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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

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HIGHLIGHTS

- In 2010–2011, 23.5% of Northern gannets breeding on Bonaventure Island overwintered in the Gulf of Mexico.
- Breeding colony on Bonaventure has decreased substantially during the last few years.
- Exposure to petroleum could not be confirmed based on PAH analyses in blood cells of gannets.
- Corticosterone status and prolactin status were not different between birds returning from the two overwintering sites.

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ABSTRACT

The Deepwater Horizon oil spill caused the death of a large number of seabirds in the Gulf of Mexico in 2010. However, the long term consequences of oil exposure on migratory birds overwintering in this area have received limited attention. The present study aimed to investigate the impact of oil contamination (e.g., polycyclic aromatic hydrocarbons (PAHs)) on the circulating status of prolactin and corticosterone, two hormones that influence reproductive success in birds, in Northern gannets (*Morus bassanus*) breeding on Bonaventure Island, Eastern Canada. Using light-based geolocators, it was found that 23.5% of Northern gannets from Bonaventure Island overwintered in the Gulf of Mexico in 2010–2011; the remainder of this population overwintered along the Atlantic Coast of the United States. PAH concentrations (eight compounds) in gannet blood cells were all found to be under the method limits of quantification, which could be the result of the ability of seabirds to metabolize these compounds and the time elapsed between oil exposure and blood sampling. Corticosterone and prolactin levels as well as body mass did not differ between the two major birds' wintering sites. Moreover, levels of both these hormones did not vary from early to late incubation period. Present results suggest that if Bonaventure Island-breeding Northern gannets had been exposed to oil in the Gulf of Mexico in the aftermath of this historical spill, this exposure could not be associated with changes in hormonal status and body mass in breeding individuals.

1. Introduction

Accidental oil spills are responsible for the introduction of large volumes of crude oil into the marine ecosystem, often causing the death of numerous marine organisms, most of which are seabirds (Castege et al., 2007). Between April 20th and July 15th, 2010, a historically large volume (approximately 780 million liters) of crude oil was spilled into the Gulf of Mexico following the explosion of the Deepwater Horizon drilling platform (Atlas, 2011; BP, 2010a; Camilli et al., 2010; Hagerty and Ramseur, 2010), thus forming an extensive plume off the coasts of Louisiana, Mississippi, and Alabama (BP, 2010b; Hagerty and Ramseur, 2010). Considering that many organisms depend on the marine environment to fulfill their daily energetic needs, the magnitude of the consequence related to the presence of this quantity of oil is undeniable. Seabirds are dependent on this habitat to feed and rest (Nelson, 2002), and are particularly vulnerable to oil spills due to exposure to potentially elevated levels of toxic polycyclic aromatic

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hydrocarbons (PAHs) (Neilson and Hutzinger, 1997; Tricart, 1987; Troisi and Borjesson, 2005). The ingestion of oil residues by preening or via the consumption of contaminated preys can thus cause long-term repercussions on their organism and general health status (Alsop, 2004; Giese et al., 2000; Guéguen et al., 2006; Tricart, 1987). Chronic exposure to sub-lethal concentrations of PAHs can elicit various physiological effects in birds including increased oxidative stress in the liver and kidney, neurological impairments, endocrine disruption, immune suppression, and poorer health condition (Alonso-Alvarez et al., 2007; Balseiro et al., 2005; Chastel et al., 2005; Golet et al., 2002; Neilson, 1963; Troisi and Borjesson, 2005). This can, in turn, have a negative impact on their reproductive success (Alonso-Alvarez et al., 2007; Castege et al., 2007; Heubeck et al., 2003). Nonetheless, very few studies have addressed the sub-lethal physiological effects and ecological consequences of petroleum exposure on breeding birds exposed in their wintering grounds (Heubeck et al., 2003). Studies investigating the long-term impacts of such environmental disasters on migratory birds are thus critically needed as this can potentially have far reaching consequences on their population dynamics.

