

1 **Breeding stage and tissue isotopic consistency suggests colony-level flexibility in niche**  
2 **breadth of an Arctic marine bird**

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11 **Running Title:** Consistency in isotopic niche of an Arctic seabird

12

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20 **Abstract**

21 Organisms must overcome environmental limitations to optimize their investment in life history  
22 stages to maximize fitness. Human-induced climate change is generating increasingly variable  
23 environmental conditions, impacting the demography of prey items and therefore the ability of  
24 consumers to successfully access resources to fuel reproduction. While climate change effects  
25 are especially pronounced in the Arctic, it is unknown whether organisms can adjust foraging  
26 decisions to match such changes. We used a 9-year blood plasma  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  dataset from  
27 over 700 pre-breeding Arctic common eiders (*Somateria mollissima*) to assess breeding-stage  
28 and inter-annual variation in isotopic niche, and whether inferred trophic flexibility was related  
29 to colony-level breeding parameters and environmental variation. Eider blood isotope values  
30 varied both across years and breeding stages, and combined with only weak relationships  
31 between isotopic metrics and environmental conditions suggests that pre-breeding eiders can  
32 make flexible foraging decisions to overcome constraints imposed by local abiotic conditions.  
33 From an investment perspective, an inshore, smaller isotopic niche predicted a greater  
34 probability to invest in reproduction, but was not related to laying phenology. Proximately, our  
35 results provide evidence that eiders breeding in the Arctic can alter their diet at the onset of  
36 reproductive investment to overcome increases in the energetic demand of egg production.  
37 Ultimately, Arctic pre-breeding common eiders may have the stage- and year-related foraging  
38 flexibility to respond to abiotic variation to reproduce successfully.

39 **Keywords: isotopic niche, foraging flexibility, phenology, trophic interactions, reproductive**  
40 **investment, adaptive capacity, carbon-13, nitrogen-15**

41

## 42 **Introduction**

43 Investment in various life history stages is significantly influenced by an individual's ability to  
44 obtain energetic resources and optimally allocate them to meet the energetic demands of  
45 associated life history (McNamara and Houston 1996). Consequently, resource limitation is one  
46 of the strongest constraints influencing the ability of an individual to optimize foraging decisions  
47 to maximize fitness (Stephens and Krebs 1986; Newton 1998). Since the quality and quantity of  
48 available dietary resources can be influenced by variability in the surrounding environment,  
49 variation in environmental conditions can play an important role in shaping the relationship  
50 between resource acquisition, and fitness and population demography (Boggs 1992). However,  
51 as climate change continues to generate increases in mean annual temperatures and variability in  
52 climatic conditions (IPCC 2018), animals are expected to be increasingly impacted by mounting  
53 instability in resource availability (Cushing 1990; Tylianakis et al. 2008).

54         Relative to other temperate and tropical ecosystems, the Arctic is experiencing amplified  
55 rates of climate change (Wassmann et al. 2011), which is reducing sea-ice extent (Johannessen et  
56 al. 2004; Comiso et al. 2008; Hoegh-Guldberg and Bruno 2010; Ciancio et al. 2016), and leading  
57 to bottom-up trophic disruptions (Wassmann et al. 2011; Boeitus et al. 2013; Jones et al. 2014;  
58 Meier et al. 2014). As such, many key prey sources are declining or their distributions are  
59 shifting (Both et al. 2006), complicating species' ability to acquire resources and their ability to  
60 optimize investment decisions in energetically demanding life history stages, such as  
61 reproduction (Ward et al. 2009; Seyboth et al. 2016). Whether Arctic species have the required  
62 adaptive capacity to be flexible enough to optimize breeding decisions to proximately keep pace  
63 with the current rate of environmental change has therefore become an important topic of  
64 investigation (Kovacs et al. 2010; Moore and Huntington 2011; Descamps et al. 2017).

65           Determining the downstream influence of environmental variation on reproductive  
66 investment first requires consideration of which prey items organisms consume to fuel  
67 reproduction (Walther et al. 2002; Rutschmann et al. 2016). The use of tissue stable isotope  
68 measurements to represent foraging niche is well established in several taxa (Bearhop et al.  
69 2004) and is increasingly used to assess individual- and population-level responses to rapid  
70 environmental change (Dawson and Siegwolf 2011; Mancinelli and Vizzini 2015; Pethybridge et  
71 al. 2017). Specifically, the combination of stable isotope measurements of carbon ( $\delta^{13}\text{C}$ ), which  
72 provides information on basal sources reflective of habitat use (i.e., inshore vs offshore), and  
73 nitrogen ( $\delta^{15}\text{N}$ ), which allows relative estimation of trophic level (Peterson and Fry 1987),  
74 provides a non-lethal method of quantifying isotopic niche (Newsome et al. 2007; Matich and  
75 Shipley 2021). Quantifying isotopic niche space or volume can provide insight on the degree of  
76 trophic specialization (Seamon and Adler 1996), where groups with larger isotopic niches are  
77 predicted to have more diverse diets (i.e., more generalist; Moreno et al. 2010). The degree of  
78 trophic specialization can then be used to predict how resilient organisms or populations will be  
79 to further environmental change (Polito et al. 2015). For example, groups with a more generalist  
80 isotopic niche might be expected to be more successful investing in reproduction, regardless of  
81 environmentally induced trophic disruptions because of their greater dietary flexibility (Seamon  
82 and Adler 1996). Further, isotopic niche provides a useful tool to assess shifts in community-  
83 wide trophic dynamics in response to environmental change (Hobson 1992a,b, 1999; Newsome  
84 et al. 2007; Herman et al. 2017), and insight into how foraging decisions might affect key  
85 fitness-related decisions (Hutchinson 1957; Vandermeer 1972; Alatalo 1982; Bolnick et al.  
86 2003). Finally, quantification of isotopic niche also provides a testable framework in which to  
87 investigate how environmental variability mediates trophic dynamics and ultimately influences

88 reproductive investment decisions (Chesson 1986; Leibold 1995); however, this framework  
89 relies on a number of assumptions (Matich and Shipley 2021). The primary assumption being  
90 that baseline isotope values remain constant or are accounted for through periods of  
91 investigation. Secondly, tracing nutrients isotopically during reproduction is complex and  
92 depends on the degree to which birds may be income or capital breeders (Hobson 2006, Hobson  
93 et al. 2015, Whiteman et al. 2021). Even considering these caveats, establishing temporal  
94 variability in the isotopic niches of populations can be a useful tool for examining the influence  
95 of environmental change in polar regions which are historically relatively slow to change over  
96 time compared to more southern regions (Yurkowski et al. 2020).

