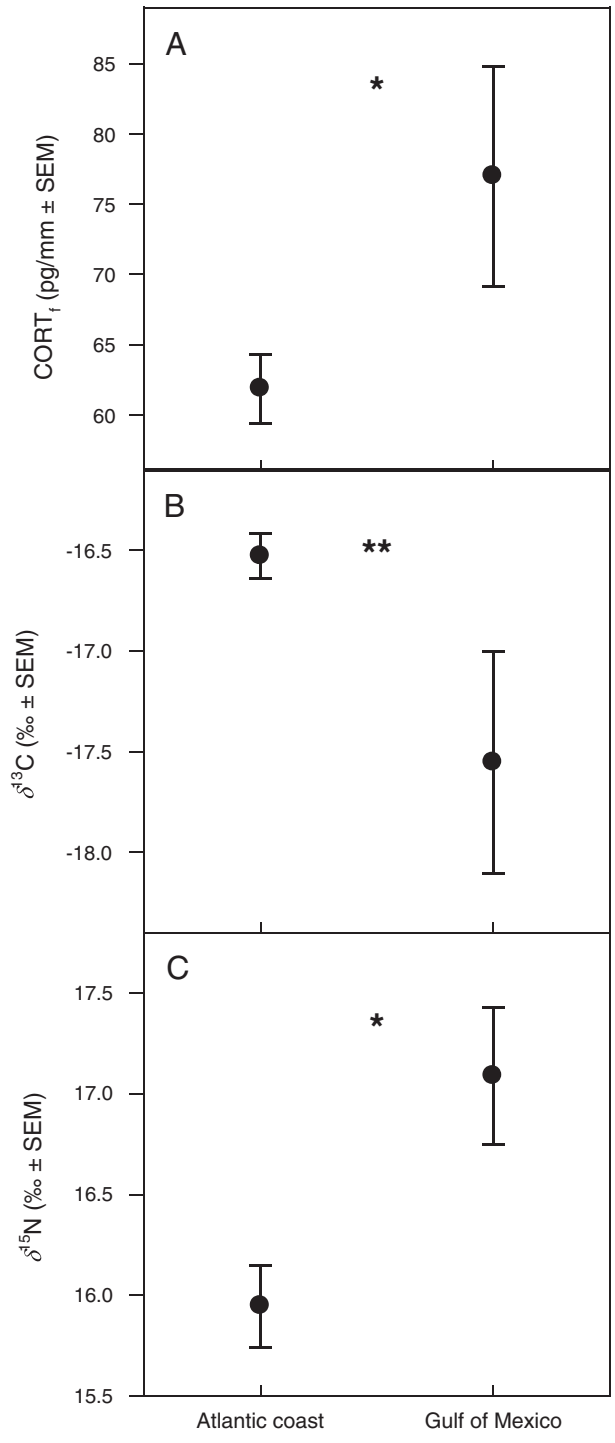

Fig. 3. Northern gannets that were known to visit the Gulf of Mexico in at least one of the three non-breeding periods prior to capture ($n = 5$) had (A) higher levels of feather corticosterone (CORT$_f$), (B) lower δ^{13}C values, and (C) higher δ^{15}N values during the 2012 non-breeding period compared to individuals that wintered along the Atlantic coast ($n = 23$). * = groups differed at $P < 0.05$; ** = groups differed at $P < 0.01$.

and health (particularly due to parasite infestations; Boughton et al., 2006; Garvin et al., 2008; Hõrak et al., 1998), as well as increased physiological stress (Dickens et al., 2009). Other studies have found results opposite to these or no relationship between hematocrit and body condition (Bókony et al., 2012; Dawson and Bortolotti, 1997a, 1997b; Ots et al., 1998; Quillfeldt et al., 2004), and some authors have instead interpreted hematocrit as a measure of metabolic activity, workload, or energetic stress (for a review of hematocrit in birds, see Fair et al., 2007; Hõrak et al., 1998; Krause et al., 2016a; Mazerolle and Hobson, 2002; Ots and Hõrak, 1998; Piersma et al., 1996; e.g., Saino et al., 1997). Triglyceride level is positively associated with feeding, fat deposition, mass gain, and cell-mediated immune response (Forero et al., 2006; Guglielmo et al., 2005; Jenni-Eiermann and Jenni, 1998; Masello and Quillfeldt, 2004; Quillfeldt et al., 2004; Svensson and Merilä, 1996), and thus has been used to indicate that birds are refueling and (presumably) in better nutritional condition. Triglyceride levels can also covary negatively with reproductive effort (Masello and Quillfeldt, 2004), and high levels are detected immediately following endurance flights (Jenni-Eiermann and Jenni, 1991, 1992).

Hematocrit and levels of triglyceride are context specific and must be interpreted cautiously (Bókony et al., 2012; Fair et al., 2007; Ots et al., 1998). These variables reveal different aspects of physiological state and therefore might be expected to vary, to some extent, independently of one another. For example, hematocrit can reflect physiological condition days to weeks prior to blood sampling (Carpenter, 1975), whereas triglyceride levels can reflect metabolic processes occurring over the hours before sample collection (Jenni-Eiermann and Jenni, 1998). Although hematocrit is a heritable trait (Fair et al., 2007; Sakaluk et al., 2014; Shlosberg et al., 1998) and can be "programmed" by stress during development (Careau et al., 2014), suggesting it may be less affected by current environmental conditions than triglyceride, other studies show a strong effect of the environment on hematocrit (Potti, 2007; Potti et al., 1999; Simon et al., 2005).

Interpreting multiple measures of physiology across time and space is challenging, and our correlative study cannot draw conclusions about the causes of the relationships we report. Nevertheless, we can speculate that if gannets with higher CORT$_f$ arrived on breeding grounds in relatively poor condition (e.g., Harms et al., 2015), they may have also exhibited relatively poor condition during incubation (i.e., low hematocrit). If so, they would be expected to spend more time flying and foraging (Angelier et al., 2007a), and thus high triglyceride levels could reflect extended bouts of feeding undertaken to improve condition. Alternatively, gannets with higher CORT$_f$ values may have arrived to the breeding grounds in relatively good body condition but then condition deteriorated during incubation (e.g., Franci et al., 2015). Indeed, elevated CORT levels and low hematocrit are seen in birds coping with food restrictions (Kempster et al., 2007; Kitaysky et al., 1999a, 1999b). However, gannets overall were likely not experiencing nutritional stress because triglyceride levels were, on average, higher than levels seen in the previous two years (Franci et al., 2015) and H:L ratios, which would be expected to be high during stress (Davis et al., 2008), were among the lowest scores reported in the literature (Brousseau-Fournier et al., 2014). Hematocrit scores were also similar to those reported previously (Dawson and Bortolotti, 1997a; Sánchez-Guzmán et al., 2004).

Regardless of the exact causes, hematocrit and triglyceride are associated with energetic state. That they were significantly related to an energy-regulating hormone (CORT) secreted several months earlier provides evidence of the link between non-lethal variation in a physiological mediator in one life-history period and physiological consequences in a subsequent period. Our results indicate that this relationship was unrelated to foraging habitat (estimated using stable isotopes) during non-breeding. Diet during the later months of the non-breeding period is a known driver of carry-over effects (Kouwenberg et al., 2013; Sorensen et al., 2009), yet diet during the earlier months of non-breeding apparently is not (Sorensen et al., 2009). Thus, if gannet feathers were grown early in the non-breeding period, diet at that time may have been too temporally segregated from breeding physiology for an association to be detected. Future studies could address this possibility by better understanding the exact periods of feather growth and by studying diet directly during this time.

