



Stable isotopes of carbon reveal flexible pairing strategies in a migratory Arctic bird

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Received: 1 October 2018 / Revised: 8 March 2019 / Accepted: 25 March 2019 / Published online: 13 April 2019
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Abstract

Many birds change their partners every year and pairing may occur before arrival on the breeding grounds. Early pairing strategies can benefit mates by strengthening pair-bonds and increasing the rate of pre-breeding resource acquisition, leading to increased reproductive output and success, especially for migratory species breeding in seasonally-constrained environments like the Arctic. Despite the theorized and documented advantages of early pairing, we know rather little about pairing phenology in many species. Here, we test the use of a stable isotope (carbon $\delta^{13}\text{C}$) method to assign geographic origin of paired birds to examine pairing phenology in Arctic-breeding Common Eiders (*Somateria mollissima borealis*). During two consecutive years, we captured paired individuals upon their arrival at breeding grounds approximately 2–3 weeks before laying. Pairs with similar $\delta^{13}\text{C}$ in their claws indicates that they paired during winter, while similar blood values (with no similarity in claws) would reveal pairs formed much later, during the pre-breeding period near or on the breeding grounds. While a large proportion of pairs (43%) appeared to pair on wintering grounds, an almost equal number (52%) likely paired within 1 month prior to arrival on the breeding grounds. The remaining 5% did not have an obvious pairing time. Despite this variability in pairing phenology, we found no significant differences in bodycondition between females or males which paired in winter or spring. In the year characterized with more challenging winter conditions, pairs formed in spring tended to have a higher breeding propensity than those formed in winter, although there were no detectable links to body condition. Delaying pairing until spring may be advantageous for Arctic-breeding eiders, although a specific mechanism is unknown. Future research focusing on the energetic costs and benefits for male eiders during these periods would help further understand pairing phenology and potential impacts on males of female breeding decisions.

Keywords Pair bond · Pairing phenology · Sea duck · Spring staging · Stable isotope analysis · Winter migration

Zusammenfassung

Stabile Isotope des Kohlenstoffs offenbaren flexible Paarungsstrategien bei einem arktischen Zugvogel

Viele Vögel wechseln jedes Jahr ihren Partner, wobei Paarbildungen bereits vor der Ankunft im Brutgebiet entstehen können. Bei der Strategie, sich frühzeitig zu verpaaren, können die Partner von einer stärkeren Paarbindung und einem erhöhten Maß der Ressourcennutzung während der Vorbrutzeit profitieren. Dies kann vor allem bei Zugvogelarten, die in Regionen mit jahreszeitlich begrenzt günstigsten Bedingungen wie der Arktis brüten, zu einer Erhöhung von Reproduktionsleistungen und -erfolg führen. Trotz der theoretisierten und dokumentierten Vorteile der frühzeitigen Paarbildung wissen wir bei vielen Arten ziemlich wenig über die Phänologie der Paarung. Wir testeten die Anwendung der Stabilisotopenmethode (Kohlenstoff $\delta^{13}\text{C}$), um die geographische Herkunft der verpaarten Vögel zu bestimmen und somit die Phänologie der Paarung bei den in arktischen Regionen brütenden Eiderenten (*Somateria mollissima borealis*) zu untersuchen. In zwei aufeinanderfolgenden Jahren haben wir verpaarte Individuen nach deren Ankunft im Brutgebiet ungefähr 2–3 Wochen vor der Eiablage gefangen. Paare mit ähnlichen $\delta^{13}\text{C}$ -Werten in den Krallen weisen darauf hin, dass die Paarbildung im Winter stattfand, wohingegen ähnliche Blutwerte, jedoch keine ähnlichen $\delta^{13}\text{C}$ -Werte in den Krallen, zeigen würden, dass die Paarbildung viel später

Communicated by F. Bairlein.

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im Laufe der Vorbrutzeit in Brutgebietsnähe erfolgt wäre. Es zeigte sich, dass sich ein großer Anteil der Paare (43%) bereits in den Überwinterungsgebieten bildete, während sich ein ungefähr gleichgroßer Teil (52%) vermutlich erst innerhalb eines Monats vor Ankunft im Brutgebiet verpaarte. Die verbleibenden 5% hatten keinen eindeutigen Paarungszeitpunkt. Ungeachtet der Variabilität in der Phänologie der Paarung konnten wir zwischen Weibchen und Männchen, welche sich im Winter oder Frühjahr verpaarten, keine signifikanten Unterschiede in der Körperkondition finden. In dem Jahr, in dem schwierigere Winterbedingungen herrschten, tendierten im Frühjahr entstandene Paare zu einer höheren Brutbereitschaft als die im Winter entstandenen Paare, wenngleich es keinen feststellbaren Zusammenhang mit der Körperkondition gab. Eine Verzögerung der Paarung bis in das Frühjahr hinein könnte vorteilhaft für die in arktischen Regionen brütenden Eiderenten sein, auch wenn der genaue Mechanismus dahinter unbekannt ist. Zukünftige Forschungen zu den energetischen Kosten und Nutzen der männlichen Eiderenten während dieser Zeiträume würden dazu beitragen, die Phänologie der Paarung und die möglichen Folgen der weiblichen Brutentscheidungen für die Männchen zu verstehen.

