

Relationships between isotopic ratios, body condition and breeding success in a High Arctic seabird community

Johanna EH Hovinen^{1,*}, Arnaud Tarroux^{1,2,*}, Francisco Ramírez³, Manuela Forero⁴, Sébastien Descamps^{1*, \$}

Running page head: Seabird breeding success and isotopic ratios

* Authors contributed equally

¹Norwegian Polar Institute, Fram Centre, 9296 Tromsø, Norway

²Norwegian Institute for Nature Research, Fram Centre, 9296 Tromsø, Norway

³Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Universitat de Barcelona, 08028 Barcelona, Catalonia, Spain

⁴Estación Biológica de Doñana CSIC, Seville 41092, Spain

^{\$}Corresponding author:

Sébastien Descamps

sebastien.descamps@npolar.no

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ABSTRACT: Predators such as seabirds are often used as bio-indicators of the marine environment. This is based on the assumption that changes in seabird populations are driven by changes in their prey. We tested this assumption in a High Arctic seabird community by assessing the relationships between the diet, body condition and breeding performance of four ecologically different species: the little auk *Alle alle*, black-legged kittiwake *Rissa tridactyla*, Brünnich's guillemot *Uria lomvia*, and glaucous gull *Larus hyperboreus*, breeding in Svalbard. Interannual changes in seabird diet (2009-2015) were assessed by estimating their carbon and nitrogen isotopic ratios ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) during the breeding and non-breeding seasons (i.e. using blood and feather tissues). We found interannual variation in the isotopic ratios during both seasons in all four species. These variations differed among species, thus suggesting dietary changes, instead of changes in isotopic baselines, as the most plausible mechanism underlying such patterns. We also found that seabirds had a lower average hatching success when the average $\delta^{15}\text{N}$ during the previous non-breeding season was higher. Our results suggest that changes in the average prey composition during the non-breeding season may partially explain changes in breeding performance of Svalbard seabirds.

KEY WORDS: carbon, carry-over effects, diet, marine birds, nitrogen, reproductive output, stable isotopes, Svalbard, trophic level

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1. INTRODUCTION

Food abundance and quality are key determinants of animal demography and population dynamics (Martin 1987, Zera & Harshman 2001, Ruffino et al. 2014, Louzao et al. 2015). Poor food availability or quality generally results in reduced breeding outcomes across species (e.g. snails, Martone & Micheli 2012; reindeers, Ballesteros et al. 2013; swallows, Winkler et al. 2014; water fleas, Choi et al. 2016). However, in many trophic systems, and especially in marine food webs, changes in resource availability are very difficult to monitor due to the dynamic nature of primary and secondary production at large spatial scales (Nicol et al. 2000, Perry et al. 2010, Afán et al. 2015). The breeding performance of high-trophic level predators may respond to changes in the structure and function of an ecosystem, including the availability of the resources on which they rely (e.g. Furness & Camphuysen 1997, Thompson & Ollason 2001, Piatt et al. 2007, Parsons et al. 2008). This has led to the concept of bio-indicator species, which has been widely applied to seabirds (Bost & Le Maho 1993, Durant et al. 2009, Fort et al. 2016). However, this concept does not always apply (Piatt et al. 2007) and relationships between food and reproduction may be more complicated than expected. Indeed, breeding performance *per se* may not be sufficient to infer changes in resource availability (Gremillet & Charmantier 2010), as predators may compensate for poor resource availability by increasing foraging effort, or by switching prey type or foraging area (e.g. Furness & Camphuysen 1997, Schwemmer & Garthe 2008, Erikstad et al. 2009). Thus, data on diet composition should also be incorporated to detect such changes.

The analysis of naturally occurring stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) constitutes an integrative tool that can be used to estimate the trophic niche (i.e. the portion of the ecological niche that describes the food resources and foraging habitat of a

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given consumer (Hobson & Bond 2012, Cherel et al. 2014, Swanson et al. 2015). The isotopic niche projects the n-dimensional trophic niche onto a reduced number of axes, e.g. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, and can be interpreted as an n-dimensional simplification of, and thus a proxy for, the trophic niche (Newsome et al. 2007). In the marine environment, a natural inshore-offshore gradient in $\delta^{13}\text{C}$ may be used to identify the foraging area of marine predators (lower values often indicating more offshore foraging, but see Saupe et al. 1989, Dunton et al. 2006), while $\delta^{15}\text{N}$ varies according to trophic position (higher values indicate higher trophic position, Newsome et al. 2007, Hussey et al. 2014). Stable isotopes integrate dietary information over different time scales depending on the tissue type (Bearhop et al. 2004, Newsome et al. 2007). Isotopic ratios from blood provide information for a period of two weeks to one month preceding the sampling event (Bearhop et al. 2002, Ogden et al. 2004), whereas isotopic ratios from body feathers reflect the diet of an individual during the period of feather growth (which can take place several months before the actual sampling event, Hobson & Bond 2012). Thus, by sampling different tissues, a consumer's isotopic ratios may provide insight into its foraging ecology at varying temporal scales.

Here, we tested whether interannual changes in the isotopic ratios were associated with variation in the body condition and breeding success of a High Arctic seabird community. We considered four seabird species breeding in Svalbard, Norway: the little auk *Alle alle*, black-legged kittiwake *Rissa tridactyla*, Brünnich's guillemot *Uria lomvia*, and glaucous gull *Larus hyperboreus*. These species are characterized by different foraging and feeding habits (see details in Materials and Methods and Wold et al. 2011). The Arctic in general, and the Svalbard Archipelago in particular, are experiencing rapid and directional environmental changes (Nordli et al. 2014, Laidre et al. 2015, Descamps et al. 2017a), with changes in seabirds' diet and foraging habits already documented (Vihtakari et al. 2018b). This area

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provides us with a unique opportunity to investigate how potential changes in seabird diet can affect their condition and breeding performance.

First, we assessed interannual changes in carbon and nitrogen isotopic ratios during the breeding and non-breeding seasons using seven years of data (2009-2015). We considered isotopic ratios from blood and feather samples to be representative of the average diet during part of the breeding and non-breeding seasons, respectively. Second, we tested the hypothesis that variation in seabird body condition and breeding performance can be explained by inter-annual changes in their isotopic ratios during the breeding and non-breeding seasons. Diet during the non-breeding season may potentially affect breeding performance indirectly through carry-over effects on individual body condition (e.g. Sorensen et al. 2009, Kouwenberg et al. 2013, Salton et al. 2015), whereas diet during the breeding season may influence breeding performance both directly via chick provisioning (Martin 1987) and indirectly through an effect on parent body condition, which could translate into lower feeding activity.