Our findings highlight the importance of the location of non-breeding areas to gannet ecophysiology. We found that gannets wintering within the Gulf of Mexico had higher levels of CORT$_f$ and showed differences in feather stable isotopes compared to birds that wintered along the Atlantic coast. Although differences in $\delta^{15}N_f$ and $\delta^{13}C_f$ may be

expected based on geographic location (Cherel et al., 2000; Hobson, 1999; Hobson et al., 1994; Kelly, 2000), the difference in $CORT_f$ is an interesting finding. Gannets have to undertake a farther and presumably more energetically demanding migration to reach the Gulf of Mexico and may incur a cost for doing so. Although it can be hypothesized that overall higher $CORT_f$ values reflect that cost, the lack of relationships between stable isotopes and $CORT_f$ suggest that the cost, if it was present, was related to an additional (unmeasured) ecological variable. For example, dietary restrictions can result in elevated CORT levels (Kitaysky et al., 1999a, 1999b), so gannets wintering in the Gulf of Mexico may have experienced nutritional restrictions or low prey densities that increased commuting distances between foraging sites. It is also possible that residual chemical exposure from the 2010 *Deepwater Horizon* oil blowout is responsible for the differences in $CORT_f$ values we found. Although oiling (i.e., plumage fouling) can increase CORT levels (Fowler et al., 1995), ingestion of sub-lethal doses of oil can reduce CORT levels (Gorsline and Holmes, 1981; Lattin et al., 2014), though results are mixed (Leighton, 1993). Levels of CORT measured in plasma during incubation in the two years before our study (2011, 2012) were not associated with prior visitation to the Gulf of Mexico during previous non-breeding periods (Franci et al., 2014). So, even if the differences in $CORT_f$ we detected during non-breeding were caused by visiting the Gulf of Mexico, the legacy of those effects on gannet CORT physiology was probably limited. Taken together, this suggests that use of the Gulf of Mexico has consequences for gannet energy management during non-breeding (measured by $CORT_f$) that can carry over to the breeding period (e.g., via hematocrit and triglyceride), but effects on CORT physiology do not persist to incubation. Considering that gannets have a lifespan of 16 years (Mowbray, 2002) and exhibit very high fidelity to non-breeding areas (Fifield et al., 2014), longitudinal studies could help clarify long-term effects of repeated use of specific non-breeding areas. Indeed, in songbirds, the intensity of CORT responses during non-breeding has been linked to return rates to non-breeding areas (Angelier et al., 2009).

Additional research is needed to determine how the individual state of gannets upon arrival on breeding grounds (unknown in our study) is related to both their non-breeding ecophysiology and subsequent physiological condition throughout breeding. Quantifying actual dietary composition, quantities, and energetic values for the birds in both periods would provide better resolution of the diet and its impact on physiology, particularly during molt when isotopic integration into feathers occurs. When possible, experimentation and measuring exact feather growth periods should likewise be goals of future research. Nevertheless, our results provide evidence that CORT physiology during non-breeding is associated with subsequent physiological profile during incubation. Considering that the location of gannet wintering areas appears to be influential, further studying the links among movements, environmental conditions, and CORT physiology during non-breeding could shed light on resulting condition during breeding. Investigations of the fitness consequences of this variation in physiology will be essential to fully understanding the mechanistic role CORT appears to play in carry-over effects, and how this relates to exposure to natural and anthropogenic stressors during the non-breeding period.

Acknowledgments

We would like to thank the Parc National de l'Île-Bonaventure-et-du-Rocher-Percé, as well as C. Brousseau-Fournier, J. Chardine, R. Cotter, M. Drolet-Lambany, C. Franci, E. Lacaze and Y. Seyer for assistance in field work. We are grateful to T. Marchant for the use of her endocrine lab, and we thank G. Treen for kindly assisting with the CORT analyses. We also thank A. Adamowicz and J.-F. Hélie (Université du Québec à Montréal) for assistance with stable isotope analyses. This work was funded by Environment and Climate Change Canada, a Canada Research Chair in Comparative Avian Toxicology to J.V., NSERC Discovery Grants to M.G. and W.A.M., and CRSNG-ANR for the program IPOC on climate change to P.B.

Appendix 1. Rankings of models in each model set for 14 physiological response variables measured in northern gannets during breeding in 2013. Model rankings are based on Akaike's information criterion adjusted for small sample size (AIC_c) and model weights were normalized to sum to 1 (Burnham and Anderson, 2002).

Response variable	Rank	Model terms	AIC_c	ΔAIC_c	ω_i
Body mass	1	Sex	307.7	0.00	0.61
	2	$CORT_f$ + sex	310.4	2.70	0.16
	3	Null	311.7	4.00	0.08
	4	$CORT_f$ + sex + $CORT_f$ * sex	313.5	5.80	0.03
	5	$\delta^{15}N$	313.6	5.90	0.03
	6	$CORT_f$	314.1	6.40	0.02
	7	$\delta^{13}C$	314.1	6.40	0.02
	8	$CORT_f$ + $\delta^{15}N$	316.3	8.60	0.01
	9	$\delta^{13}C$ + $\delta^{15}N$	316.5	8.80	0.01
	10	$CORT_f$ + $\delta^{13}C$ + $\delta^{15}N$ + sex	316.7	9.00	0.01
	11	$CORT_f$ + $\delta^{13}C$ + sex + $CORT_f$ * sex	316.7	9.00	0.01
	12	$CORT_f$ + $\delta^{13}C$	316.8	9.10	0.01
	13	$CORT_f$ + $\delta^{15}N$ + sex + $CORT_f$ * sex	317.2	9.50	0.01
	14	$CORT_f$ + $\delta^{13}C$ + $\delta^{15}N$ + sex + $CORT_f$ * sex	321.1	13.40	0.00
Hematocrit	1	$CORT_f$	106.5	0	0.35
	2	$CORT_f$ + sex	106.8	0.3	0.30
	3	$CORT_f$ + $\delta^{13}C$	109.3	2.8	0.09
	4	$CORT_f$ + $\delta^{15}N$	109.5	3	0.08
	5	$CORT_f$ + sex + $CORT_f$ * sex	110	3.5	0.06
	6	Null	110.5	4	0.05
	7	Body mass	112.3	5.8	0.02
	8	$\delta^{13}C$	113.2	6.7	0.01
	9	$\delta^{15}N$	113.2	6.7	0.01
	10	Sex	113.2	6.7	0.01
	11	$CORT_f$ + $\delta^{13}C$ + sex + $CORT_f$ * sex	113.4	6.9	0.01
	12	$CORT_f$ + $\delta^{15}N$ + sex + $CORT_f$ * sex	113.8	7.3	0.01
	13	$CORT_f$ + $\delta^{13}C$ + $\delta^{15}N$ + sex	113.9	7.4	0.01
	14	$\delta^{13}C$ + $\delta^{15}N$	116.1	9.6	0.00
	15	$CORT_f$ + $\delta^{13}C$ + $\delta^{15}N$ + sex + $CORT_f$ * sex	117.8	11.3	0.00
Glucose	1	$CORT_f$	77.7	0	0.29

(*continued*)