Reproductive performance of seabirds is tightly associated with their ability to provide adequate parental care to their progeny (Nelson, 2002; Schreiber and Burger, 2002), which is mainly regulated by prolactin (Buntin, 1996; El Halawani and Rozenboin, 1993). Circulating prolactin levels remain in general high in seabirds at the beginning and during most of the incubation period (Buntin, 1996; Lormée et al., 1999, 2000). Levels of this pituitary hormone can be influenced by a number of biological factors such as reproductive status and maturity (age) of the individual (Angelier et al., 2007c, 2006; Chastel et al., 2005). Environmental contaminants including oil components (mainly PAHs) can also alter prolactin levels in birds (Cavanaugh et al., 1983), and thus lead to impairment of reproductive behaviors (e.g., attendance and protection of the nest and incubation) (Cavanaugh et al., 1983; Giese et al., 2000). More specifically, Cavanaugh et al. (1983) have shown that mallard ducks (*Anas platyrhynchos*) dietary-dosed with oil experienced a significant decrease in blood prolactin concentrations during the egg laying and incubation periods through disruption of synthesis and release of this hormone. Other studies have also found reduced plasma levels of prolactin in breeding female ducks fed diet containing crude oil (Cavanaugh et al., 1983; Cavanaugh and Holme, 1987; Harvey and Philips, 1981). Overall, these findings suggest an underlying toxic mechanism of oil exposure affecting prolactin status in birds, which in turn resulted in failure to incubate and successfully reproduce (Ainley et al., 1981; Barrett, 1979).

Corticosterone plays a central role in the energy metabolism of birds, and levels of this glucocorticoid hormone have been shown to slightly increase during reproduction (Chastel et al., 2005; Love et al., 2004; Romero and Remage-Healey, 2000). In fact, the stimulating effect of moderately elevated corticosterone levels on foraging activities of breeding birds (Angelier et al., 2007a; Astheimer et al., 1995) may be necessary for successful reproduction (Love et al., 2004). However, Peakall et al. (1981) showed that an oral dose of 0.1 to 1.0 mL of crude oil or its aromatic fraction caused an important rise in plasma corticosterone levels in herring gulls (*Larus argentatus*). Consistent findings were reported in several species such as common guillemots (*Uria aalge*) impacted by the Exxon Valdez spill (Khan and Ryan, 1991) and magellanic penguins (*Spheniscus magellanicus*) exposed to a spill off the Coast of Patagonia (Fowler et al., 1995). In a few situations, a reduction in corticosterone levels associated with oil exposure was reported to be related to a decreased adrenal response to the adrenocorticotropic hormone (ACTH) due to extensive damage to the inner cortex of the adrenal gland (Rattner et al., 1984). Altered corticosterone status may adversely impact reproductive behavior including territoriality (Wingfield et al., 1998; Wingfield and Sapolsky, 2003), and ultimately also lead to reproduction failure (e.g., nest abandonment) (Love et al., 2004; Silverin, 1986; Wingfield et al., 1998). Repeated years with poor reproductive success due to endocrine system impairment may have deleterious long-term consequences on the population size of long-lived seabird species (Atlas, 2011; Balseiro et al., 2005; Weimerskirch et al., 2003).

The Gulf of Mexico supports a large number of seabirds during the winter including the Northern gannet (*Morus bassanus*) (Clapp et al., 1982; Montevecchi et al., 2011). The Bonaventure Island in the Gulf of St. Lawrence, Eastern Canada (Nelson, 2002), hosts one of the largest colonies of Northern gannets in the world (59,586 breeding pairs in 2009 [Chardine et al., 2013]). Because one quarter of Northern gannets from this colony were shown to migrate annually to the Gulf of Mexico (Montevecchi et al., 2011), the remainder of the population overwintering along the Atlantic Coast of the United States, it can be postulated that these birds were potentially exposed to oil and PAHs via direct ingestion of crude oil and/or the consumption of contaminated prey in the aftermath of the Deepwater Horizon spill. Oil-related exposure of gannets from Bonaventure Island may thus lead to adverse health impacts, and ultimately affect their population dynamics. In fact, the population size of this breeding colony showed slight decrease (13.2%) between 2009 and 2012 (J.-F. Rail; personal communication), which could be attributed, in part, to the 2010 oil spill. The objective of the present study was to investigate whether Northern gannets that overwintered in the Gulf of Mexico in 2010–2011 (potentially oil-exposed) had altered hormonal status (prolactin and corticosterone) compared to birds that migrated along the Atlantic Coast (reference site). We hypothesized that: i) PAHs are found at higher levels in blood of gannets that overwintered in the Gulf of Mexico relative to birds that did so along the Atlantic Coast, and ii) levels of corticosterone are elevated and prolactin decreased in gannets that overwintering in the oil-exposed area compared to Atlantic Coast birds.