Introduction

The ability for individuals to optimally time life-history events can be a key driver of variation in fitness. For example, in seasonally-breeding birds, migration and reproduction are often timed to match peak resource and territory availability on the breeding grounds (Drent et al. 2003; Descamps et al. 2011), with the aim of ensuring an optimal laying date that maximizes the probability of offspring survival (Love et al. 2010; Rockwell et al. 2012; Hennin et al. 2016a). An important potential driver of (or constraint on) variation in the phenology of seasonal breeding is the location of mate pairing given its potential influence on the timing of arrival at breeding grounds during spring migration, and by extension the timing of laying with correlated effects on clutch size, hatching dates, and fledging dates (Spurr and Milne 1976; Bluhm 1988; Hennin et al. 2018).

Within the waterfowl family (Anatidae), a key factor affecting the timing of pair formation is whether pairing provides some discernible benefit to a mate (e.g., by conferring a competitive advantage to resource accrual and foraging success), or by providing mate defense benefits to the guarding sex (Fowler 1995; Robertson et al. 1998). Since waterfowl populations often have male-biased sex ratios (Rohwer and Anderson 1988), females can afford to be choosy in their selection of a mate (Rodway 2007), and sexual selection is expected to favor pair formation as early as possible before breeding (Bluhm 1988; Rohwer and Anderson 1988). As such, in a number of species, pair formation can even occur as early as immediately following the previous breeding season (e.g., American Wigeon *Anas americana*, Mini et al. 2014; Harlequin ducks *Histrionicus histrionicus*, Robertson et al. 1998). Although the phenology of seasonal pair formation varies significantly across species and can be driven by differences in life history, breeding strategies, and levels of parental investment (Rohwer and Anderson 1988), we know rather little about the influence of pairing date and location on downstream performance or fitness traits. Males

of most waterfowl species typically do not engage in incubation or offspring-rearing behaviors, but they can nonetheless invest during pre-breeding via the defense of their female mates which maximizes pre-laying foraging success (Rodway 2007). Given the known influence of pre-breeding body condition on fitness proxies such as laying date, clutch size, and hatching date (Descamps et al. 2011; Hennin et al. 2016a, 2018), the timing of pairing, and how it influences breeding investment, may be key to both male and female fitness. However, in highly seasonal environments such as the Arctic, individuals might be reluctant to pair in winter due to potentially greater resource limitations and because there is considerable variation in ultimate overwintering destination, the choice of which is linked to individual pre-migratory condition (Bottitta et al. 2003). Unfortunately, studying pairing phenology in any seasonally-breeding seabird system remains difficult since individuals tend to overwinter in remote locations and spend the pre-breeding period offshore (Merkel et al. 2006), limiting the possibility of directly observing winter and spring behavior among males and females.

Here, we apply a recently developed method for determining the overwinter location of Common Eiders, based on stable isotope analysis (Steenweg et al. 2017), to examine the phenology of pair formation and its subsequent downstream effects on breeding decisions in Arctic-nesting Common Eiders (*Somateria mollissima borealis*). We examine these questions within an Arctic-breeding colony (East Bay Island, Nunavut, Canada), which uniquely enabled us to simultaneously capture both mates prior to breeding, assess their wintering location and arrival body condition, and then later observe breeding behaviors (breeding propensity and laying date) and reproductive investment (clutch size). Previous remote tracking of eiders breeding at this colony revealed two primary overwinter locations: Southwest Greenland and Newfoundland, Canada (Mosbech et al. 2006), characterized by different winter climatological conditions (Descamps et al. 2010). Common Eiders arriving

at the breeding colony at East Bay have isotopic values in their claw tips that indicate their wintering grounds in either Newfoundland or Western Greenland, 90–110 days before sampling (Steenweg et al. 2017). Stable isotope ratios in different tissues reflect assimilated diet based on location, diet, and the growth or turnover rate specific to each tissue (Hobson 1999; Clark et al. 2006). Values in red blood cells (hereafter: blood), which has a quicker turnover rate, reflect their more recent spring-staging period 30–40 days before sampling (Oppel and Powell 2010; Steenweg et al. 2017). As such, we aimed to use the tissue-specific turnover rates of stable isotopes in claws and red blood cells to examine whether eiders form their pairs in the winter or spring. A strong correlation between paired members in claw isotopic values would suggest pairing occurred in winter, while a strong correlation in blood (and a corresponding weak correlation in claws) would suggest pairing in spring.