Response variable	Rank	Model terms	AIC_c	ΔAIC_c	ω_i
	2	$CORT_f + \delta^{13}C$	78.4	0.7	0.21
	3	Null	79.5	1.8	0.12
	4	$\delta^{13}C$	80.1	2.4	0.09
	5	$CORT_f$ + sex	80.6	2.9	0.07
	6	$CORT_f + \delta^{15}N$	80.6	2.9	0.07
	7	$\delta^{15}N$	82	4.3	0.03
	8	Sex	82	4.3	0.03
	9	Body mass	82.2	4.5	0.03
	10	$\delta^{13}C + \delta^{15}N$	83.1	5.4	0.02
	11	$CORT_f + \delta^{13}C$ + sex + $CORT_f$ * sex	83.8	6.1	0.01
	12	$CORT_f$ + sex + $CORT_f$ * sex	83.8	6.1	0.01
	13	$CORT_f + \delta^{13}C + \delta^{15}N$ + sex	84.4	6.7	0.01
	14	$CORT_f + \delta^{15}N$ + sex + $CORT_f$ * sex	87.4	9.7	0.00
	15	$CORT_f + \delta^{13}C + \delta^{15}N$ + sex + $CORT_f$ * sex	88.14	10.44	0.00
Triglyceride[a]	1	$CORT_f$	−30.4	0	0.50
	2	$CORT_f + \delta^{13}C$	−28.1	2.3	0.16
	3	$CORT_f + \delta^{15}N$	−27.5	2.9	0.12
	4	$CORT_f$ + sex	−27.3	3.1	0.11
	5	$CORT_f$ + sex + $CORT_f$ * sex	−25.5	4.9	0.04
	6	Null	−23.9	6.5	0.02
	7	Sex	−22.6	7.8	0.01
	8	$\delta^{13}C$	−22	8.4	0.01
	9	$CORT_f + \delta^{13}C$ + sex + $CORT_f$ * sex	−21.8	8.6	0.01
	10	$CORT_f + \delta^{15}N$ + sex + $CORT_f$ * sex	−21.7	8.7	0.01
	11	$\delta^{15}N$	−21.5	8.9	0.01
	12	Body mass	−21.2	9.2	0.01
	13	$CORT_f + \delta^{13}C + \delta^{15}N$ + sex	−20.9	9.5	0.00
	14	$\delta^{13}C + \delta^{15}N$	−19.1	11.3	0.00
	15	$CORT_f + \delta^{13}C + \delta^{15}N$ + sex + $CORT_f$ * sex	−17.4	13	0.00
Cholesterol	1	$\delta^{15}N$	57.9	0	0.26
	2	Body mass	58.1	0.2	0.23
	3	Null	58.5	0.6	0.19
	4	Sex	60.7	2.8	0.06
	5	$\delta^{13}C + \delta^{15}N$	60.8	2.9	0.06
	6	$CORT_f + \delta^{15}N$	60.9	3	0.06
	7	$\delta^{13}C$	61	3.1	0.05
	8	$CORT_f$	61.1	3.2	0.05
	9	$CORT_f$ + sex	63.5	5.6	0.02
	10	$CORT_f + \delta^{13}C$	63.9	6	0.01
	11	$CORT_f + \delta^{15}N$ + sex + $CORT_f$ * sex	66.8	8.9	0.00
	12	$CORT_f$ + sex + $CORT_f$ * sex	66.8	8.9	0.00
	13	$CORT_f + \delta^{13}C + \delta^{15}N$ + sex	68	10.1	0.00
	14	$CORT_f + \delta^{13}C$ + sex + $CORT_f$ * sex	70.1	12.2	0.00
	15	$CORT_f + \delta^{13}C + \delta^{15}N$ + sex + $CORT_f$ * sex	71.4	13.5	0.00
Uric acid[a]	1	Null	6.3	0	0.35
	2	Body mass	7.3	1	0.21
	3	$\delta^{13}C$	8.9	2.6	0.09
	4	Sex	9	2.7	0.09
	5	$CORT_f$	9.1	2.8	0.09
	6	$\delta^{15}N$	9.1	2.8	0.09
	7	$\delta^{13}C + \delta^{15}N$	11.8	5.5	0.02
	8	$CORT_f + \delta^{13}C$	11.9	5.6	0.02
	9	$CORT_f$ + sex	12	5.7	0.02
	10	$CORT_f + \delta^{15}N$	12.2	5.9	0.02
	11	$CORT_f$ + sex + $CORT_f$ * sex	14.1	7.8	0.01
	12	$CORT_f + \delta^{13}C$ + sex + $CORT_f$ * sex	16.8	10.5	0.00
	13	$CORT_f + \delta^{15}N$ + sex + $CORT_f$ * sex	18	11.7	0.00
	14	$CORT_f + \delta^{13}C + \delta^{15}N$ + sex	19.1	12.8	0.00
	15	$CORT_f + \delta^{13}C + \delta^{15}N$ + sex + $CORT_f$ * sex	21.3	15	0.00
Alkaline phosphatase	1	Body mass	277.9	0	0.79
	2	Null	283.6	5.7	0.05
	3	$CORT_f$	283.6	5.7	0.05
	4	$CORT_f + \delta^{15}N$	284.6	6.7	0.03
	5	$\delta^{15}N$	284.8	6.9	0.03
	6	Sex	285.9	8	0.01
	7	$\delta^{13}C$	286.1	8.2	0.01
	8	$CORT_f + \delta^{13}C$	286.4	8.5	0.01
	9	$CORT_f$ + sex	286.6	8.7	0.01
	10	$\delta^{13}C + \delta^{15}N$	287.1	9.2	0.01
	11	$CORT_f$ + sex + $CORT_f$ * sex	289.8	11.9	0.00
	12	$CORT_f + \delta^{15}N$ + sex + $CORT_f$ * sex	290.8	12.9	0.00
	13	$CORT_f + \delta^{13}C + \delta^{15}N$ + sex	291	13.1	0.00
	14	$CORT_f + \delta^{13}C$ + sex + $CORT_f$ * sex	293.6	15.7	0.00
	15	$CORT_f + \delta^{13}C + \delta^{15}N$ + sex + $CORT_f$ * sex	294.9	17	0.00
Alanine aminotransferase	1	Body mass	146.3	0	0.62

(*continued on next page*)

(*continued*)