97       Female common eiders (*Somateria mollissima*) make an ideal study species to test these  
98 linkages given that a key environmental factor limiting Arctic-nesting eiders is sea ice cover,  
99 particularly during spring migration and the pre-laying period which can restrict access to  
100 foraging grounds of this diving seabird (Jean-Gagnon et al. 2018). Additionally, female eiders  
101 must meet a minimum body condition threshold to invest in reproduction (Hennin et al. 2016),  
102 and their ability to do so is influenced by access to resources just prior to breeding (Love et al.  
103 2010; Jean-Gagnon et al. 2018). This is an important consideration because female eiders that  
104 can fatten more quickly lay earlier (Hennin et al. 2017, 2019), invest in larger clutches  
105 (Descamps et al. 2011a; Hennin et al. 2018) and ultimately recruit more ducklings into the  
106 breeding colony (Love et al. 2010; Descamps et al. 2011b). Since eiders rely on lipid and protein  
107 sources consumed on the breeding grounds to produce their eggs (Sénéchal et al. 2011), and prey  
108 items used during egg formation differ in nutritional value (Paiva et al. 2013), the ability to  
109 access nutritious prey likely influences breeding decisions and outcomes (e.g., Kitaysky et al.  
110 2010), especially under climatically unpredictable conditions (Barbraud et al. 2012). With

111 isotopic niche capturing a general snapshot of female foraging prior to and during laying, it may  
112 act as an important predictor of variation in reproductive investment (Sénéchal et al. 2011).

113         Here we used a 9-consecutive-year (2010-2018) isotopic dataset collected from over 700  
114 Arctic-nesting female common eiders (hereafter eiders) to investigate the linkages between  
115 environmental variability, variation in important breeding metrics, and temporal variation in  
116 isotopic niche at an Arctic-breeding colony. Specifically, our first objective was to quantify  
117 variation in isotopic niche across breeding stages and years. Given the nutritional demands of  
118 egg formation (Descamps et al. 2010; Love et al. 2010; Sénéchal et al. 2011; Hennin et al. 2015,  
119 2016, 2018, 2019), we predicted that as birds approached laying, they would have higher  $\delta^{15}\text{N}$   
120 values and higher  $\delta^{13}\text{C}$  values as birds targeted higher trophic level prey (Forero et al. 2002;  
121 Becker et al. 2007; González-Medina et al. 2018) found closer to shore, respectively. Likewise,  
122 given the energetic demands of initiating and fueling egg formation, we predicted that in years  
123 when the colony exhibited a larger isotopic niche (more generalized foraging strategy) more  
124 birds would have greater access to a diversity of resources, and therefore be able to fatten more  
125 quickly, generating shorter mean delays before laying, earlier mean laying dates, and higher  
126 colony-level breeding propensity (Love et al. 2010; Descamps et al. 2011; Hennin et al. 2015,  
127 2016, 2018). Finally, we predicted significant inter-annual variation in isotopic niches, driven by  
128 inter-annual variation in climate and trophic dynamics. Considering the highly variable sea ice  
129 conditions during the pre-breeding period (Love et al. 2010; Jean-Gagnon et al. 2018), and that  
130 local environmental conditions can influence seabird foraging behaviour (Hobson 1999; Paiva et  
131 al. 2013), our second objective was to examine whether broad-scale environmental conditions  
132 explained inter-annual variation in isotopic niche. We predicted that in years with warmer  
133 winters, warmer springs, and higher overall ambient temperatures (as indicated by the North

134 Atlantic Oscillation [NAO] index), there ought to be a greater degree of open water, and  
135 therefore a wider variety of possible prey items available to eiders, resulting in a broader colony-  
136 wide isotopic niche.

137

## 138 **Methods**

### 139 *Study species and breeding parameters*

140 From 2010 to 2018, sampling was undertaken at the largest and longest continually monitored  
141 colony of common eiders in the eastern Canadian Arctic; at East Bay Island (EBI), which is  
142 found within in the Qaqsauqtuuq Migratory Bird Sanctuary, Nunavut, Canada (64°02'N,  
143 81°47'W). EBI is a small (800 m x 400 m), low lying island (<8m elevation). Females breeding  
144 at this colony migrate from their wintering grounds off the western coast of Greenland and the  
145 northern coast of Newfoundland and Labrador, Canada in May (Mosbech et al. 2006; Steenweg  
146 et al. 2017), arrive at EBI in early to mid-June, and lay their eggs in mid-June to early-July  
147 (Hennin et al. 2015; Jean-Gagnon et al. 2018). Using flight nets, we captured female common  
148 eiders as they flew over the colony in mid-June, coinciding with their timing of arrival at the  
149 breeding grounds (Descamps et al. 2010; see Supplementary Materials Table S1).

150       After capture, females were blood sampled within three minutes of capture (Romero and  
151 Reed 2005) from the tarsal vein using a 1-mL heparinized syringe and 23G thin-wall, 0.5-inch  
152 needle (see Hennin et al. 2015, 2016 for details). Plasma was separated from red blood cells, and  
153 both components were frozen at -20°C. After sampling, females were assigned a metal band and  
154 alpha-numeric Darvic bands, then affixed with a unique combination of coloured and shaped  
155 nasal tag plastic discs using UV degradable monofilament. Females were identified within the  
156 breeding colony by their nasal tags using spotting-scopes from seven permanent blinds

157 positioned around the periphery of the island. By observing the females and their associated  
158 behaviours, we obtained: breeding propensity (probability of breeding) and lay date (and  
159 therefore the interval in days between arrival at the colony and laying). From these data, we  
160 assigned reproductive stage to all birds as either laying (LAY), rapid follicle growth (RFG), pre-  
161 recruiting (PR), and non-breeding (NB) (see Hennin et al. 2015 for details; see Supplementary  
162 Material). Laying and incubating females were determined based on careful observations from  
163 blinds and monitoring of nests, along with noting the presence of an egg in the oviduct at  
164 capture. All work was approved by the animal care committees of the University of Windsor  
165 (AUPP 11-06 and 19-11) and Environment and Climate Change Canada (EC-PN-15-026).