2. MATERIALS AND METHODS

2.1. Study sites and species

The study took place during seven consecutive years (2009-2015) at four breeding sites in west Spitsbergen, Svalbard (Fig. 1), during incubation and chick-rearing, from mid June to late July (little auks, black-legged kittiwakes and Brünnich's guillemots) and from late May to late June (glaucous gulls). Little auks and black-legged kittiwakes were caught in Isfjorden (Bjørndalen; 78°24'N 15°34'E, and Grumantbyen; 78°17'N 15°10'E, respectively), Brünnich's guillemots at the Ossian Sarsfjellet colony in Kongsfjorden (78°93'N 12°44'E), and glaucous gulls at various locations in the Kongsfjorden area. However, not all species

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were caught in all seven years of study (*Supplementary Material 1, Table S1*). Maximum foraging distance to the breeding site ranges from <20 km in guillemots (Ramírez et al. 2017) to ca. 200-300 km in little auks (Jakubas et al. 2016) and kittiwakes (Goutte et al. 2014). No movement data were available for glaucous gulls, but they likely forage most of the time within fjords (S. Descamps pers. obs.). Spitsbergen guillemots spend the winter north of Iceland and in southwest Greenland (Frederiksen et al. 2016), little auks in the Greenland Sea (Fort et al. 2013), kittiwakes on the Great Banks, east of Canada (Frederiksen et al. 2012), and glaucous gulls disperse widely over most of the northeast Atlantic (B. Moe pers. comm.).

The little auk is a colonial alcid, which lays a single egg in rocky crevices in talus slopes (Stempniewicz 1981), and preferentially forages on high-lipid copepods associated with Arctic waters (Harding et al. 2009, Jakubas et al. 2012), especially *Calanus glacialis*, which represents >80 % of the chick diet in Bjørndalen (Hovinen et al. 2014). Black-legged kittiwakes are colonial cliff-breeders that typically lay 1 or 2 eggs in Svalbard (Strøm 2006). They feed mostly on fish, crustaceans and other marine invertebrates (Reiertsen et al. 2014, Vihtakari et al. 2018a). Brünnich's guillemots are colonial cliff-breeders, and lay a single egg. Their diet consists mainly of fish and crustaceans (Anker-Nilssen et al. 2000). Glaucous gulls breed in or close to other seabird colonies, often on an elevated point at the top of a cliff or on rocks beneath the colony, and lay one to three eggs (Strøm 2006). Gulls are generalist feeders and their diet consists of a wide variety of prey from both marine and terrestrial food webs: fish, mollusks, crustaceans, insects, offal, and eggs, chicks and adults of other seabird species (Anker-Nilssen et al. 2000). Black-legged kittiwakes and glaucous gulls are surface feeders, while little auks and Brünnich's guillemots are divers. In all of our study species, females and males share the incubation and chick-rearing duties, and they molt their chest feathers during the non-breeding season (Dwight 1925, Gaston & Jones 1998, Coulson 2011). The molt

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pattern is not always known in detail but there is typically a partial molt of body feathers during the pre-breeding season (Dwight Jr 1901, Gaston & Jones 1998) and chest feathers of our four study species are therefore expected to have grown during this period (spring).

2.2. Bird captures

Birds were caught with a noose-carpet (little auks), a noose pole (black-legged kittiwakes and Brünnich's guillemots), or an air-propelled net or a noose triggered at a distance (glaucous gulls). All captured birds were marked with a combination of a stainless steel ring and plastic color ring(s). Birds were captured and sampled for feathers and blood only once annually during the breeding season (June-July). The annual number of individuals caught averaged 15 ± 2 SD for little auks, 15 ± 8 SD for kittiwakes, 14 ± 7 SD for guillemots, and 18 ± 4 SD for glaucous gulls. A total of 4 little auks, 21 kittiwakes, 13 guillemots, and 1 glaucous gull were sampled more than once for stable isotopes during the study period (average number of replicates and their range: 2.3 [2, 3] for little auks, 2.4 [2, 4] for guillemots, 3.3 [2, 5] for kittiwakes, and 2 replicates for one glaucous gull). Birds were weighed using a Pesola scale (± 1 g for little auks, ± 5 g for kittiwakes and guillemots and ± 10 g for glaucous gulls) and the length of their wing (i.e. length of the longest primaries) was measured with a wing rule (to the nearest mm). We defined bird body condition as the residual from a linear regression of individual body mass on individual capture date (in Julian days) and wing length (a proxy of body size, Jakob et al. 1996, Schulte-Hostedde et al. 2005, *Supplementary Material 2, Fig. SI*).

Feather and blood samples were collected for analyses of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Blood samples (0.2-0.5 ml) were collected from the brachial vein and stored in 70% ethanol, or frozen in Eppendorf tubes (-20°C ; kittiwake blood only), until preparation for stable isotope

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analyses (70% ethanol does not alter the isotopic composition of tissues, Hobson et al. 1997). Five feathers were taken randomly from the chest (or from the head; little auk feathers in 2009 and 2011) and stored in sealed plastic bags. Little auk chest and head feathers had similar isotopic ratios (Wilcoxon rank sum test; carbon: $W = 310.5$, $P = 0.63$; nitrogen: $W = 338.5$, $P = 0.99$; compared when both feather types were collected in 2013 and 2014 from 27 individuals in total), and thus, the feather type used to infer the little auk's diet should not influence the interpretation of isotopic data.

2.3.Nest surveys

Nests were located and marked during the incubation period and monitored every 2-4 days from early/mid-incubation until hatching (glaucous gulls) or until the mid-chick rearing period (little auks, kittiwakes and guillemots) to estimate hatching success and chick survival until 15 days of age. The chick rearing period averages 27-30 days for little auks, 35-49 days for black-legged kittiwakes, and 16-30 days for Brünnich's guillemots (i.e. chicks leave the colony with one parent at 16-30 days of age but stay under one parent's supervision for another four weeks at least, del Hoyo et al. 1996). Our nest survey thus allowed us to estimate the egg and early chick survival for little auks, kittiwakes and guillemots. Monitoring stopped at hatching for glaucous gulls and only hatching success was available to assess the breeding performance of glaucous gulls.

Light-burrow scopes (Moritex Europe Ltd, Cambridge, UK; little auks only) or direct observations (other species) were used to determine the presence of egg(s) or chick(s) in the nest. The annual number of nests monitored averaged 34 ± 8 SD for little auks, 47 ± 11 SD for black-legged kittiwakes, 52 ± 11 SD for Brünnich's guillemots, and 36 ± 11 SD for glaucous gulls.

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2.4. Stable isotope analyses

Whole blood was used in the analyses, except in little auks (2011), guillemots (2010), and kittiwakes (2009-2015), for which the red blood cells (RBCs) were analyzed. Because whole blood is made up primarily of RBCs (in terms of dry mass, upon which isotopic measurements are made), we assumed that whole blood and RBCs have similar isotopic ratios. Removing these years (little auk data from 2011 and guillemot data from 2010) from the analyses did not change our results (*Supplementary Material 3, Table S4*).

Lipid content in tissues can strongly bias $\delta^{13}\text{C}$ measurements (Post et al. 2007) and therefore, their interpretation in trophic studies (Tarroux et al. 2010). Thus, feathers were washed in a 2:1 chloroform:methanol solution to remove surface lipids and were cut into small pieces with fine scissors before encapsulation. Because there can be a strong inter-feather variation in isotopic ratios (Jaeger et al. 2009), all feathers collected from the same individual in a given season were pooled together and feather pieces homogenized before proceeding with encapsulations. All blood samples (RBC and whole blood) included in the analyses had C/N ratios <3.9 , and thus there was no need to extract lipids (*Supplementary Material 1, Table S1*, Logan et al. 2008). The $\delta^{13}\text{C}$ values of feather samples for which the lipid removal was deemed incomplete, based on their C/N ratios being ≥ 3.9 , were excluded from further analyses ($N = 42$ out of 281 samples). Their $\delta^{15}\text{N}$ were maintained in the analyses as nitrogen isotopic ratios are only marginally affected by lipid concentration (Tarroux et al. 2010).