2. Materials and methods

2.1. Study area and sample collection

The fieldwork was conducted in 2010 (September 10th to 15th) and 2011 (May 30th to June 14th, and June 28th to July 6th), on Bonaventure Island (48° 30′ 08″ N, 64° 10′ 07″ W) located in the Rocher-Percé-et-de-l'île-Bonaventure National Park (QC, Canada). In September 2010, adult male and female gannets ($n = 58$) were captured randomly using a noose-pole in the peripheral section of the colony prior to the annual migration to the wintering sites. These birds have been monitored since 2008 (M. Guillemette; unpublished data), and thus were all marked with a US Fish and Wildlife Service steel ring. Each bird was equipped with a color-coded plastic band and a light-level geolocator (MK15, British Antarctic Survey, Cambridge, United Kingdom) attached using ty-raps to the steel ring for wintering site determination (latitude ± 200 km and longitude ± 87 km) (Montevecchi et al., 2011). The weight of the light-level geolocator (2.5 g) represented approximately 0.1% of the bird's body mass (Fig. 1). Two geolocators were left on Bonaventure Island for reference during the entire study period (Section 2.2). The following year, the birds were recaptured using the methods described above, and the data loggers were recovered (see below).

Blood samples of gannets were collected twice from the same individuals during the incubation period, that is, in early (May 30th to June 14th, 2011) and late incubation (June 28th to July 6th, 2011), from approximately 10 AM to 4 PM in order to minimize changes of hormone levels related to the daily cycle. A volume of 10–15 mL of blood (corresponding to less than 1% of the Northern gannet's body mass) was obtained from the brachial vein using butterfly needles, 5 mL syringes, and heparinized vacutainer tubes immediately following capture (mean ± SD: 2.44 ± 0.96 min). A drop of blood was smeared on a carton and kept in an envelope for subsequent sexing via DNA analysis. Wing length and body mass were recorded, and the birds were released near their nesting site. Blood samples were kept on ice in a cooler while in the field and were processed in the laboratory within 8 h of collection. In the laboratory, blood samples were

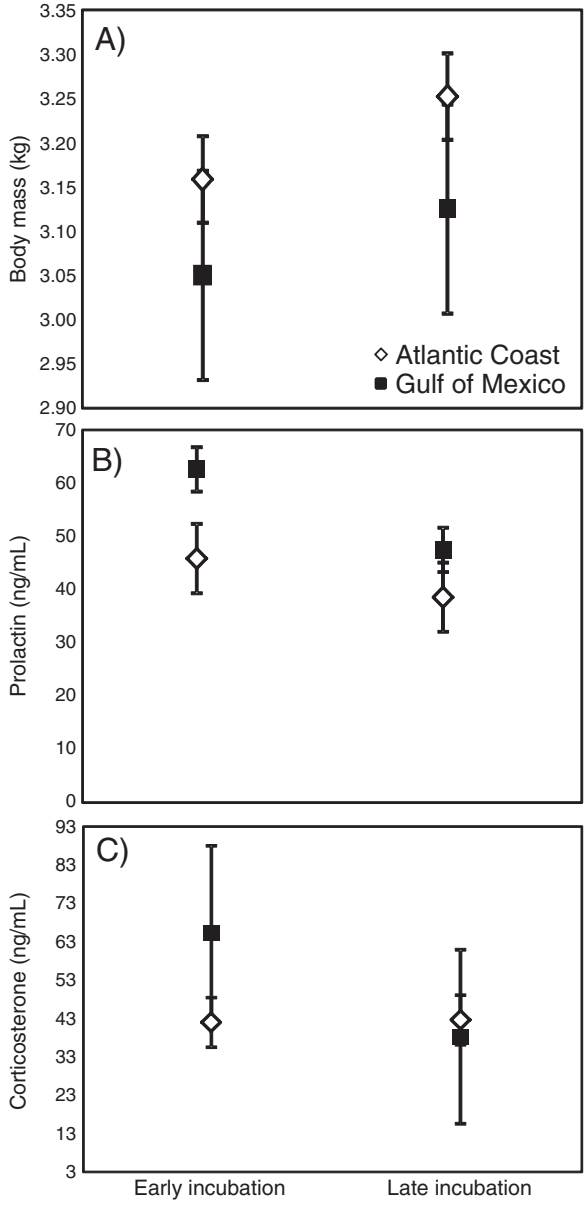

Fig. 1. (A) Mean (±SD) body mass, (B) plasma prolactin levels, and (C) plasma corticosterone levels in Northern gannets during early and late incubation periods categorized by wintering site (Gulf of Mexico and Atlantic Coast).