166

### 167 *Environmental indices*

168 We selected climate variables predictive of the storm activity and ice conditions eiders face  
169 during the pre-breeding period (see Supplementary Materials Table S2). The North Atlantic  
170 Oscillation (NAO) index was used as a proxy for inter-annual variation in environmental  
171 conditions, as it impacts a wide area across the Northern Atlantic Ocean. The relationship  
172 between temporal variation in NAO values and energetic constraints has been validated in  
173 multiple seabird species (Stenseth et al. 2003; Hallett et al. 2004; Sandvik and Erikstad 2008),  
174 including eiders (Descamps et al. 2010). We calculated the average winter NAO (December-  
175 March), which directly impacts the arrival body condition of female eiders (Descamps et al.  
176 2010) and the average spring NAO (April-July; pre-breeding conditions for eiders at MI). All  
177 NAO values were obtained from the National Weather Service  
178 (<https://www.cpc.ncep.noaa.gov/>). As a proxy for localized environmental conditions at the  
179 breeding grounds, we used air temperature ( $T_a$ ) measured at the Coral Harbour Airport Weather

180 Station (70 km from the breeding colony). We first calculated the mean Ta for each individual on  
181 the dates that coincided with the isotopic half-life of plasma (i.e., air temperature roughly 3 days  
182 prior to sample collection; Hobson and Clark 1993; Hahn et al. 2012). This value was then  
183 averaged across all the individuals in the colony for each year.

184

#### 185 *Stable isotope analysis and niche metrics*

186 Female eiders caught at arrival to EBI ranged in body mass from 1.5-2 kg (Hennin et al. 2015),  
187 making the use of plasma (with a half-life of plasma approximately three days; Hobson and  
188 Clark 1992; Hahn et al. 2012) appropriate to assess the most recent isotopic niche space occupied  
189 by these individuals (Supplementary Materials Table S3). We freeze-dried 100 uL of plasma  
190 from each individual until achieving a constant mass (minimum of 78 hours). All samples were  
191 then ground into a homogenized, fine powder using a metal spatula. Since plasma is often high in  
192 lipids we then lipid extracted all plasma samples using a 2:1 chloroform:methanol solution  
193 (Bligh and Dyer 1959). We weighed between 0.3-0.5 mg of each sample, using a four-digit  
194 balance (Sartorius AG, Model CP2P, Gottingen, Germany), into individual 3.5x5 mm tin  
195 capsules for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analysis. Analyses for plasma isotopes were conducted using  
196 continuous-flow isotope-ratio mass spectrometry (CFIRMS) at the Environment Canada Stable  
197 Isotope Hydrology and Ecology Research Laboratory in Saskatoon, Saskatchewan. Encapsulated  
198 plasma was combusted at 1030°C in a Carlo Erba NA1500 or Eurovector 3000 elemental  
199 analyser. The resulting  $\text{N}_2$  and  $\text{CO}_2$  were separated chromatographically and introduced to an  
200 Elementar Isoprime or a Nu Instruments Horizon isotope ratio mass spectrometer. We used two  
201 reference materials to normalize the results to VPDB and AIR: BWBIII keratin ( $\delta^{13}\text{C} = -20.18$ ,  
202  $\delta^{15}\text{N} = +14.31$  ‰, respectively) and PRCgel ( $\delta^{13}\text{C} = -13.64$ ,  $\delta^{15}\text{N} = +5.07$  ‰, respectively).

203 Within-run ( $n = 5$ ) precisions as determined from both reference and sample duplicate analyses  
204 were  $\pm 0.1$  ‰ for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ .

205 We used a bivariate approach to calculate isotopic niche size for each year and each  
206 breeding stage within the SIBER package (Jackson et al. 2011) in R (R Core Team 2014,  
207 Version 4.0.3). Calculated niche metrics included: mean next-neighbor distance (MNND),  
208 standard ellipse area ( $\text{SEAC}$ ), X range (i.e., maximum range of  $\delta^{13}\text{C}$ ) and Y range (i.e., maximum  
209 range of  $\delta^{15}\text{N}$ ) (see Supplementary Material Table S3). We then ran a principal component  
210 analysis (PCA) to collapse down our eight isotopic metrics and four environmental metrics. This  
211 generated three principal components for isotopic metrics, and three principal components for  
212 environmental metrics used for further analysis (Table 1, see Supplementary Materials).

213

#### 214 *Statistical analyses*

215 We had four goals in our statistical analyses, namely examining whether: (1) isotopic niche at the  
216 colony-level varied across years, (2) breeding stages and (3) inter-annual variation in isotopic  
217 metrics predicted variation in key breeding parameters (Table S1), and (4) inter-annual variation  
218 in environmental indices (winter NAO, spring NAO; pre-breeding Ta PC groups; Table S2)  
219 predicted inter-annual variation in isotopic metrics.

220 First, to assess annual variation in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values at the colony-level, we ran a  
221 MANCOVA (with  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  as dependent variables) using our 9-year dataset for common  
222 eider females including year, breeding stage, the interaction between year and breeding stage,  
223 body mass, and relative arrival date as independent variables. Since each isotope represents  
224 different trophic dynamics (i.e.,  $\delta^{15}\text{N}$ : trophic position;  $\delta^{13}\text{C}$ : spatial foraging), we followed the  
225 MANCOVA with two separate one-way ANCOVAs for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  to disentangle the effects