Methods

Study area and sample collection

Common Eiders (hereafter eiders) breeding on East Bay Island (Migratory Bird Sanctuary, Nunavut, Canada; 64°02'N, 81°47'W) overwinter off the coast of either Newfoundland, Canada, or Western Greenland (Mosbech et al. 2006), and arrive at the staging areas in the spring during their staging period in late May to early June; they arrive at the breeding colony in early June, before laying in late June (Jean-Gagnon et al. 2018). During the spring staging and pre-breeding periods in mid-May to late June, female eiders must forage locally to both invest in reproduction (Sénéchal et al. 2011; Hennin et al. 2015) and to obtain sufficient energetic stores to maintain a fasting incubation (Bottitta et al. 2003). We captured female eiders and their paired mates (given that male eiders closely follow their female mate up to and including the end of the egg-laying period; Hario and Hollmén 2004) using flight nets during the pre-breeding period from 19 June to 4 July 2015 ($n=40$ pairs) and from 21 to 30 June 2016 ($n=29$ pairs). We obtained both blood and claw samples from 65 of these pairs (2015: 38 pairs; 2016: 27 pairs, 130 individuals in total). We collected blood samples from the tarsal vein using a heparinized 23-gauge, 1 in. (2.54 cm), thin-wall needle and syringe, and stored samples in heparinized Eppendorf tubes which were kept cool. Blood was centrifuged at 10,000 rpm for 10 min, and red blood samples were separated from plasma and stored at -80°C until further analysis (Hennin et al. 2015). We collected claw samples by clipping the distal 2 mm from the middle toe of the left foot and stored them in small paper coin envelopes (Steenweg et al. 2017). Prior to release, all individuals were weighed, measured and banded with metal

and alpha-numeric darvic bands. In addition, females were outfitted with uniquely colored and shaped temporary plastic nasal tags attached through their nostrils with UV-degradable monofilament. Unique nasal tags enable the assignment of laying date and breeding investment through observation of individuals via multiple permanent blinds and spotting scopes (Descamps et al. 2009; Love et al. 2010).

Assignment of wintering location using stable isotopes

$\delta^{13}\text{C}$ in claws reflect approximately 90–110 days prior to sampling (Hopkins III et al. 2013). Recently, stable isotopes in claws have been successfully used to infer the winter location of individuals (blackcaps *Sylvia atricapilla*, Rolshausen et al. 2010; common eiders, Steenweg et al. 2017). Specifically, eiders have been successfully assigned to their wintering locations upon arrival at their breeding sites by comparing stable isotope values in claws collected from wintering birds to those collected from eiders arriving to their breeding grounds (Steenweg et al. 2017). In addition, since $\delta^{13}\text{C}$ in red blood cells reflects approximately 30–40 days prior to sampling (Hahn et al. 2012), they can be used in our study to infer a spring location since they coincide with the spring-staging periods (Steenweg et al. 2017). As such, here we use stable isotopes in claws and blood in arriving eiders during the pre-breeding period to reflect values from their winter and spring periods, respectively.

Blood samples were freeze-dried for 30 h and lipid-extracted to reduce the impact of lipids on $\delta^{13}\text{C}$ values, and surface oils were removed from claw samples. To extract the lipids and remove the surface oils from the blood and claw samples, a 2:1 chloroform:methanol solution was added to vials containing the samples, vortexed for 15 s and soaked for 24 h. Vials were centrifuged at 10,000 rpm for 10 min, the supernatant was then siphoned off with a pipette, and the samples were rinsed again with the chloroform:methanol solution, vortexed for 15 s, centrifuged, and the remaining supernatant was again siphoned. The samples were then dried under a fume-hood for 24 h. Subsamples of blood and claws were weighed to 0.30–0.50 mg and folded into a tin capsule. Stable isotope analysis was conducted at the Queen's Facility for Isotope Research, Queen's University (Kingston, Ontario, Canada) using a Costech ECS4010 coupled to a DELTA^{plus} XP Continuous-Flow Isotope Ratio Mass Spectrometer. All stable isotope results are reported within accuracy of 0.1‰ based on analyses of the international standard Vienna Pee Dee Belemnite and in house keratin (COW1: $-13.17\text{‰} \pm 0.21$, UC1: $-25.7\text{‰} \pm 0.14$) run alternately every five samples. Duplicates were run every nine samples with an accuracy of 0.2‰. All $^{13}\text{C}/^{12}\text{C}$ are reported in delta notation (δ) in parts per mil (‰).