centrifuged (7 min; 2500 ×*g*), and the resulting plasma was stored in liquid nitrogen for the remainder of the fieldwork season. The plasma was then transferred into a −80 °C freezer until hormone analysis (Sections 2.4 and 2.5). Red blood cells were kept at −20 °C for subsequent chemical analysis (Section 2.3). Bird capture and handling methods were approved by the Institutional Animal Care Committee (ACC) of the Université du Québec à Rimouski, and complied with the guidelines of the Canadian Council on Animal Care (CCAC).

2.2. Telemetry data analysis

Telemetry data were analyzed at the Université du Québec à Rimouski (Rimouski, QC). Briefly, data retrieved from the light-level geolocators included light levels recorded every min and maximal values registered every 10 min. In addition, immersion in water (wet/dry sensor) was verified every 3 s and integrated over 10 min intervals, thereby providing the proportion of time birds spent in water. Light level data were analyzed using TransEdit2 in the BASTrack software (version 18) developed by British Antarctic Survey. Sunset and sunrise times as well as latitude and longitude were determined as described by Phillips et al. (2004). To determine the elevation angle of the sun for each month the difference between the pre- and post-calibration of the units was applied. Preliminary data selection was done according to criteria suggested by Garthe et al. (2007) including the elimination of positions around the equinox (Hill, 1994), elimination of continental positions (farther than 200 km from the North American coast) because non-breeding gannets are exclusively pelagic, and elimination of locations associated with a traveling distance higher than the maximum distance that a gannet can travel in a 24 h period (Garthe et al., 2007). The wintering sites were determined using the Kernel density estimation method (Bächler et al., 2010) with the Geospatial Modelling Environment software (Version 0.6.0.0). Wintering grounds were separated into two areas using ArcGIS 10 (Esri, France): 1) area encompassing the entire Gulf of Mexico, west of the tip of Florida, and 2) the Atlantic Coast, encompassing the south-eastern tip to the north-eastern tip of Florida. Residence time and arrival and departure dates were determined based on wet/dry data using the Kernel method (Bächler et al., 2010). Since spring migration coincided with spring equinox, departure date from the wintering site was determined using fall migration duration and the return date to Bonaventure Island. Residence time in the wintering grounds was calculated as the difference between the date of departure and the arrival to the wintering grounds. In addition, the distance between the bird's main wintering location and the Deepwater Horizon platform (N 28°12′, W 088°48′) was estimated for each bird that wintered in the Gulf of Mexico. However, it should be noted that the calculated distances from the oil-covered area, which was more than 35 km in length (Camilli et al., 2010), represented an approximate estimate as both the plume and the birds were in continuous movement.

2.3. Chemical analysis

Chemical analyses were performed at the Institut des sciences de la mer de Rimouski, Université du Québec à Rimouski (QC, Rimouski). Red blood cell samples were screened for eight PAH compounds: phenanthrene, anthracene, fluoranthene, perylene, pyrene, chrysene, benzo[a]anthracene, and benzo[a]pyrene (Wellington Laboratories, Guelph, ON, Canada) following methods by Yeudakiamau et al. (2010). Briefly, red blood cells (1.0 g) were spiked with 50 μL of the internal standard acenaphthalene and left to equilibrate for 2 min. The red blood cells were then lysed using a 0.1 M sodium chloride solution. The extraction was performed using 2 mL of n-hexane (high performance liquid chromatography (HPLC) grade), and the samples were vortexed for 30 s. The solution was then centrifuged (6 min; 2500 ×*g*) and the supernatant transferred into a glass culture tube. This procedure was repeated three times. The combined extract was then concentrated to 2 mL under a nitrogen flow. Extract clean-up was achieved using solid-phase extraction (SPE) columns (Certified Sep-Pak Alumina N 6 mL Vac, Waters, ON, Canada) conditioned with 2 mL of n-hexane and eluted with 5 mL of dichloromethane. The final cleaned-up fraction was then solvent-exchanged to acetonitrile. Identification and quantification of PAHs were performed using an Accela HPLC (ThermoScientific, MA, USA) coupled to a fluorescence detector (Finnigan Surveyor FL Plus, ThermoScientific, MA, USA). The compounds were separated on a Supelcosil LC-PAH column (25 cm × 3 mm × 5 μm) (Supelco Analytical, PA, USA).