226 of our independent variables on each of our isotopic metrics (dependent variables). In the  
227 ANCOVAs, we included year, breeding stage, the interaction between year and breeding stage,  
228 body mass, and relative arrival date as independent variables. Secondly to examine finer-scale,  
229 breeding-stage specific changes in foraging strategies *via* variation in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , we  
230 conducted break-point analyses. This analysis identifies sudden and significant positive or  
231 negative changes in the dataset (Mugge 2003) through estimating breakpoints by iteratively  
232 fitting a model with a linear predictor. For each iteration, a standard linear model is fitted, and  
233 the breakpoint value is updated until convergence occurs. We performed break point analyses for  
234 both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  separately including the delay before laying as an independent variable using  
235 the Segmented R package (Mugge 2003; R Core Team 2014). Thirdly, we ran an ANCOVA to  
236 test whether mean inter-annual isotopic metrics (i.e., ISOPC1 (Spatial Foraging Breadth),  
237 ISOPC2 (Niche Breadth), and ISOPC3 (Trophic Position) predicted variation in colony mean  
238 arrival dates and breeding parameters by including colony mean breeding parameters as  
239 dependent variables (i.e., breeding propensity, the delay between arrival at the colony and laying,  
240 and relative lay date). Lastly, to determine whether inter-annual variation in isotopic metrics  
241 could be predicted by inter-annual variation in environmental traits, we ran separate ANCOVAs  
242 with the isotopic PC scores as our dependent variables (ISOPC1, ISOPC2, and ISOPC3) and the  
243 environmental PC scores (ENVPC1 and ENVPC2) as our independent variables. All our  
244 analyses met the assumptions of a parametric test. All statistical tests were run using JMP  
245 (Version 14.1.0 SAS) unless otherwise stated.

246

## 247 **Results**

248 *Inter-annual and breeding stage variation in isotopic values*

249 The MANCOVA analysis detected a significant interaction between year and breeding stage in  
250 predicting variation in female eider plasma  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  (Table 2; Figs. 1-3). ANCOVAs  
251 examining the two isotopes separately, revealed that only  $\delta^{15}\text{N}$  showed significant year- and  
252 breeding-stage effects (with no year by stage interaction). Variation in  $\delta^{13}\text{C}$  was negatively  
253 correlated with arrival date, with earlier arriving females having higher  $\delta^{13}\text{C}$  values (Table 3).

254

#### 255 *Fine-scale changes in isotopic values across breeding stages*

256 While  $\delta^{15}\text{N}$  values were relatively consistent throughout the pre-laying period, breakpoint  
257 analyses detected a significant increase approximately two days prior to laying (breakpoint  
258 value:  $1.8 \pm 5.4$  days, Fig. 3b). A breakpoint was also detected for  $\delta^{13}\text{C}$  where values were  
259 relatively consistent across the pre-laying period, until 7.4 days prior to laying. This occurred at  
260 approximately the initiation of the rapid follicle growth (RFG) stage, when  $\delta^{13}\text{C}$  values began  
261 increasing significantly (breakpoint value:  $7.4 \pm 2.5$  days, Fig. 3a).

262

#### 263 *Using isotopic metrics to predict breeding parameters*

264 There was a significant negative relationship between ISOPC2 (Niche Breadth) and breeding  
265 propensity (one-way ANCOVA:  $F_{1,7}=15.37$ ,  $p=0.01$ ,  $w=0.60$  Table 4). We found that females  
266 that foraged more inshore (higher  $\delta^{13}\text{C}$  values) and within a narrower niche had a higher  
267 probability of breeding. However, we found no other significant relationships between colony-  
268 level isotopic metrics and arrival or breeding parameters (Table 4).

269

#### 270 *Climate and isotopic metrics*

271 We found a significant negative relationship between ENVPC2 (North Atlantic Oscillation  
272 values) and ISOPC3 (Trophic Position) (ANCOVA,  $F_{1,1}=8.26$ ,  $p=0.03$ ,  $w=0$ ), suggesting that

273 milder spring environmental conditions were associated with more variable trophic position.  
274 However, we did not detect any other relationships between environmental variables and isotopic  
275 metrics (Table 3).

276

## 277 **Discussion**

278 Using a 9-consecutive-year data set we asked whether information on annual- and reproductive  
279 stage-based variation in isotopic niche dynamics predict whether a breeding colony of eiders has  
280 the foraging flexibility respond to current and projected environmental change. Female eiders  
281 demonstrated significant variation in their  $\delta^{15}\text{N}$  values across years and breeding stages  
282 suggesting that either access to prey or selective choice to forage at certain trophic levels differs  
283 across breeding stages. However,  $\delta^{15}\text{N}$  values significantly increased 2-3 days prior to laying,  
284 suggesting the increased energetic demand of ovarian follicle production during the rapid follicle  
285 growth period may drive a change in trophic decisions and/or that internal nutrient mobilizations  
286 associated with egg formation occurred (Whiteman et al. 2020). We also detected an increase in  
287  $\delta^{13}\text{C}$  as birds transitioned from the pre-breeding to the rapid follicle recruitment stage. This shift  
288 could similarly be associated with diet shifts and/or internal isotopic processes associated with  
289 nutrient mobilization to developing eggs. Assuming a dietary effect, this, combined with our  
290 result indicating isotopic niche breadth (more inshore, narrow niche) positively predicted  
291 breeding propensity, suggests that eiders may shift foraging locations inshore to respond to the  
292 increased energetic demand of the reproductive organ load. We also found that isotopic niche  
293 breadth (more inshore, narrow niche) positively predicted breeding propensity, although not  
294 laying date. Further, we found that breeding birds tended to feed more benthically when  
295 producing eggs. Despite these linkages to breeding investment, we detected significant

296 relationships between environmental conditions and trophic dynamics, but not spatial foraging  
297 indices (i.e.,  $\delta^{13}\text{C}$ ). Our results suggest that common eiders may use flexible foraging strategies  
298 to overcome environmental constraints to invest in reproduction. Considering the rapid and  
299 substantial changes occurring in Arctic marine ecosystems, these findings provide a first step  
300 towards bridging key mechanistic gaps in determining how large-scale environmental processes  
301 proximately impact the foraging decisions and physiology of female eiders expected to influence  
302 colony-level resiliency.