Each sample (0.7 mg) was encapsulated before combustion in a Flash HT Plus elemental analyzer coupled to a Delta-V Advantage isotope ratio mass spectrometer via a CONFLO IV interface (Thermo Fisher Scientific, Bremen, Germany). All analyses were run

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at the Stable Isotopes Laboratory (LIE) at the Doñana Biological Station, Seville, Spain. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are expressed in ‰ of the deviation from isotopic ratios of international standards, i.e. Pee Dee Belemnite carbonate (PDB) for carbon and atmospheric air (AIR) for nitrogen (DeNiro & Epstein 1978). The following internal standards were used, once calibrated with international standards supplied by the International Atomic Energy Agency (IAEA, Vienna): EBD-23 (cow horn), LIE-BB (whale baleen), and LIE-PA (bird feathers). Replicate assays of standards routinely inserted within the sampling sequence indicated analytical measurement errors of $\pm 0.1\text{‰}$ and $\pm 0.2\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Consumer-prey discrimination factors were assumed to be similar for all seabird species. In addition, we did not compare the isotopic ratios among tissues and all isotopic values presented throughout are thus uncorrected values.

Individuals were sampled only once during the breeding season at different time periods (most of them being sampled during chick-rearing). Previous studies found significant individual specialization in the diet of little auks, Brünnich's guillemots, black-legged kittiwakes and glaucous gulls (Bustnes et al. 2000, Woo et al. 2008, Ceia & Ramos 2015, Bond et al. 2016), which is also confirmed by our own stable isotope data for Svalbard kittiwakes (see *Supplementary material 4, Fig. S2*). Such individual specialization supports the assumption that our single measures of individual isotopic ratios per individual during a breeding or non-breeding season are a good proxy of their diet.

2.5. Statistical analyses

All data processing and statistical analyses were performed in R.3.2.4 (R Core Team 2016). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ during the breeding season ($\delta^{13}\text{C}_{\text{breeding}}$ and $\delta^{15}\text{N}_{\text{breeding}}$) were adjusted for the sampling date to remove the intra-seasonal variation in these two variables during the

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breeding season (*Supplementary Material 5, Figs. S3-S5*) and the residuals were used in all models described below.

Interannual variation in isotopic ratios, body condition and reproductive performance

To test for interannual variation in $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and body condition during the breeding and non-breeding seasons for each species, we ran generalized linear mixed-effect models using individual-level data (GLMM, with an identity link function and Gaussian error distribution) with year, species and their interaction as fixed effects and bird identity as a random factor (to take into account non-independence in repeated measurements on the same individuals). We ran separate GLMMs for breeding (blood isotopic ratios) and non-breeding seasons (feather isotopic ratios) using the function *lmer* in the package “lme4” (Bates et al. 2011). To test for interannual differences in reproductive performance (hatching success and chick survival), we ran linear models using one randomly selected year per nest (among all years in which the nest was monitored) because mixed models including the nest as a random factor could not converge. The hatching success represents the probability of hatching at least one chick while the chick survival represents the probability of keeping at least one chick alive until 15 days of age.

We performed model selection with the Akaike Information Criterion (AIC). If the difference in AIC (or AIC_C, the AIC adjusted for small samples) values between two models was <2, we considered the models to have equal statistical support and in the case of nested models, the simplest was preferred (Burnham & Anderson 2002).

Relationships between changes in isotopic ratios, body condition and breeding performance

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We tested for the effect of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (during the breeding and non-breeding seasons) on seabird body condition, hatching success and chick survival by running GLMs (with an identity link function and Gaussian error distribution) for the breeding and non-breeding seasons separately, using the mean annual. We included the species as a covariate. The best model was selected using the AIC following the procedure described above. We did not test for these relationships using individual level data because most birds sampled for blood and feathers were captured late in the season (during chick-rearing) and were thus mostly successful breeders. As a consequence, the breeding success of these sampled birds overestimated the average breeding success in each colony. Therefore, we considered the average annual hatching success and chick survival based on all nests monitored within each colony (see details above).

All data are available in *Supplementary Material 1 (Tables S1-S3)*.

3. RESULTS

Isotopic ratios of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ during the breeding and non-breeding season varied among years and these variations were generally not parallel among species (i.e. the interaction between year and species was selected for all variables considered with a $\Delta\text{AIC} > 2$ compared to the null model or model with year only; Table 1; *Supplementary Material 6, Fig. S6*). Only values of $\delta^{13}\text{C}$ during the non-breeding season indicated potential parallel variation among species (i.e. equivalent statistical support for the additive and interactive effect, Table 1; *Supplementary Material 6, Fig. S6*). However, the amplitude of these interannual variations was limited (Fig. 2). The body condition of the four species considered did not vary among years (Table 1; *Supplementary Material 6, Fig. S6*) while the hatching success and chick

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survival varied among years and not in parallel among species (Table 1; *Supplementary Material 6, Fig. S6*).

Interannual variations in $\delta^{13}\text{C}$ during both the breeding and non-breeding seasons and interannual variation in $\delta^{15}\text{N}$ during the breeding season were not related to Svalbard seabird body condition in our Svalbard seabird study system (Table 2). However, we found a negative relationship between the interannual variation in $\delta^{15}\text{N}_{\text{non breeding}}$ and the average seabird hatching success (slope of 0.59 ± 0.20 SE; Table 2; Fig. 3). Interannual variation in $\delta^{15}\text{N}_{\text{non breeding}}$ explained more than a third of the interannual variation in hatching success ($R^2=35\%$).

4. DISCUSSION

We used seven years of isotope data ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) to investigate interannual dietary changes for four, ecologically-different seabird species from the High Arctic, and their ultimate consequences in terms of breeding performance (hatching success and chick survival). The interspecific differences in feeding ecology likely explain the different variation in isotopic ratios we observed among species. Overall, the planktivorous, at-sea foraging little auks had lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than omnivorous glaucous gulls, which forage both on land and at sea (Anker-Nilssen et al. 2000, Hovinen et al. 2014, Vihtakari et al. 2018a). Intermediate $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in kittiwakes and guillemots likely reflect their diet, based on both fish and crustaceans, compared to that of little auks (plankton) and glaucous gulls (from fish to birds). Although the feeding ecology of these four species may vary slightly between the summer and winter (Erikstad 1990, Gaston & Jones 1998), the similar isotopic patterns for both blood and feather samples suggested that the previous descriptions remain generally true independent of the season considered.