Response variable	Rank	Model terms	AIC_c	ΔAIC_c	ω_i
	2	Null	149.3	3	0.14
	3	$\delta^{13}C$	150.8	4.5	0.07
	4	$\delta^{15}N$	151.1	4.8	0.06
	5	$CORT_f$	152.2	5.9	0.03
	6	Sex	152.2	5.9	0.03
	7	$CORT_f + \delta^{13}C$	153.7	7.4	0.02
	8	$\delta^{13}C + \delta^{15}N$	153.8	7.5	0.01
	9	$CORT_f + \delta^{15}N$	154.3	8	0.01
	10	$CORT_f$ + sex	155.4	9.1	0.01
	11	$CORT_f$ + sex + $CORT_f$ * sex	159	12.7	0.00
	12	$CORT_f + \delta^{13}C + \delta^{15}N$ + sex	161.6	15.3	0.00
	13	$CORT_f + \delta^{13}C$ + sex + $CORT_f$ * sex	161.7	15.4	0.00
	14	$CORT_f + \delta^{15}N$ + sex + $CORT_f$ * sex	162.3	16	0.00
	15	$CORT_f + \delta^{13}C + \delta^{15}N$ + sex + $CORT_f$ * sex	166.7	20.4	0.00
Gamma-glutamyl transpeptidase	1	Null	159.2	0	0.34
	2	$CORT_f$	161.3	2.1	0.12
	3	Body mass	161.4	2.2	0.11
	4	Sex	161.8	2.6	0.09
	5	$\delta^{13}C$	161.9	2.7	0.09
	6	$\delta^{15}N$	161.9	2.7	0.09
	7	$CORT_f$ + sex	163.7	4.5	0.04
	8	$CORT_f$ + sex + $CORT_f$ * sex	164.1	4.9	0.03
	9	$CORT_f + \delta^{15}N$	164.3	5.1	0.03
	10	$CORT_f + \delta^{13}C$	164.3	5.1	0.03
	11	$\delta^{13}C + \delta^{15}N$	164.9	5.7	0.02
	12	$CORT_f + \delta^{13}C$ + sex + $CORT_f$ * sex	167.1	7.9	0.01
	13	$CORT_f + \delta^{15}N$ + sex + $CORT_f$ * sex	167.9	8.7	0.00
	14	$CORT_f + \delta^{13}C + \delta^{15}N$ + sex	170.8	11.6	0.00
	15	$CORT_f + \delta^{13}C + \delta^{15}N$ + sex + $CORT_f$ * sex	171.5	12.3	0.00
Lactate dehydrogenase	1	$\delta^{13}C$	247.2	0	0.31
	2	Null	248.3	1.1	0.18
	3	$CORT_f + \delta^{13}C$	249	1.8	0.13
	4	$CORT_f$	249.8	2.6	0.08
	5	Body mass	250	2.8	0.08
	6	$\delta^{13}C + \delta^{15}N$	250.1	2.9	0.07
	7	Sex	250.5	3.3	0.06
	8	$\delta^{15}N$	251	3.8	0.05
	9	$CORT_f$ + sex	252.7	5.5	0.02
	10	$CORT_f + \delta^{15}N$	252.8	5.6	0.02
	11	$CORT_f$ + sex + $CORT_f$ * sex	255.4	8.2	0.01
	12	$CORT_f + \delta^{13}C + \delta^{15}N$ + sex	256	8.8	0.00
	13	$CORT_f + \delta^{13}C$ + sex + $CORT_f$ * sex	256.2	9	0.00
	14	$CORT_f + \delta^{15}N$ + sex + $CORT_f$ * sex	259.2	12	0.00
	15	$CORT_f + \delta^{13}C + \delta^{15}N$ + sex + $CORT_f$ * sex	260.4	13.2	0.00
Aspartate aminotransferase	1	$\delta^{13}C$	264.9	0	0.43
	2	Null	267.3	2.4	0.13
	3	$\delta^{13}C + \delta^{15}N$	267.5	2.6	0.12
	4	$CORT_f + \delta^{13}C$	267.9	3	0.10
	5	Sex	268.4	3.5	0.07
	6	Body mass	269.9	5	0.04
	7	$CORT_f$	270	5.1	0.03
	8	$\delta^{15}N$	270	5.1	0.03
	9	$CORT_f$ + sex	271.1	6.2	0.02
	10	$CORT_f$ + sex + $CORT_f$ * sex	272.6	7.7	0.01
	11	$CORT_f + \delta^{13}C$ + sex + $CORT_f$ * sex	273	8.1	0.01
	12	$CORT_f + \delta^{15}N$	273	8.1	0.01
	13	$CORT_f + \delta^{13}C + \delta^{15}N$ + sex	273.2	8.3	0.01
	14	$CORT_f + \delta^{15}N$ + sex + $CORT_f$ * sex	276.4	11.5	0.00
	15	$CORT_f + \delta^{13}C + \delta^{15}N$ + sex + $CORT_f$ * sex	277.2	12.3	0.00
Creatine kinase[a]	1	Body mass	−21.3	0	0.96
	2	Sex	−12.1	9.2	0.01
	3	Null	−11.6	9.7	0.01
	4	$\delta^{15}N$	−11.1	10.2	0.01
	5	$CORT_f$	−10.9	10.4	0.01
	6	$CORT_f + \delta^{15}N$	−10.5	10.8	0.00
	7	$CORT_f$ + sex	−9.7	11.6	0.00
	8	$\delta^{13}C$	−9.4	11.9	0.00
	9	$CORT_f + \delta^{13}C$	−8.5	12.8	0.00
	10	$\delta^{13}C + \delta^{15}N$	−8.2	13.1	0.00
	11	$CORT_f$ + sex + $CORT_f$ * sex	−6.3	15	0.00
	12	$CORT_f + \delta^{13}C + \delta^{15}N$ + sex	−5	16.3	0.00
	13	$CORT_f + \delta^{15}N$ + sex + $CORT_f$ * sex	−4.8	16.5	0.00
	14	$CORT_f + \delta^{13}C$ + sex + $CORT_f$ * sex	−3.6	17.7	0.00
	15	$CORT_f + \delta^{13}C + \delta^{15}N$ + sex + $CORT_f$ * sex	−1.3	20	0.00
Total protein	1	Null	142.5	0	0.28
	2	Body mass	143.1	0.6	0.21

(*continued*)

Response variable	Rank	Model terms	AIC_c	ΔAIC_c	ω_i
	3	$\delta^{15}N$	144.2	1.7	0.12
	4	Sex	144.7	2.2	0.09
	5	$\delta^{13}C$	144.8	2.3	0.09
	6	$CORT_f$	145.1	2.6	0.08
	7	$\delta^{13}C + \delta^{15}N$	146.5	4	0.04
	8	$CORT_f + \delta^{15}N$	147.2	4.7	0.03
	9	$CORT_f$ + sex	147.7	5.2	0.02
	10	$CORT_f + \delta^{13}C$	147.8	5.3	0.02
	11	$CORT_f$ + sex + $CORT_f$ * sex	148	5.5	0.02
	12	$CORT_f + \delta^{15}N$ + sex + $CORT_f$ * sex	149.2	6.7	0.01
	13	$CORT_f + \delta^{13}C$ + sex + $CORT_f$ * sex	151.8	9.3	0.00
	14	$CORT_f + \delta^{13}C + \delta^{15}N$ + sex	153.5	11	0.00
	15	$CORT_f + \delta^{13}C + \delta^{15}N$ + sex + $CORT_f$ * sex	153.6	11.1	0.00
H/L ratio	1	Null	−50.3	0	0.35
	2	Sex	−47.9	2.4	0.10
	3	$CORT_f$	−47.8	2.5	0.10
	4	$\delta^{13}C$	−47.7	2.6	0.09
	5	$\delta^{15}N$	−47.7	2.6	0.09
	6	Body mass	−47.6	2.7	0.09
	7	$CORT_f$ + sex + $CORT_f$ * sex	−46.6	3.7	0.05
	8	$CORT_f$ + sex	−45.4	4.9	0.03
	9	$CORT_f + \delta^{15}N$	−45.0	5.3	0.02
	10	$CORT_f + \delta^{13}C$	−44.9	5.4	0.02
	11	$\delta^{13}C + \delta^{15}N$	−44.8	5.5	0.02
	12	$CORT_f + \delta^{13}C$ + sex + $CORT_f$ * sex	−43.3	7	0.01
	13	$CORT_f + \delta^{15}N$ + sex + $CORT_f$ * sex	−42.8	7.5	0.01
	14	$CORT_f + \delta^{13}C + \delta^{15}N$ + sex + $CORT_f$ * sex	−38.9	11.4	0.00
	15	$CORT_f + \delta^{13}C + \delta^{15}N$ + sex	−38.4	11.9	0.00

[a] Values were log-transformed to achieve normality.