303

#### 304 *Links between isotopic niche variation and breeding investment decisions*

305 Given the energetic demands leading up to laying (Sénéchal et al. 2011; Hennin et al. 2015), we  
306 predicted that shifts in  $\delta^{15}\text{N}$  related to breeding stage would indicate adjustments in foraging  
307 strategies to the changing energetic demands of breeding. We found that  $\delta^{15}\text{N}$  was indeed higher  
308 during the pre-recruiting and RFG stages compared to the laying stage (Table 2; Fig. 2,3b).  
309 Interestingly, we did not find any changes in  $\delta^{15}\text{N}$  either between pre-recruitment stage, despite  
310 birds needing to gain significant body fat (i.e., body mass of 500-750g) to invest in breeding, and  
311 initiation of rapid follicle growth (although see details below for changes in  $\delta^{13}\text{C}$  values).  
312 However, we detected a significant breakpoint, and the highest  $\delta^{15}\text{N}$  values, nearly two days  
313 prior to laying (i.e., during RFG). This coincides with the most energetically demanding rapid  
314 follicle growth (RFG) stage of reproduction (see Hennin et al. 2015). This suggests that females  
315 may shift their prey consumption to match the energetic requirements of laying. We suggest that  
316 combined, these results provide evidence that females make biologically relevant trophic  
317 decisions to fuel the energetic costs of flight and diving while carrying the additional weight of  
318 developing yolks and their supporting reproductive tissues (see Vézina and Williams 2002;

319 Vézina and Salvante 2010; reviewed in Williams 2012). We acknowledge however, that it is  
320 plausible that isotopic effects of RFG may have led to these switches in  $\delta^{15}\text{N}$  values. Previous  
321 work on species relying on some degree of capital (i.e., stored) resources to fuel egg production  
322 have indicated that  $\delta^{15}\text{N}$  fractionation can increase in tandem with the increased energetic  
323 demand associated with egg production *via* protein catabolism (Hobson et al. 1993; Vanderklift  
324 & Ponsard 2003). It is therefore important to note that previous work at EBI has shown that pre-  
325 breeding eiders rely heavily on income-based resources to fuel egg production (Sénéchal et al.  
326 2011) and only enter a fasting (protein catabolism) state during incubation (Bottitta et al 2003).  
327 As such, we would expect minimal impact of fractionation on stable isotope values in plasma  
328 due to fasting or rapid follicle growth in our focal birds. Nevertheless, we acknowledge that such  
329 processes require further examination in Arctic-breeding female eiders.

330         We found that early arriving birds foraged closer to shore in agreement with our  
331 predictions. This could be the result of birds needing to forage at the mouths of rivers as  
332 freshwater inflow into the bay begins to open up small areas of open water prior to marine ice off  
333 where birds can access resources (Jean-Gagnon et al. 2018). We also detected a significant  
334 breakpoint in  $\delta^{13}\text{C}$  values in which females moved to forage at more inshore locations as they  
335 transitioned into the RFG period. This suggests that when females are under significant energetic  
336 demands at the onset of ovarian follicle recruitment, they may switch from foraging on offshore  
337 benthic macroinvertebrates, to prey with lower digestive and foraging energetic costs, such as  
338 amphipods (*Gammarus* spp.). This trophic switch may be driven by a variety of non-exclusive  
339 reasons, including fueling the growth of reproductive organs and follicles. Amphipods are an  
340 eider prey species found more inshore near the surface of the water (Sénéchal et al. 2011). They  
341 require less metabolic energy and time to digest compared to hard-shelled benthic prey (e.g.,

342 blue mussels, sea urchins) (Zhang et al. 2019), while simultaneously reducing the energetic costs  
343 of diving as females become more buoyant as they continuously accumulate needed fat stores for  
344 reproduction (Sénéchal et al. 2011). Conserving fat stores for their upcoming incubation fast is  
345 critical. Foraging on amphipods close to the colony may reduce the costs of commuting and  
346 foraging, and may be an important energy-conserving strategy.

347         Interestingly, we found that an inshore, smaller isotopic niche, predicted higher breeding  
348 propensity (Table 4; Fig. 1,3a). Previous studies have demonstrated that in years with later ice  
349 breakup, females were less likely to breed (Jean-Gagnon et al. 2018). Additionally, previous  
350 research at EBI has shown that unpredictable food shortages during the RFG stage reduce the  
351 probability that an individual breeds, regardless of reproductive readiness (Legagneux et al.  
352 2016), suggesting that reproductive decisions are highly responsive to environmentally driven  
353 changes in resource availability typically related to ice cover and access to prey (see below).  
354 Considering the short Arctic breeding season (Lepage et al. 2000) and the role that ice dynamics  
355 play in impacting the decision to breed (Jean-Gagnon et al. 2018), the relationship between  
356 breeding propensity and isotopic niche may only be evident in years with the greatest  
357 environmental, and therefore, energetic constraints and may only impact individuals with lower  
358 body condition.

359

#### 360 *Lack of a relationship between environmental conditions and isotope values*

361 We predicted that in years with milder winters, milder springs, and higher overall ambient  
362 temperatures, there would be more open water and a wider variety and quantity of prey items  
363 available, resulting in a broader colony-based isotopic niche. In contrast, we only detected a  
364 significant, negative relationship between trophic position (ISOPC3) and pre-breeding NAO

365 (ENVPC2) (Table 3). In years with higher winter storm activity and milder springs at EBI (i.e.,  
366 breeding grounds), females had a greater range and variance in  $\delta^{15}\text{N}$  values on breeding grounds,  
367 potentially related to accessing resources from multiple trophic levels. In years with harsh winter  
368 conditions, mussel beds and other prey sources may be depleted due to the increased storm  
369 activity on wintering grounds (Reusch and Chapman 1995). Consequently, eiders may employ a  
370 more generalist foraging strategy upon arrival to breeding areas to compensate for diminished  
371 abundance of preferred prey during winter explaining the higher MNND values calculated during  
372 these conditions. Similarly, we predicted that  $\delta^{13}\text{C}$  would also be strongly related to  
373 environmental indices, but this relationship was not observed (Table 3). This was surprising  
374 considering that eiders are known to adjust their foraging areas based on extent of sea ice (Jean-  
375 Gagnon et al. 2018), and given the impacts of environmental conditions on regional sea-ice  
376 dynamics near the nesting colony, although we are still learning about benthic-pelagic coupling  
377 in the marine system. However, since variation in  $\delta^{13}\text{C}$  is largely driven by input from primary  
378 producers, it is possible that the lack of diversity of primary production around the nesting  
379 colony in EBI, consistent with the circumpolar Arctic (Ramírez et al. 2017), limits our ability to  
380 detect a relationship between  $\delta^{13}\text{C}$  and environmental conditions. Thus, the ability to apply bulk  
381 stable isotopes in this context could be constrained by the biogeochemical processes of isotopic  
382 incorporation (see Boecklen et al. 2011, Whiteman et al. 2021). Combining compound-specific  
383 stable isotope analyses of individual amino acids and spatial tracking will provide future  
384 opportunities to investigate colony-level resiliency to changes in prey availability predicted by  
385 climate change.