Data analysis

We used two methods to determine the relative phenology of pair formation in eiders. First, we used linear regression analyses to investigate the strength of the relationship between the stable isotope values of paired females and males using claw (winter) and blood (spring) samples. Secondly, to identify overwintering locations, we used a *k*-means cluster analysis (Garcia-Perez and Hobson 2014; Pomerleau et al. 2014) of $\delta^{13}\text{C}$ obtained from claws of pre-breeders, and set the starting centroid values to those obtained from eiders captured and sampled at each overwintering location (Greenland and Newfoundland; Steenweg et al. 2017). We then calculated the 'ordinal distance' between the $\delta^{13}\text{C}$ values in claws (winter) and blood (spring) by taking the absolute value of the numerical difference between isotopic values in each pair. We assumed individuals overwintering or migrating in proximity to each other will have similar isotopic values. As a proxy for similarity, we use the standard deviation (SD) of $\delta^{13}\text{C}$ values acquired from previously published values of the claw (0.59‰) and blood (0.86‰) samples obtained from individuals in their overwintering areas (Steenweg et al. 2017; this study). $\delta^{13}\text{C}$ claws values of paired individuals within one SD were considered isotopically similar and we assumed those pairs wintered in the same location. If $\delta^{13}\text{C}$ claw values from paired individuals differed by more than one SD, we considered those individuals to winter in separate locations even if their general wintering area (inferred from $\delta^{13}\text{C}$ values) was similar. Although eiders breeding at East Bay Island generally overwinter in either Newfoundland or Western Greenland, they may nevertheless cover large areas within each region (Mosbech et al. 2006). Therefore, individuals of the same pair may winter in the same general region, but spend time in geographically distant portions of that region. Paired individuals could therefore experience different ecological conditions and consume different prey items with dissimilar isotopic values. There is variability in stable isotope values in coastal habitats. Individuals with dissimilar isotopic values are unlikely to have been geographically close together even if they were foraging on similar prey, as the stable isotopes of carbon change with latitude (Graham et al. 2010). In addition, we conducted a sensitivity analysis by considering different threshold values with ordinal distances of 0.5 and 1.5 times the SD. We then used a linear model to examine relationships among eiders who paired in the winter (claw $\delta^{13}\text{C}$ values) and during spring-staging (blood $\delta^{13}\text{C}$ values). We only included pairs in these analyses with claw or blood $\delta^{13}\text{C}$ values within the ordinal distance window, as we could not be confident in the timing of pairing of the others.

Finally, to investigate links between pairing phenology, female and male body mass and reproductive parameters, we used logistic regression analyses to examine relationships

between the timing of pairing (spring versus winter) and male and female arrival body mass, including year as a fixed effect. We subsequently used logistic regression analyses to examine the role that the timing of pairing and female body mass play in predicting the subsequent breeding propensity (females re-sighted breeding in the colony). We used linear models to examine the relationship between the timing of pairing and the interval between arrival at the colony and laying (pre-laying interval) and laying date of female eiders. Since body mass, timing of arrival and seasonal conditions are known to collectively impact reproductive decisions (Descamps et al. 2011; Harms et al. 2015; Hennin et al. 2016a, 2018), our null model consisted of body mass, capture date and year. We tested for additional effects of timing of pairing and interaction with year. If a significant interaction was found between year and pairing phenology, we broke down the interaction and provided the model summary for each year separately. All data analyses were conducted using R v.3.4.3 (2017-11-30) using packages MASS package (Venables and Ripley 2002) and cluster (Maechler et al. 2016).

Results

Patterns in pairing phenology

Linear models of the $\delta^{13}\text{C}$ values in claws and blood indicated that pairs had more similar isotopic values during the spring ($R=0.66$, $F_{(1,62)}=50.25$, $P<0.001$) compared to the winter ($R=0.35$, $F_{(1,67)}=10.79$, $P=0.001$; Fig. 1). Linear models of $\delta^{13}\text{C}$ values between individuals that paired in the winter and in the spring were statistically significant for 0.5, 1, and 1.5 times the SD ($P<0.001$ for all; Table 1) indicating that all of the three SD windows resulted in significant relationships between paired individuals. The strength of correlation was highest for 0.5 times the SD (winter: 0.98, spring: 0.83) compared to 1 times the SD (winter: 0.88, spring: 0.71, Fig. 2) and 1.5 times the SD (winter: 0.77, spring: 0.70) indicating that 0.5 times the SD shows the strongest relationship, but that any of the three SD windows could be used. Using 0.5, 1, and 1.5 times the SD resulted in 11, 3, and 1 pairs without a pairing time, respectively. Because using 0.5 times the SD resulted in more pairs without a pairing time, and decreased sample size, we used 1 times the SD for subsequent analyses.