Quality control and assurance procedures included method blanks for each batch of ten samples and standard reference material (SRM 2977 mussel tissue) for every two batches of ten samples. Background contamination was present in method blanks and hence, blank correction was performed for the following compounds: phenanthrene, fluoranthene, perylene, pyrene, and chrysene. Concentrations of PAHs were determined using an external standard method, and were recovery-corrected. The method limits of detection (MLODs) and the method limits of

quantification (MLOQs) were determined by using the lowest concentration of the external standards producing a signal for all compounds analyzed. MLOQs (defined as a minimum amount of analyte producing a peak with a signal-to-noise ratio (S/N) of 10 and MLODs (defined as S/N = 3) can be found in Table S1 of the Supporting information section.

2.4. Prolactin analysis

Analysis of prolactin in Northern gannet plasma was performed at the Centre d'Études Biologiques de Chizé, Centre National de la Recherche Scientifique (Villiers en Bois, Deux-Sèvres, France) using a heterologous radioimmunoassay (RIA) based on the methods described by Cherel et al. (1994), and validated for several seabird species (e.g., Angelier et al., 2007b; Angelier et al., 2006; Lormée et al., 2000; Verreault et al., 2008). Pooled plasma samples of Northern gannets produced a dose–response curve that paralleled a chicken prolactin standard curve indicating that this RIA was appropriate to determine prolactin levels in this species. Only one assay was performed; the intra-assay coefficient of variation was 8.4% (n = 3 replicates).

2.5. Corticosterone analysis

Plasma samples of Northern gannets were analyzed for corticosterone levels at the Université du Québec à Montréal (Montreal, QC) using a commercially available double antibody RIA (ImmuChem Double Antibody Corticosterone I^{125}kit, MP Biomedicals, Orangeburg, NY, USA) designed for mice and rats, but validated for birds (Troisi et al., 2006; Verboven et al., 2010; Washburn et al., 2002). The analytical procedure of the kit was followed with a minor modification, that is, a number of plasma samples were diluted (1:4) such that values would fall within the mid-portion of the standard curve. Samples were run in four assays; the coefficient of inter-assay variation was 7.24% (n = 3 replicates).

2.6. Data treatment

Differences in body mass as well as plasma prolactin and corticosterone levels in Northern gannets between wintering sites (Gulf of Mexico and Atlantic Coast) were tested using analysis of variance (ANOVA), followed by the Student's t post-hoc test, while paired t-tests were used to test differences between early and late incubation (controlled for wintering sites). Residuals of all variables followed the normal distribution with the exception of corticosterone levels, which were log-transformed to achieve the normal distribution. All statistical analyses were carried out using the statistical package JMP 10 (SAS, Cary, NC, USA) and results with $p \leq 0.05$ were considered significant.

3. Results

3.1. Wintering site determination

Among the 58 light-level geolocators that were deployed on Northern gannets in September 2010, 40 were recovered the following year (May–June 2011). Among the 18 light-level geolocators that were not recovered, four had fallen off the birds while the remaining 14 units were on birds that were either not recaptured or not sighted in the colony. Data could not be retrieved from six defective geolocators, thus resulting in a total of 34 birds for analysis.

Analysis of the light-level geolocator data indicated that most of the Northern gannets overwintered along the Atlantic Coast (n = 26), while 23.5% overwintered in the Gulf of Mexico (n = 8). Northern gannets that overwintered in the Gulf of Mexico concentrated their foraging activities at 298 ± 167 km on average from the Deepwater Horizon oil spill site (N 28°12′, W 088°48′). Arrival dates of gannets in the Gulf of Mexico ranged from November 11th to December 23rd, 2010, and the departure dates ranged from January 29th to March 17th, 2011. Arrival dates of birds wintering along the Atlantic Coast ranged from October 25th to November 27th, 2010, while departure dates ranged from March 2nd to April 16th, 2011. The mean residence time of birds wintering in the Gulf of Mexico was significantly shorter ($F_{1,24} = 26.02$; $p = 0.0002$) compared to birds wintering along the Atlantic Coast (83.4 and 138.2 days, respectively). Gannets also arrived later to the Gulf of Mexico ($F_{1,24} = 32.1$; $p < 0.0001$) and left this wintering site before birds from the Atlantic Coast ($F_{1,24} = 21.59$; $p = 0.0001$).