386

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397

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699 **Table 1** - List of principal component correlation values based on plasma isotopic metrics  
700 derived from bulk d15N and d13C values of female common eiders breeding at the East Bay  
701 Island, Nunavut, Canada and environmental metrics (see Methods for details). Bold values  
702 indicate statistically significant relationships at the alpha level of 0.05.  
703

<b>Group</b>	<b>Variable</b>	<b>ISOPC1 (Spatial Foraging)</b>	<b>ISOPC2 (Niche Breadth)</b>	<b>ISOPC3 (TP)</b>
Isotopic	Y Range	0.20201	<b>0.51061</b>	<b>-0.57323</b>
	X Range	<b>0.45855</b>	0.13017	-0.12389
	MNND	-0.17996	<b>0.40414</b>	<b>0.63032</b>
	SEAc	<b>0.47159</b>	0.1755	0.08766
	AVG $\delta^{13}\text{C}$	0.29675	<b>-0.58426</b>	0.19752
	%CV $\delta^{13}\text{C}$	<b>-0.42799</b>	0.08641	-0.13040
	AVG $\delta^{15}\text{N}$	-0.35635	0.21296	0.01793
	CV $\delta^{15}\text{N}$	0.30971	0.36609	<b>0.44129</b>
Eigenvalue		3.7445	1.4859	1.2791
Cum. Percent		46.806	18.574	15.989
<b>Group</b>	<b>Variable</b>	<b>ENVPC1 (Spring)</b>	<b>ENVPC2 (NAO)</b>	
Environment	S NAO	<b>0.6001</b>	<b>-0.53296</b>	
	W NAO	0.35475	<b>0.84569</b>	
	Ta	<b>-0.71696</b>	-0.02764	
Eigenvalue		1.1305	1.0078	
Cum. Percent		37.685	33.592	

704  
705

706 **Table 2** - Summary of MANCOVA and ANCOVA analyses examining predictors of variance in  
 707 plasma  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in female common eiders breeding at the East Bay Island, Nunavut,  
 708 Canada. Bold values indicate statistically significant relationships.  
 709

Analysis	Variable	F	df	p
MANCOVA ( $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ )	Full Model	4.35	74, 1198	0.0001
	Year	5.22	16, 1198	<b>0.0001</b>
	Breeding stage	2.97	2, 600	<b>0.03</b>
	Year*Breeding stage	1.41	48, 1198	<b>0.04</b>
	Relative arrival date	19.50	2, 599	<b>0.0001</b>
	Body Mass	0.50	2, 599	0.61
ANCOVA ( $\delta^{15}\text{N}$ )	Full Model	5.92	37, 600	0.0001
	Year	8.67	8, 8	<b>0.0001</b>
	Breeding stage	2.96	3, 3	<b>0.03</b>
	Year*Breeding stage	1.31	24, 24	0.15
	Relative arrival date	1.41	1, 1	0.23
	Body Mass	0.13	1, 1	0.71
ANCOVA ( $\delta^{13}\text{C}$ )	Full Model	2.82	37, 600	0.0001
	Year	1.15	8, 8	0.33
	Breeding stage	0.56	3, 3	0.64
	Year*Breeding stage	1.34	24, 24	0.13
	Relative arrival date	27.00	1, 1	<b>0.0001</b>
	Body Mass	0.51	1, 1	0.47

711 **Table 3** - Summary of ANCOVA analyses using environmental metrics (ENVPC1 (Spring  
712 Weather); and ENVPC2 (NAO)) to predict variation in plasma isotopic metrics (ISOPC1 (Spatial  
713 Foraging Location); ISOPC2 (Niche Breadth); and ISOPC3 (Trophic Position)) in female  
714 common eiders breeding at the East Bay Island, Nunavut, Canada. Bold values indicate  
715 statistically significant relationships.  
716

Variable	ISOPC1			ISOPC2			ISOPC3		
	R <sup>2</sup>	F <sub>2,6</sub>	p	R <sup>2</sup>	F <sub>2,6</sub>	p	R <sup>2</sup>	F <sub>2,6</sub>	p
Full Model	0.02	0.07	0.93	0.10	0.35	0.72	0.62	4.88	<b>0.06*</b>
ENVPC1	-	0.12	0.74	-	0.17	0.69	-	1.50	0.27
ENVPC2	-	0.03	0.86	-	0.53	0.49	-	8.26	<b>0.03</b>

717 \*Marginal significance (see Results).

718 **Table 4** - Summary of ANCOVA analyses between breeding parameters (relative arrival date  
719 (RAD); percent breeding propensity (BP); delay before laying (delay); relative lay date (RLD))  
720 and isotopic metrics (ISOPC1 (Spatial Foraging Location); ISOPC2 (Niche Breadth); and  
721 ISOPC3 (Trophic Position)).  
722

PC	RAD			BP			Delay			RLD		
	R <sup>2</sup>	F <sub>1,1</sub>	p	R <sup>2</sup>	F <sub>1,1</sub>	p	R <sup>2</sup>	F <sub>1,1</sub>	p	R <sup>2</sup>	F <sub>1,1</sub>	p
Model	0.3	0.84	0.53	0.7	4.48	<b>0.07*</b>	0	0.02	1.00	0.2	0.51	0.70
ISO1	-	0.16	0.70	-	0.62	0.47	-	0.03	0.87	-	0.01	0.91
ISO2	-	1.57	0.27	-	12.67	<b>0.02</b>	-	0.00	0.97	-	1.25	0.31
ISO3	-	0.79	0.42	-	0.15	0.72	-	0.02	0.91	-	0.25	0.64

723 \*Marginal significance (see Results).

724 **Figure 1** - Inter-annual variation in plasma isotopic niche of eiders nesting at East Bay Island,  
725 NU, Canada. Each colour indicates a different year. Ellipses represent 40% of the individuals'  
726 isotopic values that comprise the sampled population within each year. Ellipses are used to  
727 represent the placement of birds within each year in isotopic space and compare placement  
728 among years.