To determine the timing of pairing, we used an ordinal distance of 1 times the SD in $\delta^{13}\text{C}$ between pairs (Fig. 3). Using this ordinal distance, 43% of pairs were isotopically similar on the wintering grounds ($n=17$ and 11 in 2015 and 2016, respectively), and 52% of the pairs were isotopically similar only at the spring staging area ($n=18$ and 16 in 2015 and 2016, respectively). Only three pairs (i.e., 5%; $n=3$ in

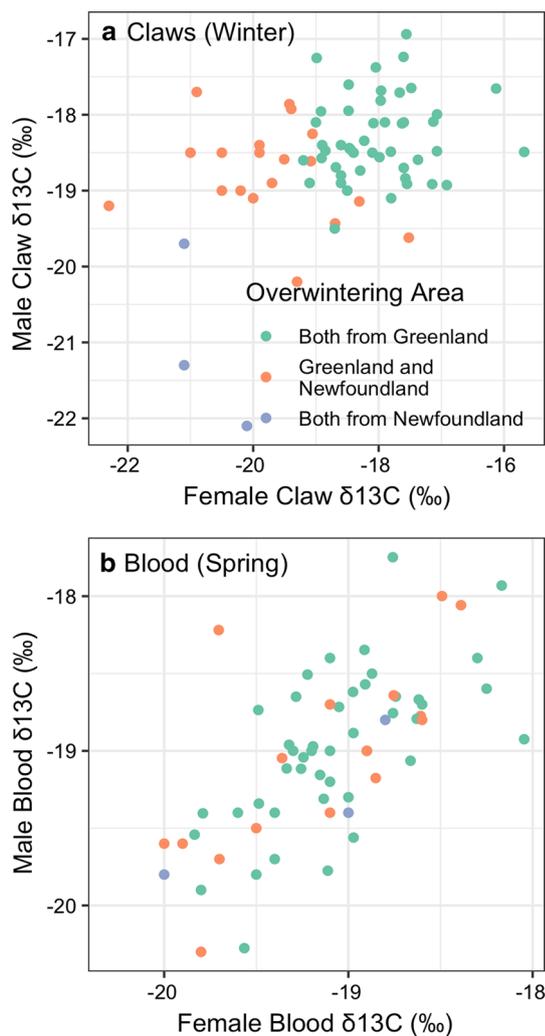


Fig. 1 Stable isotope values in the claws and blood of eider (*Somateria mollissima borealis*) pairs used to assign individuals to overwintering areas (see "Methods"). Claws represent winter values while blood represents more recent spring values

2015, $n=0$ in 2016) show no isotopic similarity in either period and were removed from subsequent analyses.

Links between pairing phenology and breeding

We estimated that, overall, 52% ($n=34$) of our sampled eiders paired in the spring, and 43% ($n=28$) paired in the winter. Of those, in 2015, 63% ($n=10$) of the breeding eiders paired in the spring and in 2016, 50% ($n=4$) of breeding birds paired in the spring (Table 2). Logistic regressions indicated that the timing of pairing was not significantly related to female or male body mass (female: timing of pairing: $P=0.52$, year: $P<0.001$, $df=2$, 58; male: timing of pairing: $P=0.54$, year: $P=0.003$, $df=2$, 58). The timing of pairing had a near-significant relationship with breeding propensity, and female body mass significantly predicted

breeding propensity in 2015 ($P=0.07$ and $P=0.01$, respectively, $df=3$, 30; Table 3), but neither were significant in 2016 ($P=0.53$, $P=0.63$, respectively, $df=3$, 23). However, the timing of pairing showed no significant link to the pre-laying interval or laying date (Table 4).

Discussion

Using a recently validated isotopic method for determining the overwinter location of eiders (Steenweg et al. 2017), we show that eiders breeding at East Bay Island in the Canadian Arctic exhibit variable pairing strategies, with some birds pairing on the overwintering grounds in Western Greenland and Newfoundland, others during spring staging, and very few individuals with unknown timing of pairing, potentially having paired on the breeding grounds. Of the eiders with conclusive pairing phenology, 55% of pairs adopted a spring-pairing strategy (2015: 51%; 2016: 59%), while 45% (2015: 49%; 2016: 41%) adopted a winter-pairing strategy. These findings provide new information about the breeding biology of Arctic-breeding eiders, elucidates mixed pairing strategies amongst breeding eiders, and suggests that variation in pairing strategies could have downstream impacts on breeding.

Patterns of pairing phenology in northern Common Eiders

Previously, little was known about the timing and variability of pair formation in Arctic eiders, other than they were expected to pair in the spring (Goudie et al. 2000). Since many populations of eiders winter and breed in remote areas, it is not possible to directly observe when pairing occurs compared to in other duck species (Heitmeyer 1995). Our results indicate that it is (1) possible to infer the timing of pairing using stable isotope analysis and (2) Arctic-breeding eiders appear to employ both spring- and winter-pairing strategies.