References

Angelier, F., Wingfield, J.C., 2013. Importance of the glucocorticoid stress response in a changing world: theory, hypotheses and perspectives. Gen. Comp. Endocrinol. 190, 118–128.

Angelier, F., Clement-Chastel, C., Gabrielsen, G.W., Chastel, O., 2007a. Corticosterone and time-activity budget: an experiment with Black-legged kittiwakes. Horm. Behav. 52, 482–491.

Angelier, F., Shaffer, S.A., Weimerskirch, H., Trouve, C., Chastel, O., 2007b. Corticosterone and foraging behavior in a pelagic seabird. Physiol. Biochem. Zool. 80, 283–292.

Angelier, F., Holberton, R.L., Marra, P.P., 2009. Does stress response predict return rate in a migratory bird species? A study of American redstarts and their non-breeding habitat. Proc. R. Soc. B 276, 3545–3551.

Arnold, T.W., 2010. Uninformative parameters and model selection using Akaike's information criterion. J. Wildl. Manag. 74, 1175–1178.

Bächler, E., Hahn, S., Schaub, M., Arlettaz, R., Jenni, L., Fox, J.W., Afanasyev, V., Liechti, F., 2010. Year-round tracking of small trans-Saharan migrants using light-level geolocators. PLoS One 5, e9566.

Bearhop, S., Waldron, S., Votier, S.C., Furness, R.W., 2002. Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. Physiol. Biochem. Zool. 75, 451–458.

Bókony, V., Seress, G., Nagy, S., Lendvai, A.Z., Liker, A., 2012. Multiple indices of body condition reveal no negative effect of urbanization in adult house sparrows. Landsc. Urban Plan. 104, 75–84.

Bonier, F., Martin, P.R., Moore, I.T., Wingfield, J.C., 2009. Do baseline glucocorticoids predict fitness? Trends Ecol. Evol. 24, 634–642.

Bonier, F., Moore, I.T., Robertson, R.J., 2011. The stress of parenthood? Increased glucocorticoids in birds with experimentally enlarged broods. Biol. Lett. 7, 944–966.

Borga, K., Fisk, A.T., Hoekstra, P.F., Muir, D.C.G., 2004. Biological and chemical factors of importance in the bioaccumulation and trophic transfer of persistent organochlorine contaminants in arctic marine food webs. Environ. Toxicol. Chem. 23, 2367–2385.

Bortolotti, G.R., 2010. Flaws and pitfalls in the chemical analysis of feathers: bad news-good news for avian chemoecology and toxicology. Ecol. Appl. 20, 1766–1774.

Bortolotti, G.R., Marchant, T.A., Blas, J., German, T., 2008. Corticosterone in feathers is a long-term, integrated measure of avian stress physiology. Funct. Ecol. 22, 494–500.

Boughton, R.K., Atwell, J.W., Schoech, S.J., 2006. An introduced generalist parasite, the sticktight flea (*Echidnophaga gallinacea*), and its pathology in the threatened Florida scrub-jay (*Aphelocoma coerulescens*). J. Parasitol. 92, 941–948.

Bourgeon, S., Leat, E.H.K., Magnusdottir, E., Fisk, A.T., Furness, R.W., Strom, H., Hanssen, S.A., Petersen, A.E., Olafsdottir, K., Borga, K., Gabrielsen, G.W., Bustnes, J.O., 2012. Individual variation in biomarkers of health: influence of persistent organic pollutants in great skuas (*Stercorarius skua*) breeding at different geographical locations. Environ. Res. 118, 31–39.

Breuner, C.W., Patterson, S.H., Hahn, T.P., 2008. In search of relationships between the acute adrenocortical response and fitness. Gen. Comp. Endocrinol. 157, 288–295.

Brousseau-Fournier, C., Lacaze, E., Champoux, L., Fournier, M., Brousseau, P., 2014. Immunologic and genotoxic profile of northern gannet (*Morus bassanus*) from Bonaventure Island. J. Xenobiotics 4, 53–55.

Brown, M.E., 1996. Assessing Body Condition in Birds. Curr OrnitholSpringer, pp. 67–135.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multiple Inference: a Practical Information-Theoretic Approach. second ed. Springer, Heidlberg.

Bustnes, J.O., Miland, O., Fjeld, M., Erikstad, K.E., Skaare, J.U., 2005. Relationships between ecological variables and four organochlorine pollutants in an artic glaucous gull (*Larus hyperboreus*) population. Environ. Pollut. 136, 175–185.

Careau, V., Buttemer, W.A., Buchanan, K.L., 2014. Early-developmental stress, repeatability, and canalization in a suite of physiological and behavioral traits in female zebra finches. Integr. Comp. Biol. 54, 539–554.

Caron-Beaudoin, É, Gentes, M.-L., Patenaude-Monette, M., Hélie, J.-F., Giroux, J.-F., Verreault, J., 2013. Combined usage of stable isotopes and GPS-based telemetry to understand the feeding ecology of an omnivorous bird, the Ring-billed Gull (Larus delawarensis). Can. J. Zool. 91, 689–697.

Carpenter, F.L., 1975. Bird hematocrits: effects of high altitude and strength of flight. Comp. Biochem. Physiol. 50, 415–417.

Chastel, O., Weimerskirch, H., Jouventin, P., 1995. Body condition and seabird reproductive performance: a study of 3 petrel species. Ecology 76, 2240–2246.

Cherel, Y., Hobson, K.A., Weimerskirch, H., 2000. Using stable-isotope analysis of feathers to distinguish moulting and breeding origins of seabirds. Oecologia 122, 155–162.

Cherel, Y., Hobson, K.A., Bailleul, F.R., Groscolas, R., 2005. Nutrition, physiology, and stable isotopes: new information from fasting and molting penguins. Ecology 86, 2881–2888.

Cherel, Y., Phillips, R.A., Hobson, K.A., McGill, R., 2006. Stable isotope evidence of diverse species-specific and individual wintering strategies in seabirds. Biol. Lett. 2, 301–303.

Crossin, G.T., Phillips, R.A., Trathan, P.N., Fox, D.S., Dawson, A., Wynne-Edwards, K.E., Williams, T.D., 2012a. Migratory carryover effects and endocrinological correlates of reproductive decisions and reproductive success in female albatrosses. Gen. Comp. Endocrinol. 176, 151–157.

Crossin, G.T., Trathan, P.N., Phillips, R.A., Gorman, K.B., Dawson, A., Sakamoto, K.Q., Williams, T.D., 2012b. Corticosterone predicts foraging behavior and parental care in macaroni penguins. Am. Nat. 180, E31–E41.

Cury, P.M., Boyd, I.L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R.J.M., Furness, R.W., Mills, J.A., Murphy, E.J., Oesterblom, H., Paleczny, M., Piatt, J.F., Roux, J.-P., Shannon, L., Sydeman, W.J., 2011. Global seabird response to forage fish depletion—one-third for the birds. Science 334, 1703–1706.

Davis, A.K., Maney, D.L., Maerz, J.C., 2008. The use of leukocyte profiles to measure stress in vertebrates: a review for ecologists. Funct. Ecol. 22, 760–772.