729

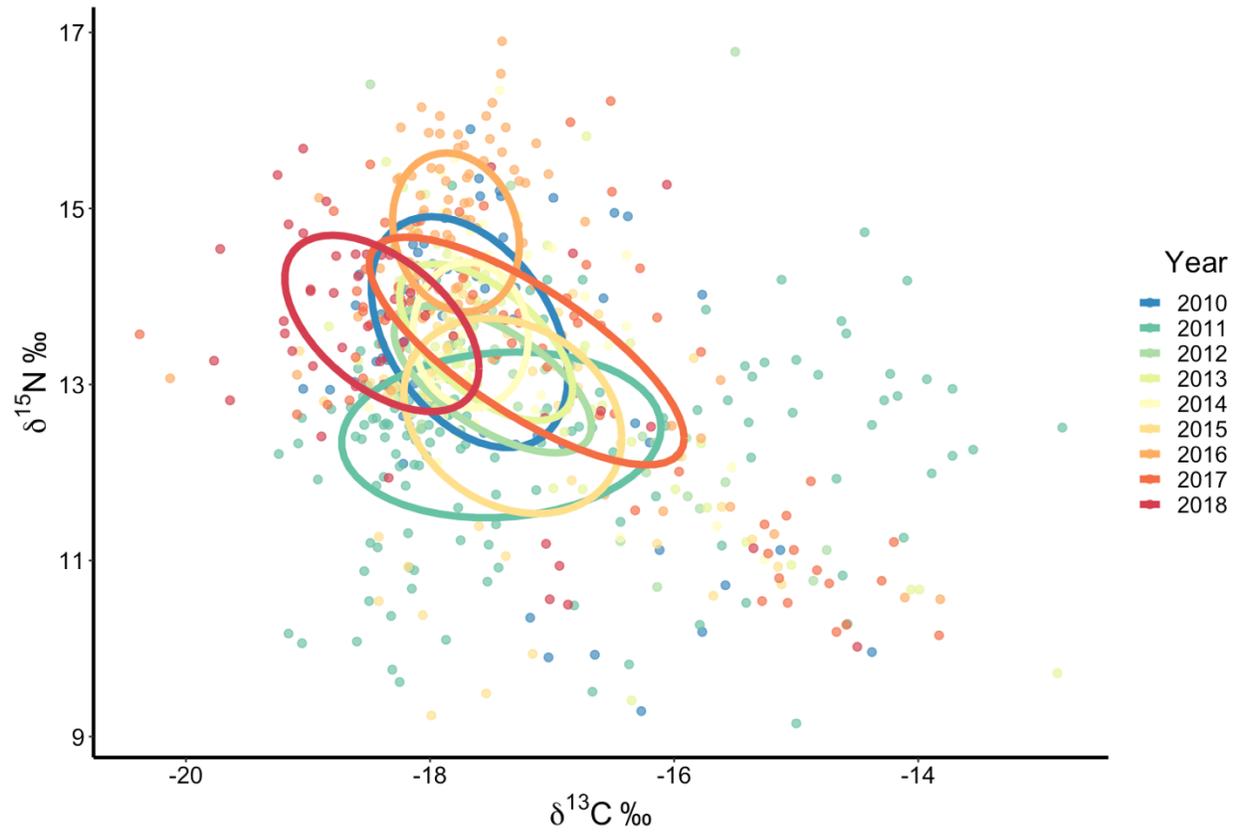
730 **Figure 2** - Breeding stage-related variation in plasma isotopic niche of eiders nesting at East Bay  
731 Island, NU, Canada. PR (green line; pre-recruiting), shows 40% of the individuals which started  
732 laying at least 8 days post-capture; RFG (blue line; rapid follicle growth), is characterized by  
733 birds that are delayed between 8-1 days before breeding and Lay (red line; laying or incubating)  
734 is the 40% ellipse of birds during laying or incubation the same day of capture.

735

736 **Figure 3** - Variation in plasma  $\delta^{13}\text{C}$  (A), and  $\delta^{15}\text{N}$  (B) values across breeding stages of female  
737 eiders nesting on East Bay Island. Values are represented as mean  $\pm$  SEM provided for each day  
738 during pre-breeding (black circle), rapid follicle growth (black square), and laying (black  
739 triangle). The size of the data points represents the sample size. Dashed, vertical lines represent  
740 statistically significant change in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values detected from breakpoint analyses.

741 **Figure 1**

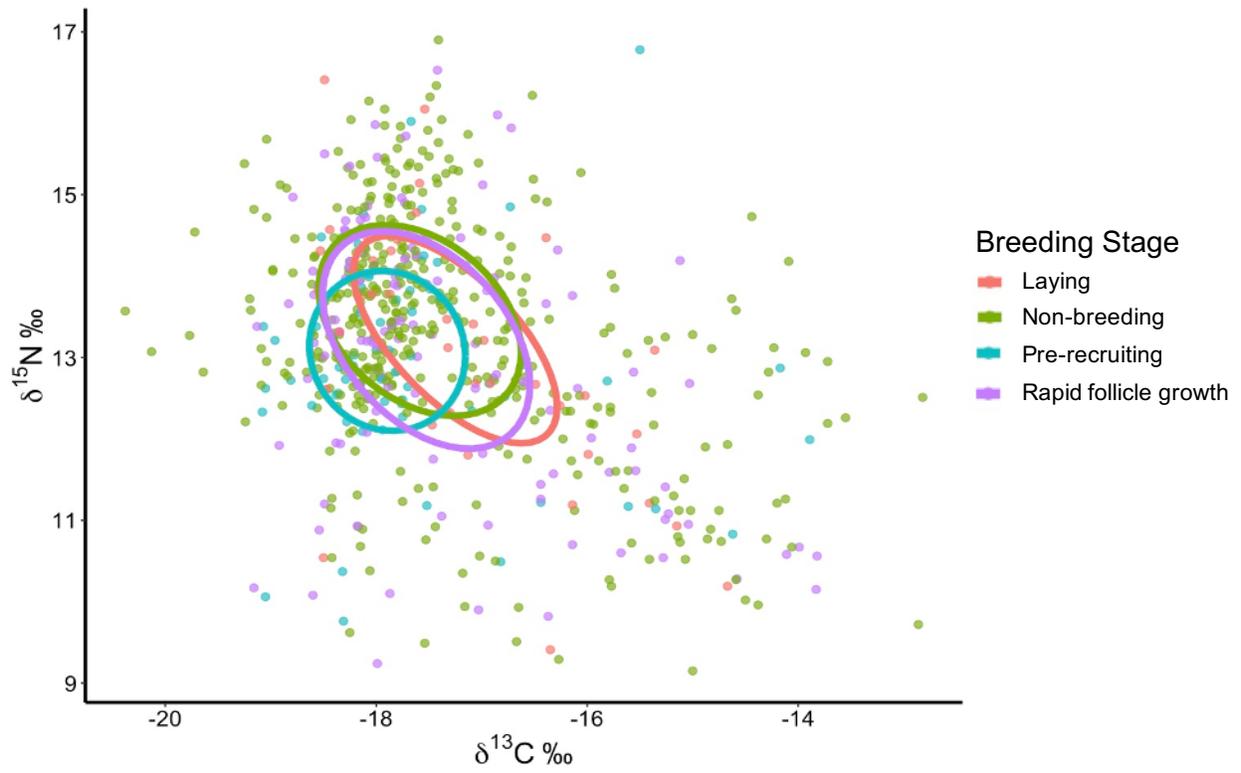
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744 **Figure 2**