3.2. PAH concentrations

PAH compounds monitored in Northern gannet red blood cells were all found to be under the MLODs and MLOQs after blank-correction. MLODs varied between 0.03 and 2.00 ng/mL, while MLOQs varied from 0.09 to 6.67 ng/mL (Table S1).

3.3. Prolactin levels

Prolactin levels in plasma of gannets were not different between males and females early in the incubation period for birds from the Atlantic Coast ($F_{1,18} = 1.14$; $p = 0.30$), although males had lower concentrations than females in late incubation ($F_{1,14} = 5.35$; $p = 0.04$). Sample size for the Gulf of Mexico was too small to test the influence of sex. Birds from the Gulf of Mexico exhibited higher plasma prolactin levels early in incubation compared to birds arriving from the Atlantic Coast ($F_{1,24} = 4.70$; $p = 0.04$) (Fig. 1). In contrast, there was no difference in prolactin levels between birds from these two wintering sites late in the incubation ($F_{1,20} = 1.57$; $p = 0.22$). For the Atlantic Coast birds, prolactin concentrations tended to decrease from early to late incubation (paired t-test $_{1,15} = -1.74$; $p = 0.10$). This tendency was also observed in birds that overwintered in the Gulf of Mexico (paired t-test $_{1,5} = -2.32$; $p = 0.07$). When considering the sex of the birds, a difference across the incubation period was only found in males, and showed a significant decrease in prolactin concentrations from early to late incubation (male: paired t-test $_{1,15} = -3.27$; $p = 0.005$; female: paired t-test $_{1,5} = -0.07$; $p = 0.95$).

3.4. Corticosterone levels

Plasma corticosterone levels in gannets were not different between early and late incubation between males (paired t-test $_{1,17} = 0.59$; $p = 0.56$) and females (paired t-test $_{1,6} = -0.59$; $p = 0.58$). Concentrations of this glucocorticoid in birds from the Atlantic Coast were also not significantly different between males and females early ($F_{1,18} = 0.86$; $p = 0.37$) and late in the incubation period ($F_{1,18} = 0.36$; $p = 0.56$). When comparing the two wintering sites (Fig. 1), no difference was detected neither in early ($F_{1,23} = 2.02$; $p = 0.17$), nor in late incubation period ($F_{1,23} = 0.28$; $p = 0.60$) between birds from the Gulf of Mexico (n = 5) and the Atlantic Coast (n = 20) (Fig. 1). Moreover, corticosterone concentrations did not vary significantly between early and late incubation in birds from both the Atlantic Coast (paired t-test $_{1,19} = -0.55$; $p = 0.59$) and the Gulf of Mexico (paired t-test $_{1,4} = 1.32$; $p = 0.26$).

3.5. Body mass

No difference in body mass was observed between males and females for birds from the Atlantic Coast for both periods in the incubation (early: $F_{1,13} = 0.05$; $p = 0.82$; late: $F_{1,12} = 0.04$; $p = 0.84$). However, this variable could not be tested statistically for birds from the Gulf of Mexico due to low sample size. Body mass in combined males and females was not significantly different between gannets arriving from the Gulf of Mexico and the Atlantic Coast early ($F_{1,15} = 0.48$; $p = 0.50$) or late ($F_{1,15} = 0.54$; $p = 0.47$) in the incubation period. Birds that overwintered along the Atlantic Coast tended to have a lower body mass

in early incubation than in late incubation (paired t-test $_{1,11} = 1.93$; $p = 0.08$). However, this tendency was not observed in birds from the Gulf of Mexico (paired t-test $_{1,2} = 0.63$; $p = 0.59$) (Fig. 1).