Differences in pairing strategies may be driven by age or experience. Within eiders in Scotland, younger females formed pairs later in the winter compared to older females which paired in the fall (Spurr and Milne 1976). Later-formed pairs typically laid later in the summer or not at all, whereas earlier-formed pairs laid throughout the season and were more successful. For this temperate population, later pairings were mostly made up of younger birds, and females pairing early probably benefited from male-assisted winter foraging compared to unpaired females (Spurr and Milne 1976). Similarly, the differences in pairing strategies in East Bay eiders could be driven by age or experience—with few known-age birds within this study colony, it is not possible

Table 1 Results of sensitivity analysis comparing the relationship in stable isotope values between paired male and female eiders (*Somateria mollissima borealis*)

Time period paired	Ordinal distance	Variable	Estimate (SE)	<i>t</i>	<i>F</i> (<i>df</i>)	<i>P</i>	<i>R</i>
Winter	0.5	Intercept	− 1.03 (0.87)	− 1.18	398.6 (1, 13)	0.26	0.98
		δ¹³C in claws	0.94 (0.04)	19.97		< 0.001	
Spring	0.5	Intercept	− 3.35 (1.70)	− 1.97	85.73 (1, 37)	0.056	0.83
		δ¹³C in blood	0.83 (0.09)	9.26		< 0.001	
Winter	1	Intercept	− 2.05 (1.65)	− 1.24	98.49 (1, 26)	0.225	0.88
		δ¹³C in claws	0.88 (0.09)	9.92		< 0.001	
Spring	1	Intercept	− 7.13 (1.98)	− 3.61	36.45 (1, 34)	< 0.001	0.71
		δ¹³C in blood	0.63 (0.10)	6.04		< 0.001	
Winter	1.5	Intercept	− 5.20 (1.79)	− 2.90	54.69 (1, 36)	0.006	0.77
		δ¹³C in claws	0.71 (0.10)	7.40		< 0.001	
Spring	1.5	Intercept	− 7.67 (2.20)	− 3.48	26.32 (1, 25)	0.001	0.70
		δ¹³C in blood	0.59 (0.11)	5.13		< 0.001	

These relationships were tested for 1, 0.5, and 1.5 times the SD (ordinal distance). Significant relationships are shown in bold

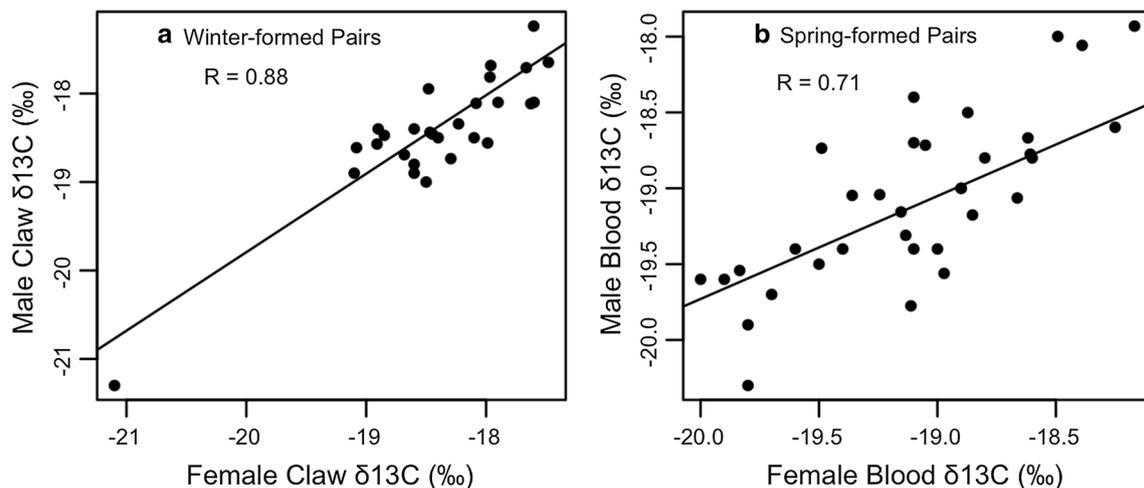


Fig. 2 Correlation of the stable isotopic values of common eider pairs inferred to have formed in the winter (a) and in the spring (b) shows a strong relationship for between individuals for both spring and winter formed pairs. The lowest isotopic value for winter is from a pair that

migrated from Newfoundland and therefore have much lower δ¹³-carbon as compared to the pairs which were inferred to have wintered in Greenland

to answer this question—or the benefits of winter pairing may differ between years.