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Isotopic composition also varied annually, although to a varying extent depending on the species, season, and isotope considered. For example, black-legged kittiwakes showed interannual variation of limited amplitude in $\delta^{15}\text{N}$ during the breeding period (0.5‰), while little auks and Brünnich's guillemot's $\delta^{15}\text{N}$ values for the same period showed larger variation ($\geq 1.0\text{‰}$). In particular, the $\delta^{15}\text{N}$ in summer was much lower in 2014 for little auks and in 2014 and 2015 for guillemots. The observed interannual variation in isotopic ratios of Svalbard seabirds may reflect changes in their trophic niche (i.e. prey) and/or changes in the isotopic composition of their prey driven by changes in isotopic baselines (Bond & Jones 2009). The $\delta^{15}\text{N}$ of bulk tissues integrates the ratios from distinct amino acids reflecting either the baseline of a given food web (source) or the trophic level of the digested prey (Lorrain et al. 2009) and can indeed theoretically be affected solely by changes in baseline $\delta^{15}\text{N}$. Changes in baseline $\delta^{15}\text{N}$ would probably have led to parallel and synchronous changes in the isotopic ratios of seabird species that feed within the same food chains, which was not the case (*Supplementary Material 6*). Even though we cannot completely rule out this hypothesis, changes in baseline isotopic ratios of such amplitude seem less likely in the context of our study.

Our results support the hypothesis that some changes in diet occurred for all four species considered during both the breeding and non-breeding seasons, and that the changes during the non-breeding season may have important consequences for seabird fitness. Indeed, we found that the average hatching success was negatively correlated to the average trophic level during the previous non-breeding season. This relationship was the same for all four species considered. These species all winter in the North Atlantic but generally in different areas: north of Iceland and in southwest Greenland for Brünnich's guillemots (Frederiksen et al. 2016), in the Greenland Sea for little auks (Fort et al. 2013), on the Great Banks, east of **Hovinen, Johanna Emilia Heidi; Tarroux, Arnaud; Ramirez, Francisco; Forero, Manuela; Descamps, Sébastien.**

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316 Canada, for kittiwakes (Frederiksen et al. 2012), and over most of the northeast Atlantic for
317 glaucous gulls (B. Moe pers. comm.). However, it is possible that they forage within the same
318 area close to Svalbard in the spring when they come back to breed. They would thus be
319 exposed to the same environmental conditions at the time of chest feather moult, which could
320 explain the lack of inter-species variation in the relationship between $\delta^{15}\text{N}$ and breeding
321 success observed here.

322 This correlation does not necessarily imply a mechanistic relationship but may
323 indicate that feeding on prey at higher trophic levels during the non-breeding season has some
324 negative carry-over consequences on the breeding performance of seabirds breeding in
325 Svalbard. One potential explanation could be that in years with generally high productivity,
326 the abundance and availability of lower trophic organisms is higher and thus represents a
327 higher proportion of the diet in the upper trophic levels, including seabirds (Miller et al. 2010,
328 Miller et al. 2011). This would lead to negative associations between overall food availability,
329 average trophic level (and thus $\delta^{15}\text{N}$) of seabirds and their reproductive output. In such a case,
330 the driver of the decreasing reproductive outputs would not be the increase in average trophic
331 level *per se* but rather the lower food availability for low productive years. An alternative
332 explanation would be that high $\delta^{15}\text{N}$ is the consequence of birds using more of their
333 endogenous reserves (Cherel et al. 2005). Low food availability during the non-breeding
334 season could thus potentially lead to this negative association between $\delta^{15}\text{N}$ and subsequent
335 breeding success in Svalbard seabirds. These two alternative explanations remain speculative
336 and further studies examining the relationships between primary productivity, plankton and
337 fish availability at the wintering grounds, seabird diet and subsequent reproduction are
338 needed.

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The apparent correlation between reproductive success and average $\delta^{15}\text{N}$ compared to the absence of a relationship between average $\delta^{15}\text{N}$ and body condition may be indicative of a trade-off between a bird's own maintenance and reproduction. Indeed, in long-lived species like seabirds, individuals are expected to prioritize their own condition and thus survival, at the expense of the survival of their egg or chicks (Saether & Bakke 2000). Seabirds may maintain a relatively constant body condition even in years with limited food availability but at the cost of a lower reproductive investment and therefore a lower reproductive success (Sæther et al. 1993, Mauck & Grubb Jr 1995, Erikstad et al. 1998). This explanation fits well with the absence of clear interannual variation in seabird body condition. Alternatively, our proxy for body condition may not provide an adequate picture of bird physiological condition and health, and/or an adequate picture of the average condition during the breeding season. We estimated bird condition only once per season and per bird and thus, it may mostly reflect near-term environmental conditions and/or bird breeding status (i.e. the condition of a bird may be dependent on its offspring developmental stage). As a consequence, there could be some relationship between trophic level during the non-breeding season and bird body condition during pre-breeding or breeding, but that were not detected using our proxy of body condition. Obtaining measures of body condition during the pre-breeding period and/or repeated measures of condition during the breeding season, may be necessary to reveal such relationships.

5. Conclusion

Food abundance is generally considered to be a key determinant of individual breeding performance in free-living populations (Martin 1987, Zera & Harshman 2001), but the importance of diet composition, in terms of prey species, is less clear. Here, we found that

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362 interannual variation in the average breeding performance of four Svalbard seabirds was
363 negatively correlated with interannual variation in their average trophic level during the non-
364 breeding season. This suggests that changes in the structure and functioning of marine food
365 webs during the non-breeding season (resulting from changes in marine productivity) may
366 have consequences for seabirds' reproductive performance. Several Svalbard seabird species
367 are currently experiencing rapid changes (Descamps et al. 2013, Petersen et al. 2015,
368 Descamps et al. 2017b) and it has generally been assumed that changes in the food chain are a
369 key driver. Our study supports the hypothesis that environmentally-driven changes in seabird
370 diet may affect their reproduction and thus, that reproductive success of Svalbard seabirds
371 may be used to some extent as bioindicators of their (non-breeding) marine environment. Our
372 results are based on indirect measures of diet that have important limitations. Further studies
373 identifying the prey consumed during the non-breeding season by seabirds and their inter-
374 annual changes are now needed to move forward.

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596 **Table 1** Interannual variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic ratios (during the breeding and non-breeding seasons), body condition and reproductive
597 performance of Svalbard seabirds. For $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and body condition, results are from generalized mixed effect models that include bird identity
598 as a random effect. For reproductive variables, results are from linear models; only one value per nest (among all available years) was randomly
599 sampled to avoid pseudo-replication (mixed models could not be used due to convergence issues). Variables $\delta^{13}\text{C}_{\text{breeding}}$ and $\delta^{15}\text{N}_{\text{breeding}}$ have been
600 adjusted for the sampling date (to remove the intra-seasonal variation in isotopic ratios during the breeding season). Body condition represents
601 the body mass adjusted for capture date and body size (wing length). Hatching success represents the probability of hatching at least one chick,
602 and the chick survival variable represents the probability of having at least one chick survive up to 15 days of age. df represents the degrees of
603 freedom, AIC the Akaike Information Criterion, and ΔAIC the difference in AIC from the model with the lowest AIC.