Dawson, R.D., Bortolotti, G.R., 1997a. Are avian hematocrits indicative of condition? American kestrels as a model. J. Wildl. Manag. 61, 1297–1306.

Dawson, R.D., Bortolotti, G.R., 1997b. Variation in hematocrit and total plasma proteins of nestling American kestrels (*Falco sparverius*) in the wild. Comp. Biochem. Physiol. A Physiol. 117, 383–390.

Dickens, M.J., Earle, K.A., Romero, L.M., 2009. Initial transference of wild birds to captivity alters stress physiology. Gen. Comp. Endocrinol. 160, 76–83.

Drent, R., Daan, S., 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68, 225–252.

Fair, J., Whitaker, S., Pearson, B., 2007. Sources of variation in haematocrit in birds. Ibis 149, 535–552.

Fairhurst, G.D., Frey, M.D., Reichert, J.F., Szelest, I., Kelly, D.M., Bortolotti, G.R., 2011. Does environmental enrichment reduce stress? An integrated measure of corticosterone from feathers provides a novel perspective. PLoS One 6, e17663.

Fairhurst, G.D., Navarro, J., González-Solís, J., Marchant, T.A., Bortolotti, G.R., 2012a. Feather corticosterone of a nestling seabird reveals consequences of sex-specific parental investment. Proc. R. Soc. B Biol. Sci. 279, 177–184.

Fairhurst, G.D., Treen, G.D., Clark, R.G., Bortolotti, G.R., 2012b. Nestling corticosterone response to microclimate in an altricial bird. Can. J. Zool. 90, 1422–1430.

Fairhurst, G.D., Marchant, T.A., Soos, C., Machin, K.L., Clark, R.G., 2013a. Experimental relationships between plasma- and feather-levels of corticosterone in a free-living bird. J. Exp. Biol. 216, 4071–4081.

Fairhurst, G.D., Vögeli, M., Serrano, D., Delgado, A., Tella, J.L., Bortolotti, G.R., 2013b. Can synchronizing feather-based measures of corticosterone and stable isotopes help us better understand habitat-physiology relationships? Oecologia 173, 731–743.

Fairhurst, G.D., Berzins, L.L., Bradley, D.W., Laughlin, A.J., Romano, A., Romano, M., Scandolara, C., Ambrosini, R., Dawson, R.D., Dunn, P.O., Hobson, K.A., Liechti, F., Marchant, T.A., Norris, D.R., Rubolini, D., Saino, N., Taylor, C.M., Whittingham, L.A., Clark, R.G., 2015a. Assessing costs of carrying geolocators using feather corticosterone in two species of aerial insectivore. R. Soc. Open Sci. 2, 150004.

Fairhurst, G.D., Bond, A.L., Hobson, K.A., Ronconi, R.A., 2015b. Feather-based measures of stable isotopes and corticosterone reveal a relationship between trophic position and physiology in a pelagic seabird over a 153-year period. Ibis 157, 273–283.

Fifield, D.A., Montevecchi, W.A., Garthe, S., Robertson, G.J., Kubetzki, U., Rail, J.-F., 2014. Migratory tactics and wintering areas of northern gannets (*Morus bassanus*) breeding in North America. Ornithol. Monogr. 79, 1–63.

Forero, M.G., Gonzalez-Solis, J., Igual, J.M., Hobson, K.A., Ruiz, X., Viscor, G., 2006. Ecological and physiological variance in T-cell mediated immune response in Cory's shearwaters. Condor 108, 865–876.

Fowler, G.S., Wingfield, J.C., Boersma, P.D., 1995. Hormonal and reproductive effects of low levels of petroleum fouling in Magellanic penguins (*Spheniscus magellanicus*). Auk 112, 382–389.

Franci, C.D., Guillemette, M., Pelletier, É., Chastel, O., Bonnefoi, S., Verreault, J., 2014. Endocrine status of a migratory bird potentially exposed to the deepwater horizon oil spill: a case study of northern gannets breeding on Bonaventure Island, eastern Canada. Sci. Total Environ. 473, 110–116.

Franci, C.D., Vézina, F., Grégoire, F., Rail, J.-F., Verreault, J., 2015. Nutritional stress in northern gannets during an unprecedented low reproductive success year: can extreme sea surface temperature event and dietary change be the cause? Comp. Biochem. Physiol. A Mol. Integr. Physiol. 181, 1–8.

Garthe, S., Montevecchi, W.A., Chapdelaine, G., Rail, J.-F., Hedd, A., 2007. Contrasting foraging tactics by northern gannets (*Sula bassana*) breeding in different oceanographic domains with different prey fields. Mar. Biol. 151, 687–694.

Garthe, S., Guse, N., Montevecchi, W.A., Rail, J.-F., Gregoire, F., 2014. The daily catch: flight altitude and diving behavior of northern gannets feeding on Atlantic mackerel. J. Sea Res. 85, 456–462.

Garvin, J.C., Dunn, P.O., Whittingham, L.A., Steeber, D.A., Hasselquist, D., 2008. Do male ornaments signal immunity in the common yellowthroat? Behav. Ecol. 19, 54–60.

Ginn, H.B., Melville, D.S., 1983. Moult in Birds. British Trust for Ornithology, Tring, Hertfordshire, UK.

Gorsline, J., Holmes, W.N., 1981. Effects of petroleum on adrenocortical activity and on hepatic naphthalene-metabolizing activity in mallard ducks. Arch. Environ. Contam. Toxicol. 10, 765–777.

Grava, T., Fairhurst, G.D., Avey, M.T., Grava, A., Bradley, J., Avis, J.L., Bortolotti, G.R., Sturdy, C.B., Otter, K.A., 2013. Habitat quality affects early physiology and subsequent neuromotor development of juvenile black-capped chickadees. PLoS One 8, e71852.

Griffiths, R., Double, M.C., Orr, K., Dawson, R.J., 1998. A DNA test to sex most birds. Mol. Ecol. 7, 1071–1075.

Guglielmo, C.G., Cerasale, D.J., Eldermire, C., 2005. A field validation of plasma metabolite profiling to assess refueling performance of migratory birds. Physiol. Biochem. Zool. 78, 116–125.

Harms, N.J., Legagneux, P., Gilchrist, H.G., Bêty, J., Love, O.P., Forbes, M.R., Bortolotti, G.R., Soos, C., 2015. Feather corticosterone reveals effect of moulting conditions in the autumn on subsequent reproductive output and survival in an Arctic migratory bird. Proc. R. Soc. B 282, 20142085.

Harriman, V.B., Dawson, R.D., Clark, R.G., Fairhurst, G.D., Bortolotti, G.R., 2014. Effects of ectoparasites on seasonal variation in quality of nestling tree swallows (*Tachycineta bicolor*). Can. J. Zool. 92, 87–96.

Harrison, X.A., Blount, J.D., Inger, R., Norris, D.R., Bearhop, S., 2011. Carry-over effects as drivers of fitness differences in animals. J. Anim. Ecol. 80, 4–18.

Hedd, A., Montevecchi, W.A., 2006. Diet and trophic position of Leach's storm-petrel *Oceanodroma leucorhoa* during breeding and moult, inferred from stable isotope analysis of feathers. Mar. Ecol. Prog. Ser. 322, 291–301.

Hennin, H.L., Legagneux, P., Bety, J., Williams, T.D., Gilchrist, H.G., Baker, T.M., Love, O.P., 2015. Pre-breeding energetic management in a mixed-strategy breeder. Oecologia 177, 235–243.