Links between pairing location/phenology and breeding decisions

The skewed sex ratios (biased toward males) of most waterfowl species and populations favor female choice (Blums and Mednis 1996), where benefits to the female outweigh the costs to the male (Rohwer and Anderson 1988). For example, if paired female eiders have better access to limited resources in winter when paired, pair formation should occur as soon as possible (early winter; Bluhm 1988). Our

data suggest that eiders were able to pair during winter, and nearly half of the birds that we studied did so (Table 2). Previous work has shown that North Atlantic Oscillation (NAO) values during the winter are associated with survival in Arctic-breeding eiders; Common Eider populations have higher survival and body condition during years with a lower NAO (Guéry et al. 2017). The winter of 2015 was characterized as a harsher winter in Greenland with a more positive NAO value, with a higher incidence of storms compared with 2016 (NOAA 2017). In 2015, females pairing in spring tended to be more likely to breed than females that paired in winter. Although this trend was only nearly significant ($P=0.07$), 55% of the spring-paired birds bred that year

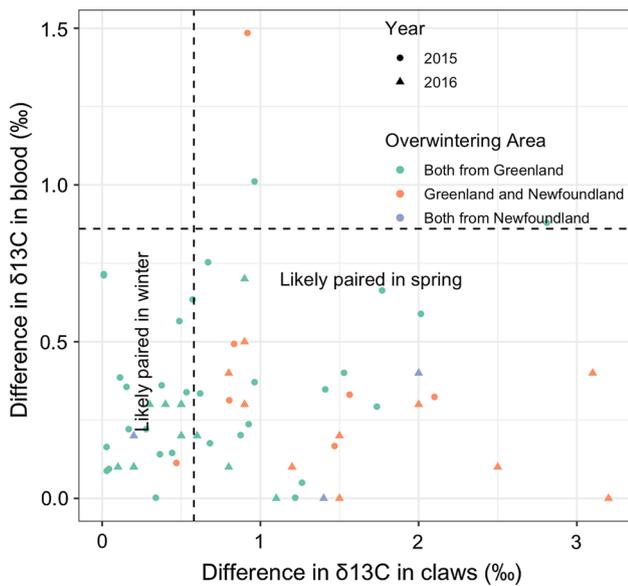


Fig. 3 The difference in stable isotopic values within pairs in both blood and claws. The vertical dotted line is drawn at the first SD of the stable isotope values in the claws of known overwintering eiders, the horizontal dotted line is at the first SD of the stable isotopic values in the blood of eiders

compared to 35% of the winter-paired birds. In 2016, when the NAO index indicated a lower incidence of storms, the proportions were reversed; 25% of the spring-paired birds bred compared to 36% of the winter-paired birds, suggesting some disadvantage to pairing in harsh winters.

Newfoundland and Western Greenland are both influenced by the NAO, but in opposite ways (Descamps et al. 2010; NOAA 2017). In years when the NAO is in a strong positive phase, such as in 2015 (1.17 average between February and April; NOAA 2017), there tends to be below-average temperatures in Greenland with a high incidence of storms, and above-average temperatures in Newfoundland, with most of the eiders wintering in Greenland (90%; Steenweg et al. 2017). These cold temperatures and frequent winter storms may have constrained the eiders’ ability to optimally thermoregulate, contributing to declining condition through the winter (Merkel et al. 2006). In any given year, the condition of eiders returning to East Bay for the spring-staging and pre-breeding periods can be highly variable (body mass ranges from 1700 to 2600 g; Descamps et al. 2011), which is a testament to the energetic demands that Arctic winters and subsequent migration can impose. However, our data suggest

Table 2 The breeding decisions of eiders which formed their pairs on the overwintering grounds (winter) and in spring staging areas (spring); results obtained from using the ordinal distance of less than 1 SD

Year	Breeding decision				Total
	Non-breeding		Breeding		
	Proportion paired in spring (n)	Proportion paired in winter (n)	Proportion paired in spring (n)	Proportion paired in winter (n)	
2015	0.42 (8)	0.58 (11)	0.63 (10)	0.37 (6)	35
2016	0.63 (12)	0.37 (7)	0.50 (4)	0.50 (4)	27

Table 3 Results of logistic regression models investing effects of the timing of pair formation on the breeding decision of pairs

Year	Response	Variable	Estimate (SE)	z	df	P
2015 and 2016	Breeding propensity	Intercept	11.57 (14.86)	0.778	(5, 55)	0.44
		Timing of pairing	− 1.34 (0.81)	− 1.65		0.09
		Female mass	0.005 (0.002)	2.49		0.01
		Year	− 2.67 (0.97)	− 2.74		0.006
		Capture date	− 0.13 (0.08)	− 1.52		0.13
		Timing of pairing:year	2.11 (1.23)	1.71		0.09
2015	Breeding propensity	Intercept	− 1.35(17.2)	− 0.08	(3, 30)	0.94
		Timing of pairing	− 1.60 (0.90)	− 1.78		0.07
		Female mass	0.008 (0.003)	2.52		0.01
		Capture date	− 0.09 (0.10)	− 0.89		0.37
2016	Breeding propensity	Intercept	68.88 (45.18)	1.52	(3, 23)	0.13
		Timing of pairing	0.59 (0.95)	0.62		0.53
		Female mass	0.002 (0.003)	0.48		0.63
		Capture date	− 0.41 (0.25)	− 1.66		0.09