604

Response variable	Fixed effects	df	AIC	ΔAIC
$\delta^{13}\text{C}_{\text{breeding}}$ (n=250 from 205 individuals)	Year×Species	20	-45.18	0.00
	Year+Species	10	43.19	88.37
	Year	8	50.32	95.50
	Species	4	210.52	255.70
	Null (intercept only) model	2	204.52	249.70
$\delta^{15}\text{N}_{\text{breeding}}$	Year×Species	20	321.30	0.00
	Year	8	382.62	61.32

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(n=251 from 205 individuals)	Year+Species	10	384.99	63.69
	Null (intercept only) model	2	446.71	125.41
	Species	4	452.70	131.40
$\delta^{13}\text{C}_{\text{non breeding}}$	Year×Species	20	525.27	0.00
(n=239 from 212 individuals)	Year+Species	10	526.01	0.74
	Species	4	534.27	9.00
	Null (intercept only) model	2	698.82	173.55
	Year	8	701.13	175.86
$\delta^{15}\text{N}_{\text{non breeding}}$	Year×Species	20	699.45	0.00
(n=281 from 224 individuals)	Species	4	720.79	21.34
	Year+Species	10	725.89	26.44
	Year	8	920.29	220.84
	Null (intercept only) model	2	922.45	223.00
Body condition	Null (intercept only) model	2	2674.23	0.00
(n=301 from 288 individuals)	Year×Species	20	2680.23	6.00
	Year	8	2680.29	6.06
	Species	4	2685.71	11.48
	Year+Species	10	2686.16	11.93
Hatching success	Year×Species	21	799.37	0.00
	Year+Species	9	853.20	53.83

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(n= 305 from 305 nests)	Species	4	922.37	123.00
	Year	7	946.06	146.69
	Null (intercept only) model	1	985.58	186.21
Chick survival	Year×Species	16	455.66	0.00
(n=194 from 194 nests)	Year+Species	9	506.73	51.07
	Species	3	526.59	70.93
	Year	7	565.66	110.00
	Null (intercept only) model	1	565.08	109.42

605

606

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607 **Table 2** Relationships between average annual carbon and nitrogen isotopic ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) during the breeding and non-breeding seasons
608 and average seabird condition and reproductive performance in Svalbard. Results are from linear models and all variables have been normalized
609 (within species normalizing) so that models with only *species* or “*species* + $\delta^{13}\text{C}$ ” or “*species* + $\delta^{15}\text{N}$ ” as fixed effects were not informative.
610 $\delta^{13}\text{C}_{\text{breeding}}$ and $\delta^{15}\text{N}_{\text{breeding}}$ have been adjusted to the sampling date (to remove the intra-seasonal variation in these two traits during the breeding
611 season). df represents the degrees of freedom, AIC_C the Akaike Information Criterion corrected for small sample size, and ΔAIC_C the difference
612 in AIC_C from the model with the lowest AIC_C and R^2 represents the proportion of variance explained by the model.

613

Response variable	n	Fixed effects	df	AIC _C	ΔAIC_C	R^2
Average body condition	17	Null (intercept only)	1	49.21	0.00	
		$\delta^{13}\text{C}_{\text{breeding}}$	2	51.17	1.96	<0.01
		$\delta^{15}\text{N}_{\text{breeding}}$	2	50.64	1.43	0.12
		$\delta^{13}\text{C}_{\text{breeding}} \times \text{Species}$	6	60.57	11.36	0.15
		$\delta^{15}\text{N}_{\text{breeding}} \times \text{Species}$	6	62.61	13.40	0.43
	17	$\delta^{13}\text{C}_{\text{non breeding}}$	2	47.62	0.00	0.16
		Null (intercept only)	1	47.95	0.33	
		$\delta^{15}\text{N}_{\text{non breeding}}$	2	48.44	0.82	0.12
		$\delta^{15}\text{N}_{\text{non breeding}} \times \text{Species}$	8	69.38	21.76	0.45

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		$\delta^{13}\text{C}_{\text{non breeding}} \times \text{Species}$	8	70.62	23.00	0.41
Average hatching success	17	Null (intercept only)	1	47.95	0.00	
		$\delta^{13}\text{C}_{\text{breeding}}$	2	49.80	1.85	0.04
		$\delta^{15}\text{N}_{\text{breeding}}$	2	50.21	2.26	0.01
		$\delta^{15}\text{N}_{\text{breeding}} \times \text{Species}$	8	73.25	25.30	0.32
		$\delta^{13}\text{C}_{\text{breeding}} \times \text{Species}$	8	73.59	25.64	0.30
	19	$\delta^{15}\text{N}_{\text{non breeding}}$	2	45.67	0.00	0.35
		Null (intercept only)	1	50.81	5.14	
		$\delta^{13}\text{C}_{\text{non breeding}}$	2	53.36	7.69	<0.01
		$\delta^{13}\text{C}_{\text{non breeding}} \times \text{Species}$	8	75.85	30.18	0.23
		$\delta^{15}\text{N}_{\text{non breeding}} \times \text{Species}$	8	68.57	22.90	0.49
Average chick survival	15	$\delta^{15}\text{N}_{\text{breeding}}$	2	42.72	0.00	0.21
		Null (intercept only)	1	43.53	0.81	
		$\delta^{13}\text{C}_{\text{breeding}}$	2	45.89	3.17	0.02
		$\delta^{13}\text{C}_{\text{breeding}} \times \text{Species}$	6	56.46	13.74	0.38
		$\delta^{15}\text{N}_{\text{breeding}} \times \text{Species}$	6	59.68	16.96	0.24
	14	Null (intercept only)	1	40.68	0.00	
		$\delta^{13}\text{C}_{\text{non breeding}}$	2	42.40	1.72	0.07
		$\delta^{13}\text{C}_{\text{non breeding}} \times \text{Species}$	6	58.08	17.40	0.26

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$\delta^{15}\text{N}_{\text{non breeding}}$	2	42.73	2.05	0.05
$\delta^{15}\text{N}_{\text{non breeding}} \times \text{Species}$	6	59.22	18.54	0.20

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FIGURE LEGENDS

Fig. 1 Breeding sites of little auks (red circle), black-legged kittiwakes (blue circle), Brünnich's guillemots (green circle), and glaucous gulls (black circle) included in the study (Svalbard Archipelago). Glaucous gulls were all breeding within Kongsfjorden and not in a specific colony.

Fig. 2 Average stable isotopic ratios ($\pm 1SD$) of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in little auks, black-legged kittiwakes, the Brünnich's guillemots, and glaucous gulls during a) breeding and b) non-breeding seasons in 2009-2015. Dots represent individual values for each species and year.

Fig. 3 Average hatching success of Svalbard seabirds in relation to nitrogen isotopic ratio during the previous non-breeding season. The line represents the prediction from a linear model and its associated 95% confidence interval (shaded areas).

Supplementary material 2. *Seabird body condition*

We defined bird body condition as the residual from a linear regression of individual body mass on individual capture date (in Julian days) and wing length (a proxy of body size). As the regression parameters may differ among species, we considered the interactions between capture date and species and between wing length and species. The year and individual identity (ring number) were included as random factors. Model was run with the *lmer* function of the package *lme4*.

The R-output is represented in Fig. S1.