4. Discussion

4.1. Wintering site, population trends, and reproductive success

This study showed that 23.5% of the breeding Northern gannet subpopulation forming our sample overwintered in the Gulf of Mexico in 2010–2011, while the remainder overwintered along the Atlantic Coast of the United States (mainly Florida). This migration pattern was consistent with results recently reported by Montevecchi et al. (2011) who estimated that approximately one quarter of Northern gannets from North America spend the winter in the Gulf of Mexico area. This suggests that roughly 24,570 adult gannets from Bonaventure Island overwintered in the Gulf of Mexico from mid-November 2010 through mid-March 2011. Because 14 light-level geolocators were not recovered (i.e., birds not sighted in the colony), this may further suggest that 25,200 adult gannets did not return to Bonaventure Island in 2011 (estimated return rate: 75.9%). In 2012, the return rate estimated from 38 deployed geolocators was 81.6% (M. Guillemette; unpublished data), which represents 5.7% more than in 2011. Unfortunately, since the fate of these 14 birds was unknown, the reasons behind this lower return rate compared to 2012 remain unexplained. In fact, a number of ecological and environmental factors have been shown to influence adult survival in seabirds such as climate (Sandvik et al., 2005; Votier et al., 2005), food availability (Furness and Camphuysen, 1997; Votier et al., 2005), and oil exposure (Castege et al., 2007). Therefore, the Deepwater Horizon spill-related petroleum exposure in the Gulf of Mexico could have accounted for an as yet undetermined number of adult gannet deaths breeding in this colony.

The population of gannets on Bonaventure Island has decreased from 59,586 ± 1788 breeding pairs in 2009 (Chardine et al., 2013) to 51,725 ± 1552 in 2012, which represented an overall breeding population decline of 13.2% during those four years (J.-F. Rail; personal communication). Furthermore, a survey undertaken in this breeding population in July 2010, which is considered the pre-oiling scenario since the birds had already departed from the Gulf of Mexico when the oil spill took place, reported 52,277 ± 1568 breeding pairs. In July 2011, the number of gannets reached the lowest count recorded in this colony during 2009–2012 (47,744 ± 1432 breeding pairs), which corresponded to an 8.9% decline relative to 2010 (J.-F. Rail; personal communication). Reproductive success of Northern gannets from Bonaventure Island has also been monitored since 2008 (M. Guillemette; unpublished data). For all birds monitored, regardless of their wintering sites, reproductive success in 2011 indicated that breeding started later than usual that year. Moreover, the number of empty nests was higher and there was a very low hatching success in general (M. Guillemette; unpublished data). This indicated that 2011 was a particularly poor recruitment year for the Northern gannet population from Bonaventure Island.

4.2. PAH levels in gannets

The turnover (half-life) of red blood cells has been estimated to be 4–5 weeks in higher vertebrates (Clark, 1988). Therefore, the occurrence of PAHs in this tissue indicates a relatively short-term accumulation during the process of erythropoiesis. However, all screened PAHs in gannet red blood cells were under the detection limits in birds that overwintered in the Gulf of Mexico and the Atlantic Coast. Considering the large reservoir of PAHs present in the Gulf of Mexico in the aftermath of the oil spill, PAH detection was expected in oil-exposed gannets arriving from this wintering site (Pereira et al., 2008; Pérez et al., 2008; Troisi and Borjesson, 2005). This absence of quantifiable PAH concentrations in gannet red blood cells may not necessarily be the result of a lack of exposure to these compounds in the Gulf of Mexico, but may be related to the (high) biotransformation and elimination capacity of gannets for PAH compounds (Malcolm and Shore, 2003). In fact, hepatic cytochrome P450 (CYP) isoenzymes are involved in the biotransformation of PAHs via epoxide hydroxylation, which leads to the formation of reactive metabolites that are conjugated to readily excretable hydrophilic molecules (Guéguen et al., 2006; Hodgson, 2004; Lauwerys et al., 2007). The efficient metabolism of PAHs can therefore accentuate the difficulty related to the detection of PAH contamination in seabirds sampled several weeks post-exposure, which can also explain the scarcity of PAH data in petroleum-exposed birds (Hall and Coon, 1988; Varanasi et al., 1989). It has been suggetsed that measuring oil-related contaminants in birds should be combined to other analyses such as metabolite bile burden or the induction of CYP isoenzymes (Troisi et al., 2006; Trust et al., 2000). However, these analyses require bird sacrifice, which could not be considered in the present study as Bonaventure Island is a migratory bird sanctuary devoted to the protection of seabirds including the Northern gannet (Rail, 2009).