Hobson, K.A., 1999. Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120, 314–326.

Hobson, K.A., Clark, R.G., 1993. Turnover of ^{13}C in cellular and plasma fractions of blood: implications for nondestructive sampling in avian dietary studies. Auk 110, 638–641.

Hobson, K.A., Piatt, J.F., Pitocchelli, J., 1994. Using stable isotopes to determine seabird trophic relationships. J. Anim. Ecol. 63, 786–798.

Hõrak, P., Ots, I., Murumagi, A., 1998. Haematological health state indices of reproducing great tits: a response to brood size manipulation. Funct. Ecol. 12, 750–756.

Hõrak, P., Männiste, M., Meitern, R., Sild, E., Saks, L., Sepp, T., 2013. Dexamethasone inhibits corticosterone deposition in feathers of greenfinches. Gen. Comp. Endocrinol. 191, 210–214.

Howell, S.N.G., 2010. Molt in North American Birds. Houghton Mifflin Harcourt.

Howlett, J.C., Bailey, T.A., Samour, J.H., Naldo, J.L., D'Aloia, M.-A., 2002. Age-related hematologic changes in captive-reared houbara, white-bellied, and rufous-crested bustards. J. Wildl. Dis. 38, 804–816.

Jenni-Eiermann, S., Jenni, L., 1991. Metabolic responses to flight and fasting in night-migrating passerines. J. Comp. Physiol. B Biochem. Syst. Environ. Physiol. 161, 465–474.

Jenni-Eiermann, S., Jenni, L., 1992. High plasma triglyceride levels in small birds during migration flight: a new pathway for fuel supply during endurance locomotion at very high mass-specific metabolic rates? Physiol. Zool. 65, 112–123.

Jenni-Eiermann, S., Jenni, L., 1998. What Can Plasma Metabolites Tell Us About the Metabolism, Physiological State and Condition of Individual Birds? An overview Biological Conservation Fauna 102 pp. 312–319

Jenni-Eiermann, S., Helfenstein, F., Vallat, A., Glauser, G., Jenni, L., 2015. Corticosterone: effects on feather quality and deposition into feathers. Methods Ecol. Evol. 6, 237–246.

Jennings, S., Warr, K., 2003. Environmental correlates of large-scale spatial variation in the $\delta^{15}N$ of marine animals. Mar. Biol. 142, 1131–1140.

Kelly, J.F., 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Can. J. Zool. 78, 1–27.

Kempster, B., Zanette, L., Longstaffe, F.J., MacDougall-Shackleton, S.A., Wingfield, J.C., Clinchy, M., 2007. Do stable isotopes reflect nutritional stress? Results from a laboratory experiment on song sparrows. Oecologia 151, 365–371.

Kitaysky, A.S., Piatt, J.F., Wingfield, J.C., Romano, M., 1999a. The adrenocortical stress-response of black-legged kittiwake chicks in relation to dietary restrictions. J. Comp. Physiol. B Biochem. Syst. Environ. Physiol. 169, 303–310.

Kitaysky, A.S., Wingfield, J.C., Piatt, J.F., 1999b. Dynamics of food availability, body condition and physiological stress response in breeding black-legged kittiwakes. Funct. Ecol. 13, 577–584.

Kitaysky, A.S., Piatt, J.F., Wingfield, J.C., 2007. Stress hormones link food availability and population processes in seabirds. Mar. Ecol. Prog. Ser. 352, 245–258.

Kitaysky, A.S., Piatt, J.F., Hatch, S.A., Kitaiskaia, E.V., Benowitz-Fredericks, Z.M., Shultz, M.T., Wingfield, J.C., 2010. Food availability and population processes: severity of nutritional stress during reproduction predicts survival of long-lived seabirds. Funct. Ecol. 24, 625–637.

Korschgen, C.E., 1977. Breeding stress of female eiders in Maine. J. Wildl. Manag. 41, 360–373.

Kouwenberg, A.-L., Hipfner, J.M., McKay, D.W., Storey, A.E., 2013. Corticosterone and stable isotopes in feathers predict egg size in Atlantic puffins *Fratercula arctica*. Ibis 155, 413–418.

Krause, J.S., Nemeth, Z., Perez, J.H., Chmura, H.E., Ramenofsky, M., Wingfield, J.C., 2016a. Annual hematocrit profiles in two subspecies of white-crowned sparrow: a migrant and a resident comparison. Physiol. Biochem. Zool. 89, 51–60.

Krause, J.S., Perez, J.H., Chmura, H.E., Meddle, S.L., Hunt, K.E., Gough, L., Boelman, N., Wingfield, J.C., 2016b. The stress response is attenuated during inclement weather in parental, but not in pre-parental, Lapland longspurs (*Calcarius lapponicus*) breeding in the low Arctic. Horm. Behav. 83, 68–74.

Krause, J.S., Perez, J.H., Chmura, H.E., Sweet, S.K., Meddle, S.L., Hunt, K.E., Gough, L., Boelman, N., Wingfield, J.C., 2016c. The effect of extreme spring weather on body condition and stress physiology in Lapland longspurs and white-crowned sparrows breeding in the Arctic. Gen. Comp. Endocrinol. 237, 10–18.

Lattin, C.R., Ngai, H.M., Romero, L.M., 2014. Evaluating the stress response as a bioindicator of sub-lethal effects of crude oil exposure in wild house sparrows (*Passer domesticus*). PLoS One 9, e102106.

Lattin, C.R., Breuner, C.W., Romero, L.M., 2016. Does corticosterone regulate the onset of breeding in free-living birds?: the CORT-flexibility hypothesis and six potential mechanisms for priming corticosteroid function. Horm. Behav. 78, 107–120.

Legagneux, P., Harms, N.J., Gauthier, G., Chastel, O., Gilchrist, H.G., Bortolotti, G., Bêty, J., Soos, C., 2013. Does feather corticosterone reflect individual quality or external stress in arctic-nesting migratory birds? PLoS One 8, e82644.

Leighton, F.A., 1993. The toxicity of petroleum oils to birds. Environ. Rev. 1, 92–103.

Marra, P.P., Hobson, K.A., Holmes, R.T., 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282, 1884–1886.

Masello, J.F., Quillfeldt, P., 2004. Are haematological parameters related to body condition, ornamentation and breeding success in wild burrowing parrots *Cyanoliseus patagonus*? J. Avian Biol. 35, 445–454.

Mazerolle, D.F., Hobson, K.A., 2002. Physiological ramifications of habitat selection in territorial male ovenbirds: consequences of landscape fragmentation. Oecologia 130, 356–363.

McNamara, J.M., Houston, A.I., 1996. State-dependent life histories. Nature 380, 215–221.

Montevecchi, W., Benvenuti, S., Garthe, S., Davoren, G., Fifield, D., 2009. Flexible foraging tactics by a large opportunistic seabird preying on forage- and large pelagic fishes. Mar. Ecol. Prog. Ser. 385, 295–306.

Montevecchi, W., Fifield, D., Burke, C., Garthe, S., Hedd, A., Rail, J.-F., Robertson, G., 2012. Tracking long-distance migration to assess marine pollution impact. Biol. Lett. 8, 218–221.

Mowbray, T.B., 2002. Northern gannet (*Morus bassanus*). In: Poole, A. (Ed.), The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, N. Y., U. S. A.