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```

Linear mixed model fit by REML ['lmerMod']
Formula: Mass ~ (Julian + wing) * Species + (1 | YR) + (1 | MetalRing)
Data: Selection

REML criterion at convergence: 5692.9

Scaled residuals:
    Min       1Q   Median       3Q      Max
-10.3800  -0.0145   0.0014   0.0377   2.7941

Random effects:
 Groups      Name      Variance Std.Dev.
MetalRing (Intercept) 32740.6  180.94
YR          (Intercept)  104.9   10.24
Residual                        982.9   31.35
Number of obs: 493, groups: MetalRing, 232; YR, 7

Fixed effects:
              Estimate Std. Error t value
(Intercept)  -5499.579   1147.655  -4.792
Julian         9.745     3.363    2.898
Wing         11.240     2.300    4.886
SpeciesLiau   5736.100   1474.300    3.891
SpeciesRitri  5584.727   1529.180    3.652
SpeciesUrlom  6617.300   1294.259    5.113
Julian:SpeciesLiau  -10.736     3.501   -3.066
Julian:SpeciesRitri -10.867     3.378   -3.217
Julian:SpeciesUrlom -11.326     3.449   -3.284
Wing:SpeciesLiau   -10.199     7.535   -1.353
Wing:SpeciesRitri   -9.648     3.916   -2.464
Wing:SpeciesUrlom  -10.511     3.526   -2.981

```

```

Analysis of Variance Table
              Df Sum Sq Mean Sq  F value
Julian         1 145379  145379  147.9138
Wing           1 438557  438557  446.2046
Species        3 701919  233973  238.0528
Julian:Species  3  12613    4204    4.2776
Wing:Species    3  11121    3707    3.7716

```

Figure S1. R-output for the linear regression of individual body mass on individual capture date and wing length (with the species as an interacting factor).

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Supplementary material 3. Relationships between Svalbard seabird body condition, breeding success and isotopic ratios (during the breeding season) when excluding the years based on different tissue samples (i.e. red blood cells instead of whole blood for little auks in 2011 and Brünnich's guillemots in 2010).

Results are from linear models and all variables were normalized (within species normalizing) so that models with only species or “species + $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ ” as fixed effects were not informative. $\delta^{13}\text{C}_{\text{breeding}}$ and $\delta^{15}\text{N}_{\text{breeding}}$ were adjusted to the sampling date (to remove the intra-seasonal variation in isotopic ratios during the breeding season). df represents the degrees of freedom, AIC_C the Akaike Information Criterion corrected for small sample size, and ΔAIC_C the difference in AIC_C from the model with the lowest AIC_C and R^2 represents the proportion of variance explained by the model.

Table S4. Results from linear models testing the effects of isotopic ratios (during the breeding season) on seabird body condition and breeding success when excluding the years based on different tissue samples

Response variable	n	Fixed effects	df	AIC _C	ΔAIC_C
Average body condition	15	Null (intercept only)	1	43.53	0.04
		$\delta^{13}\text{C}_{\text{breeding}}$	2	46.20	2.71
		$\delta^{13}\text{C}_{\text{breeding}} \times \text{Species}$	6	60.04	16.55
		$\delta^{15}\text{N}_{\text{breeding}}$	2	43.49	0.00
		$\delta^{15}\text{N}_{\text{breeding}} \times \text{Species}$	6	53.38	9.89
Average hatching success	16 ^a	Null (intercept only)	1	45.09	0.00
		$\delta^{13}\text{C}_{\text{breeding}}$	2	47.44	2.36
		$\delta^{13}\text{C}_{\text{breeding}} \times \text{Species}$	8	75.06	29.98
		$\delta^{15}\text{N}_{\text{breeding}}$	2	47.55	2.47
		$\delta^{15}\text{N}_{\text{breeding}} \times \text{Species}$	8	73.31	28.23

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Average chick survival	14 ^a	Null (intercept only)	1	40.68	0.65
		$\delta^{13}\text{C}_{\text{breeding}}$	2	43.29	3.26
		$\delta^{13}\text{C}_{\text{breeding}} \times \text{Species}$	6	55.29	15.26
		$\delta^{15}\text{N}_{\text{breeding}}$	2	40.03	0.00
		$\delta^{15}\text{N}_{\text{breeding}} \times \text{Species}$	6	58.39	18.36

657

658 ^a: no reproduction data for Brünnich's guillemot in 2010 so that the only difference here with analyses presented in Table 2
659 (main document) is the absence of little auk reproductive data for 2011.

Hovinen, Johanna Emilia Heidi; Tarroux, Arnaud; Ramirez, Francisco; Forero, Manuela; Descamps, Sébastien.

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Supplementary material 4. Repeatability in black-legged kittiwake isotopic ratios

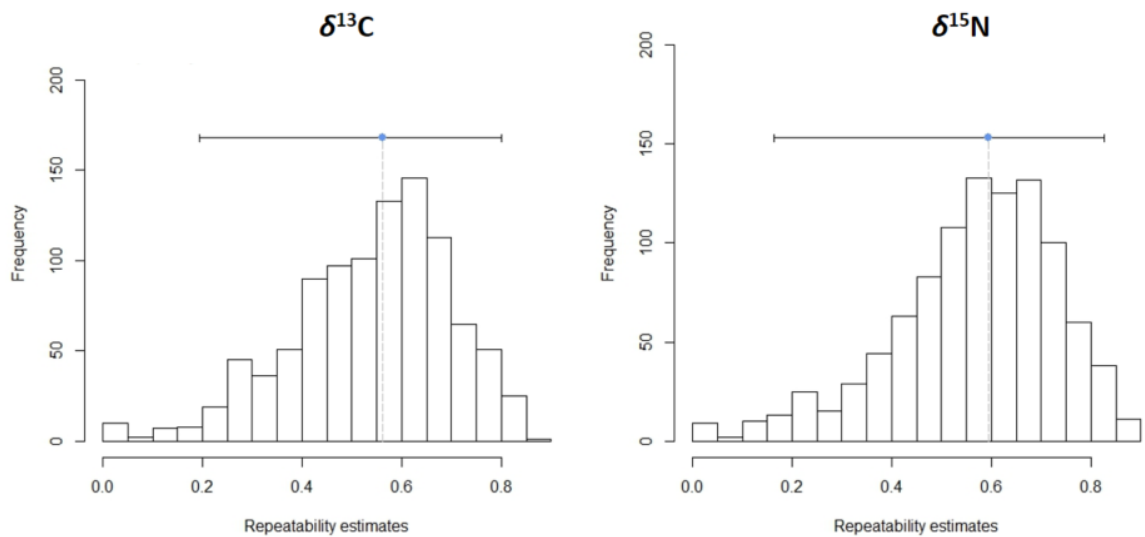


Figure S2. Bootstrapped repeatability of blood $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, and their associated 95% confidence intervals, in black-legged kittiwakes breeding on Svalbard (Grumantbyen colony, 78°17'N 15°10'E). Repeatability has been calculated using the rpt function of the rptR package (Stoffel et al., 2017). Kittiwakes were sampled during chick-rearing and isotopic ratios were centered on their annual mean (within year centering). $N=37$ samples from 18 individuals and 4 years (2011, 2012, 2014 and 2015). Likelihood ratio tests indicate that repeatability in both ratios is significantly different from zero ($\delta^{13}\text{C}$: $D=6.82$, $df=1$, $p=0.005$; $\delta^{15}\text{N}$: $D=8.78$, $df=1$, $p=0.002$).

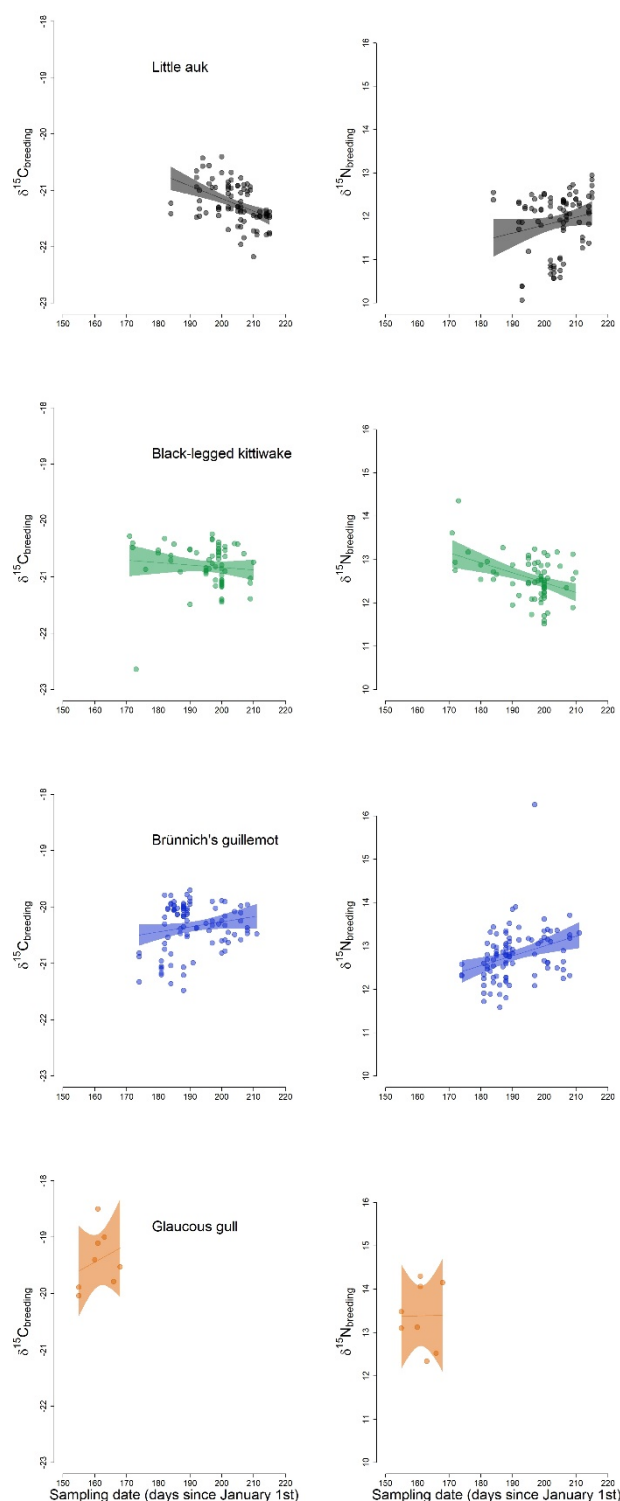
Literature cited

Stoffel MA, Nakagawa S, Schielzeth H (2017) rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Meth Ecol Evol* 8:1639-1644

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677 **Figure S3.** Raw isotope values (carbon and nitrogen) as a function of the sampling date. The line and
678 shaded areas represent the estimated relationship between isotope and sampling date, and the
679 associated 95% confidence interval.

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Results below are from a linear mixed-effects model with individual identity as a random factor. Model was run with the *lmer* function of the package *lme4*.

The R-output is represented in *Figs. S4 and S5*.