4.3. Hormonal status and parental behavior

High prolactin levels are generally found in breeding seabirds at the beginning and during most of the incubation period, and decrease gradually after hatching in most altricial birds including the gannet (Lormée et al., 1999, 2000). Despite that male Northern gannets were found to initiate the incubation period with similar plasma prolactin concentrations than females, these levels significantly decreased from early to late incubation in males, but not in females. For altricial birds, prolactin in incubating males usually follows the same pattern as females to promote parental care (Lormée et al., 1999; Schoech et al., 1996). Nonetheless, in the present study, females exhibited higher levels of plasma prolactin than males, which could be associated to a difference in parental care investment between sexes later in the incubation (Lormée et al., 2000). In gannets arriving from both wintering sites, the levels of prolactin tended to decrease from early to late incubation, but not significantly. Prolactin has been shown to be altered by environmental contaminants, including oil components, by decreasing circulating levels in breeding little penguins (Giese et al., 2000), magellanic penguins (Fowler et al., 1995), and mallard ducks (Cavanaugh et al., 1983). Hence, variations of prolactin levels in birds that overwintered in potentially oil-contaminated areas of the Gulf of Mexico could not be related to oil exposure as, oppositely, levels of this hormone were higher compared to birds from the Atlantic Coast early in the incubation. Many natural factors can influence prolactin levels in birds including the breeding experience of the individual (Angelier et al., 2006, 2007c; Chastel et al., 2005), which may explain this lack of linkage between wintering site and prolactin variation.

Corticosterone levels were found to be similar when compared between the bird's wintering site, period in the incubation, and sex. However, birds from the Gulf of Mexico showed higher corticosterone levels early in the incubation, though not significantly different from those of birds from the Atlantic Coast. Some studies have shown that corticosterone levels were slightly increased during the reproduction period in breeding red-footed Bobbies (Lormée et al., 2005), in European starlings (Love et al., 2004), northern mockingbirds (Romero and Remage-Healey, 2000), and captive starlings (Logan and Wingfield, 1995). This increase in corticosterone has been associated with modulation of breeding behavior (Siegel, 1980; Wingfield et al., 1992) and an increase in foraging activity due to a greater effort imposed by parental care (Astheimer et al., 1992; Holberton et al., 1996; Wingfield and Silverin, 1986). However, several studies suggested that ingestion of crude oil or its aromatic fractions can induce a significant rise in plasma corticosterone levels, for example, in magellanic penguins following a spill along the Coast of Patagonia (Fowler et al., 1995), common guillemots exposed to the Exxon Valdez spill (Khan and Ryan, 1991), and orally-dosed herring gulls (Peakall et al., 1981). The consistency in

corticosterone levels detected in present Northern gannet subpopulation indicated that no sign of abnormal stress potentially induced by oil contaminants before migration could be observed during the breeding season.

4.4. Body mass variation

Body mass of gannets did not differ between birds arriving to Bonaventure Island from the two wintering sites. Results of the present study was thus not representative of an oiling scenario as reported, for example, in a study of pigeon guillemots in which breeding adult body mass and body condition were significantly lower at oiled sites post-spill compared to pre-spill (Golet et al., 2002). Similarly, the body mass of birds arriving from the Gulf of Mexico was constant throughout the incubation period (early vs. late incubation). This could be explained by the fact that body mass generally is maintained throughout the incubation period in seabirds with shared incubation bouts (Moreno, 1989). However, for birds that overwintered along the Atlantic Coast, body mass early in the incubation tended to be slightly lower (although not significantly) than late in the incubation period.

5. Conclusions

To our knowledge, this is the first study that used geolocation in an oil spill context to identify long-term physiological effects of oil exposure in a long-lived migratory bird. However, comparisons in blood PAH, prolactin and corticosterone levels, as well as body mass between Northern gannets that overwintered in the oil-contaminated Gulf of Mexico and the Atlantic Coast of the United States did not allow confirming exposure-related effects in this long range migrant. However, the preoccupying 8.9% decrease in breeding population size of gannets reported in this colony between 2010 and 2011 (J.-F. Rail; personal communication) could be tentatively attributed to the Deepwater Horizon oil spill considering that gannets were among the most impacted seabirds recorded in this area during this historical spill event (Montevecchi et al., 2011). Nevertheless, the combination of migration route tracking, survival rate monitoring, and hormonal measurements may represent a promising approach to evaluate chronic effects of oil and other contaminant exposure in migratory birds. Because of ethical considerations, sampling of gannets from Bonaventure Island was limited to blood collection, and this represented a limitation in our ability to assess health status of gannets that wintered in the Gulf of Mexico as low exposure to oil components may elicit toxicity in internal organs (e.g., DNA adduct formation in liver [Lyons et al., 1997; Nagy et al., 2004]). Furthermore, present study could not ascertain that birds overwintering along the Atlantic Coast (selected as a reference site) had been unexposed to PAHs as intentional or accidental oil spills by commercial ships (or any other sources) commonly occur in this region and elsewhere.

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