Nelson, B., 2010. The Gannet. A&C Black.

Norris, D.R., Taylor, C.M., 2006. Predicting the consequences of carry-over effects for migratory populations. Biol. Lett. 2, 148–151.

Norris, D.R., Marra, P.P., Kyser, T.K., Sherry, T.W., Ratcliffe, L.M., 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proc. R. Soc. B Biol. Sci. 271, 59–64.

Ots, I., Hõrak, P., 1998. Health impact of blood parasites in breeding great tits. Oecologia 116, 441–448.

Ots, I., Murumagi, A., Hõrak, P., 1998. Haematological health state indices of reproducing great tits: methodology and sources of natural variation. Funct. Ecol. 12, 700–707.

Peterson, B.J., Fry, B., 1987. Stable isotopes in ecosystem studies. Annu. Rev. Ecol. Syst. 18, 293–320.

Piersma, T., Everaarts, J.M., Jukema, J., 1996. Build-up of red blood cells in refuelling bar-tailed godwits in relation to individual migratory quality. Condor 98, 363–370.
Potti, J., 2007. Variation in the hematocrit of a passerine bird across life stages is mainly of environmental origin. J. Avian Biol. 38, 726–730.
Potti, J., Moreno, J., Merino, S., Frias, O., Rodriguez, R., 1999. Environmental and genetic variation in the haematocrit of fledgling pied flycatchers *Ficedula hypoleuca*. Oecologia 120, 1–8.
Quillfeldt, P., Masello, J.F., Mostl, E., 2004. Blood chemistry in relation to nutrition and ectoparasite load in Wilson's storm-petrels *Oceanites oceanicus*. Polar Biol. 27, 168–176.
Rail, J.-F., Champoux, L., Lavoie, R.A., Chapdelaine, G., 2013. Monitoring of the population and contamination of the Northern Gannet in Quebec, 1966–2009, Technical Report Series No. 528. Canadian Wildlife Service, Quebec Region, Environment Canada, IX + 75 Pages + Appendices.
Rockwell, S.M., Bocetti, C.I., Marra, P.P., 2012. Carry-over effects of winter climate on spring arrival date and reproductive success in an endangered migratory bird, Kirtland's Warbler (*Setophaga kirtlandii*). Auk 129, 744–752.
Romero, L.M., Fairhurst, G.D., 2016. Measuring corticosterone in feathers: strengths, limitations, and suggestions for the future. Comp. Biochem. Physiol. A 202, 112–122.
Ronconi, R.A., Koopman, H.N., McKinstry, C.A.E., Wong, S.N.P., Westgate, A.J., 2010. Interannual variability in diet of non-breeding pelagic seabirds *Puffinus* spp. at migratory staging areas: evidence from stable isotopes and fatty acids. Mar. Ecol. Prog. Ser. 419, 267–282.
Saino, N., Bolzern, A.M., Moller, A.P., 1997. Immunocompetence, ornamentation, and viability of male barn swallows (*Hirundo rustica*). Proc. Natl. Acad. Sci. U. S. A. 94, 549–552.
Saino, N., Szep, T., Ambrosini, R., Romano, M., Moller, A.P., 2004. Ecological conditions during winter affect sexual selection and breeding in a migratory bird. Proc. R. Soc. B 271, 681–686.
Saino, N., Romano, M., Caprioli, M., Ambrosini, R., Rubolini, D., Scandolara, C., Romano, A., 2012. A ptilochronological study of carry-over effects of conditions during wintering on breeding performance in the barn swallow *Hirundo rustica*. J. Avian Biol. 43, 513–524.
Sakaluk, S.K., Wilson, A.J., Bowers, E.K., Johnson, L.S., Masters, B.S., Johnson, B.G.P., Vogel, L.A., Forsman, A.M., Thompson, C.F., 2014. Genetic and environmental variation in condition, cutaneous immunity, and haematocrit in house wrens. BMC Evol. Biol. 14.
Sánchez-Guzmán, J., Villegas, A., Corbacho, C., Morán, R., Marzal, A., Real, R., 2004. Response of the haematocrit to body condition changes in northern bald ibis *Geronticus eremita*. Comp. Biochem. Physiol. A Mol. Integr. Physiol. 139, 41–47.
Scheuhammer, A.M., Meyer, M.W., Sandheinrich, M.B., Murray, M.W., 2007. Effects of environmental methylmercury on the health of wild birds, mammals, and fish. AMBIO J. Hum. Environ. 36, 12–19.
Shlosberg, A., Bellaiche, M., Berman, E., Perk, S., Deeb, N., Neumark, E., Cahaner, A., 1998. Relationship between broiler chicken haematocrit-selected parents and their progeny, with regard to haematocrit, mortality from ascites and bodyweight. Res. Vet. Sci. 64, 105–109.
Simon, A., Thomas, D., Bourgault, P., Blondel, J., Perret, P., Lambrechts, M., 2005. Between-population differences in nestling size and hematocrit level in blue tits (*Parus caeruleus*): a cross-fostering test for genetic and environmental effects. Can. J. Zool. 83, 694–701.
Sorensen, M.C., Hipfner, J.M., Kyser, T.K., Norris, D.R., 2009. Carry-over effects in a Pacific seabird: stable isotope evidence that pre-breeding diet quality influences reproductive success. J. Anim. Ecol. 78, 460–467.
Stauss, C., Bearhop, S., Bodey, T.W., Garthe, S., Gunn, C., Grecian, W.J., Inger, R., Knight, M.E., Newton, J., Patrick, S.C., Phillips, R.A., Waggitt, J.J., Votier, S.C., 2012. Sex-specific foraging behaviour in northern gannets *Morus bassanus*: incidence and implications. Mar. Ecol. Prog. Ser. 457, 151–162.
Strack, A.M., Sebastian, R.J., Schwartz, M.W., Dallman, M.F., 1995. Glucocorticoids and insulin - reciprocal signals for energy-balance. Am. J. Phys. Regul. Integr. Comp. Phys. 37, R142–R149.
Svensson, E., Merilä, J., 1996. Molt and migratory condition in blue tits: a serological study. Condor 98, 825–831.
Votier, S.C., Bearhop, S., Witt, M.J., Inger, R., Thompson, D., Newton, J., 2010. Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. J. Appl. Ecol. 47, 487–497.
Votier, S.C., Grecian, W.J., Patrick, S., Newton, J., 2011. Inter-colony movements, at-sea behaviour and foraging in an immature seabird: results from GPS-PPT tracking, radio-tracking and stable isotope analysis. Mar. Biol. 158, 355–362.
Wayland, M., Gilchrist, H.G., Marchant, T., Keating, J., Smits, J.E., 2002. Immune function, stress response, and body condition in arctic-breeding common eiders in relation to cadmium, mercury, and selenium concentrations. Environ. Res. 90, 47–60.
Will, A.P., Suzuki, Y., Elliott, K.H., Hatch, S.A., Watanuki, Y., Kitaysky, A.S., 2014. Feather corticosterone reveals developmental stress in seabirds. J. Exp. Biol. 217, 2371–2376.
Wingfield, J.C., Kitaysky, A.S., 2002. Endocrine responses to unpredictable environmental events: stress or anti-stress hormones? Integr. Comp. Biol. 42, 600–609.
Wingfield, J.C., Sapolsky, R.M., 2003. Reproduction and resistance to stress: when and how. J. Neuroendocrinol. 15, 711–724.