```
Linear mixed model fit by maximum likelihood ['lmerMod']
Formula: D13C ~ Julian * Species + (1 | MetaRing)
Data: Select

      AIC      BIC    logLik deviance df.resid
  218.5    253.7    -99.3    198.5      240

Scaled residuals:
    Min       1Q   Median       3Q      Max
-3.08274 -0.71102  0.04843  0.84172  2.53235

Random effects:
 Groups      Name      Variance Std.Dev.
MetaRing (Intercept)  0.0000    0.0000
Residual              0.1295    0.3599
Number of obs: 250, groups: MetaRing, 205

Fixed effects:
              Estimate Std. Error t value
(Intercept)   -24.45617    4.72286  -5.178
Julian          0.03133    0.02930   1.069
SpeciesLiau     7.77766    4.85065   1.603
SpeciesRitri    6.26982    4.82887   1.298
SpeciesUrlom    2.39238    4.79335   0.499
Julian:SpeciesLiau -0.05367    0.02980  -1.801
Julian:SpeciesRitri -0.04461    0.02975  -1.500
Julian:SpeciesUrlom -0.02233    0.02961  -0.754
```

```
Analysis of Variance Table
              Df Sum Sq Mean Sq  F value
Julian         1  28.281  28.2810  218.3269
Species        3  21.186   7.0622   54.5195
Julian:Species  3   3.232   1.0773    8.3168
```

Figure S4. R-output for the linear mixed testing the effect of Julian date (with species as an interacting factor) on the carbon isotopic ratio during the breeding season.

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```

Linear mixed model fit by maximum likelihood ['lmerMod']
Formula: D15N ~ Julian * Species + (1 | MetalRing)
Data: Select

      AIC      BIC    logLik deviance df.resid
  460.6    495.8   -220.3    440.6     241

Scaled residuals:
    Min       1Q   Median       3Q      Max
-2.3288 -0.5652  0.0863  0.5757  4.8233

Random effects:
 Groups      Name      Variance Std.Dev.
MetalRing (Intercept) 0.09557   0.3091
Residual          0.24891   0.4989
Number of obs: 251, groups: MetalRing, 205

Fixed effects:
              Estimate Std. Error t value
(Intercept)    13.013977    7.701848    1.690
Julian           0.002295    0.047783    0.048
SpeciesLiau     -4.620921    7.903832   -0.585
SpeciesRitri     4.551149    7.846941    0.580
SpeciesUrlom    -4.456133    7.813495   -0.570
Julian:SpeciesLiau  0.014725    0.048569    0.303
Julian:SpeciesRitri -0.027886    0.048398   -0.576
Julian:SpeciesUrlom  0.019897    0.048277    0.412

```

```

Analysis of Variance Table
              Df Sum Sq Mean Sq F value
Julian         1 10.2616  10.2616  41.2257
Species        3 22.8421   7.6140  30.5892
Julian:Species  3  5.9638   1.9879   7.9865

```

Figure S5. R-output for the linear mixed testing the effect of Julian date (with species as an interacting factor) on the nitrogen isotopic ratio during the breeding season.