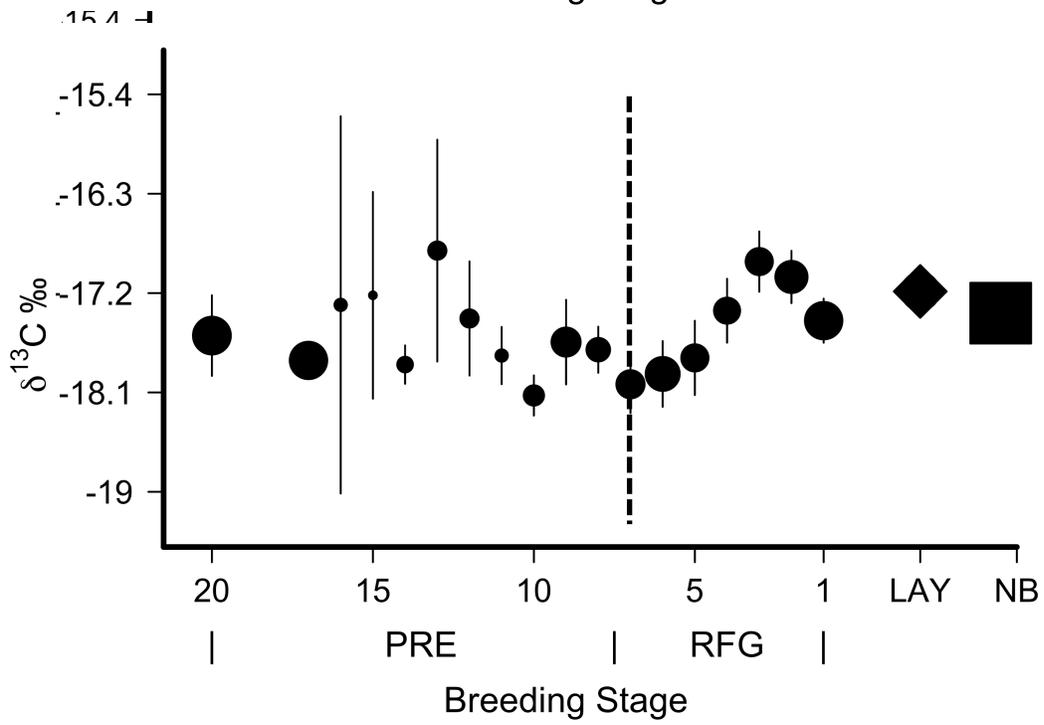
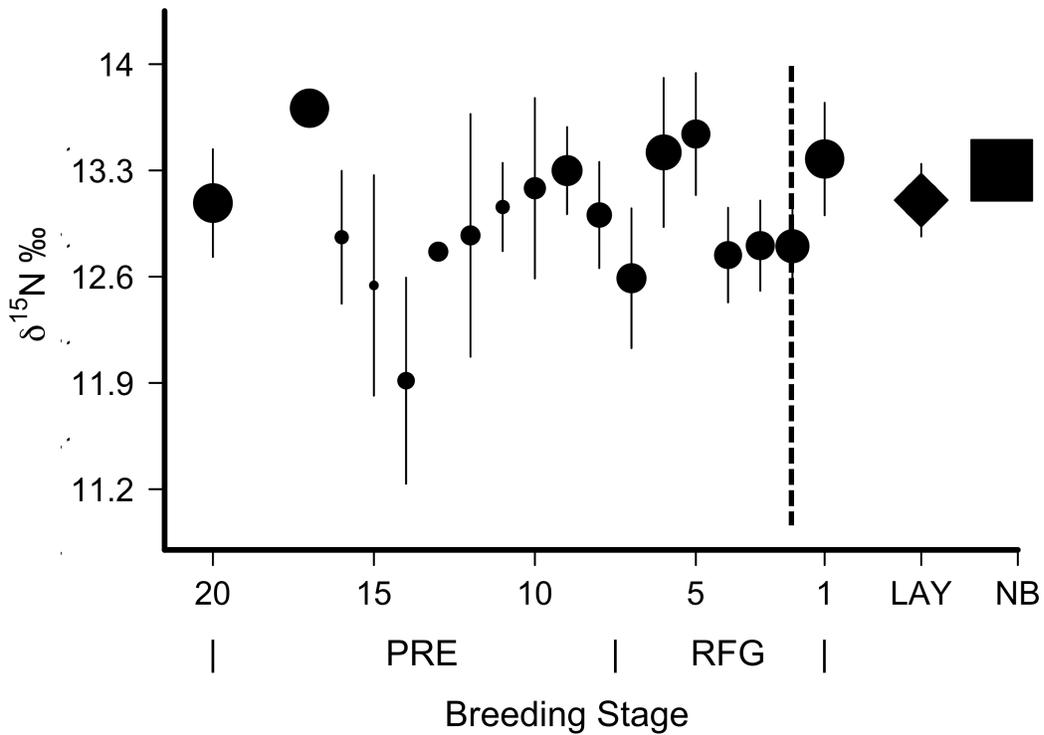
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747 **Figure 3**

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