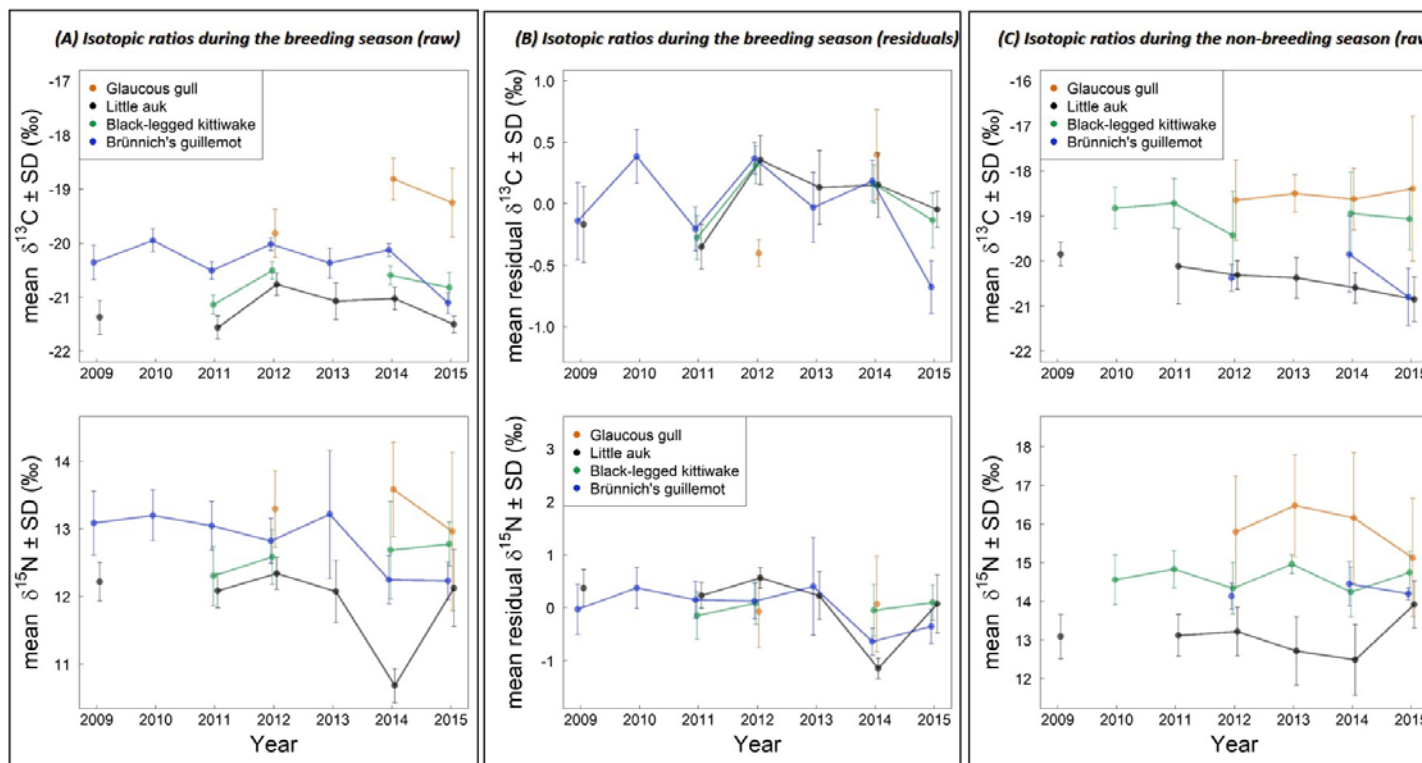
Hovinen, Johanna Emilia Heidi; Tarroux, Arnaud; Ramirez, Francisco; Forero, Manuela; Descamps, Sébastien.

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693 **Supplementary material 6. Inter-annual variation in carbon and nitrogen isotopic ratios, body condition, hatching**
694 **success and chick survival during the breeding and non-breeding season**

695 (a)



696

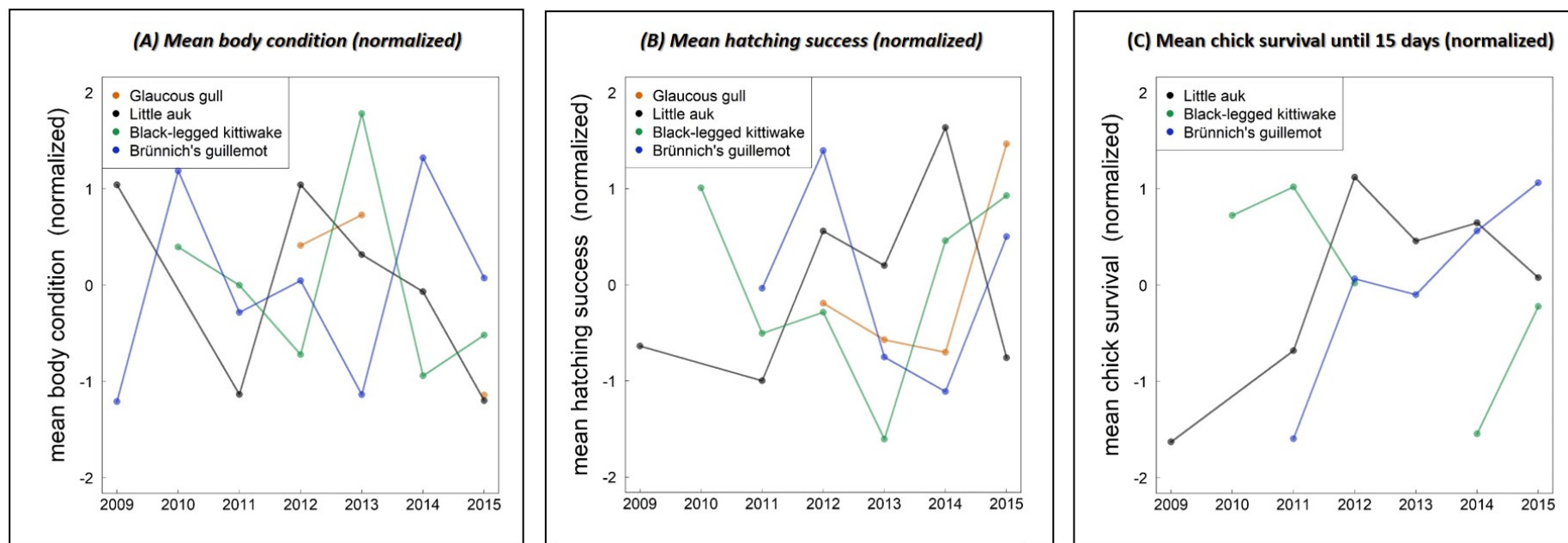
Hovinen, Johanna Emilia Heidi; Tarroux, Arnaud; Ramirez, Francisco; Forero, Manuela; Descamps, Sébastien.

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697

(b)



698

699

700 **Figure S6.** Inter-annual variation in Svalbard seabird isotopic ratios (a) and condition or breeding success (b). In (a), the left (A) and central (B) panels
 701 represent the average carbon (top) and nitrogen (bottom) isotopic ratios for the breeding season (blood samples) and right panels (C) represent the non-
 702 breeding season (feather samples). In panels (B), isotopic ratios have been adjusted for sampling date (see details in the Method section and Suppl. Mat. 5).
 703 In (b), panels represent the body condition (A), hatching success (B) and chick survival until 15 days of age (C). All variables were normalized (centered on
 704 the mean and divided by the SD).

705

Hovinen, Johanna Emilia Heidi; Tarroux, Arnaud; Ramirez, Francisco; Forero, Manuela; Descamps, Sébastien.

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