Null model include female mass and capture date (see “Methods” for details). Because of a nearly significant effect of the year:pairing interaction, we analyzed years separately. Significant relationships are shown in bold

Table 4 Results of linear models investigating effects of the timing of pair formation on the interval between arrival and laying (pre-laying interval) and laying date of the female

Year	Response	Variable	Estimate (SE)	<i>t</i>	<i>df</i>	<i>P</i>
2015 and 2016	Pre-laying interval	Intercept	2418 (5307)	0.456	5, 18	0.654
		Timing of pairing	– 369.3 (736.9)	– 0.05		0.96
		Female mass	– 0.002 (0.006)	– 0.37		0.72
		Year	– 1.143 (2.63)	– 0.43		0.67
		Capture date	– 0.587 (0.202)	– 2.89		0.009
		Timing of pairing:year	0.183 (3.66)	0.05		0.96
2015 and 2016	Laying date	Intercept	2418 (5307)	0.456	5, 18	0.65
		Timing of pairing	– 369 (736.9)	– 0.05		0.96
		Female mass	– 0.002 (0.006)	– 0.37		0.72
		Year	– 1.143	– 0.43		0.67
		Capture date	– 0.413 (0.203)	2.04		0.06
		Timing of pairing:year	0.183 (3.66)	0.05		0.96

Models include female mass as it has been established to have a significant effect on reproductive decisions in eiders, capture date, year, and the timing of pairing and year interaction. Significant relationships are shown in bold

that the timing of pairing does not appear to directly link to a female's body mass at arrival on the breeding grounds, the interval between arrival and laying, nor laying date. The differences in pairing phenology between 2015 and 2016 may be driven by differences in winter climate and how individual eiders deal with it. Given that eiders wintering in Greenland tended to pair more in springtime, and that pairing in spring increased the likelihood of breeding that year, we can speculate that pair formation in winter is likely detrimental to winter survival and/or foraging success during such conditions, and that perhaps eiders are better off unpaired in harsh winters.

Further, because Arctic winters may be harsh and stormy, in some years it may be costly for males to invest energy into mate defense, eiders may require calm conditions in order to engage in courtship behaviors, and the benefits of defense may be low. In geese, females that are paired in the winter have more foraging opportunities to facilitate the accumulation of energy stores (Choinière and Gauthier 1995). Conversely, this may not be possible for diving ducks as the defense of underwater resources is near impossible. It has been suggested that female migratory waterfowl in the north may not have an advantage to gain more nutrition when paired during the winter (Rodway 2007). In addition, the potential for mate loss due to accidental separation during migration could also affect the male's readiness to pair early. As such, sometimes it may not be advantageous for pairs to form until their arrival at the spring-staging areas. Given this high variability in individual condition across years, it may be strategic for eiders to delay pair formation until spring in years with harsh winters, which would allow them to assess the condition of potential mates who survived the winter, rather than committing to one individual who could be in poor condition by the end of migration. In

contrast to 2015, the NAO in 2016 was in a weakly positive phase (0.90; NOAA 2017), which resulted in milder conditions in both Greenland and Newfoundland. As a result, relatively more eiders opted for Newfoundland, which suggests either competitive exclusion in Greenland when conditions are milder, and/or previously unavailable foraging opportunities in Newfoundland. Whatever the case, the consequence of the 2016 winter saw the formation of pairs in both winter and spring, which were equally as likely to breed in that year.

Implications of pairing decisions (in a changing world)

In eiders, only females are philopatric to their breeding sites (Robertson and Gilchrist 1998; Mckinnon et al. 2006; Lehikoinen et al. 2008). The demographics of the East Bay eider population are changing; the population of East Bay eiders has decreased from 8000 nesting pairs in 2006 to 1300 pairs in 2016 (Gilchrist, unpublished data), due to an avian cholera outbreak (Iverson et al. 2016) and several years of sustained polar bear predation of nests (Iverson et al. 2014; Dey et al. 2017), reducing local recruitment into the population. Currently, about 90% of the breeding population overwinters in Western Greenland (Steenweg et al. 2017), whereas in early 2000 approximately 60% of the population were overwintering there (Mosbech et al. 2006). While recruitment into the breeding population is low in the East Bay colony, eider populations in Western Greenland are increasing by about 12% per year (Merkel 2010), and most Greenland-breeding eiders also overwinter in Greenland (Mosbech et al. 2006). Since male–male competition in ducks tends to be high due to their skewed sex ratios, winter pair formation, with males following their female mates to the breeding colony, may be a way in which the East Bay

colony population is able to persist even though there has been little or no natal breeding recruitment. Genetic tools could be used to assess the demographic changes within the colony to determine how the colony continues to persist following multiple years of egg loss, and whether the timing of pair formation has changed as a result of these natural perturbations.

Furthermore, the differences between years indicate that there may be carry-over effects of winter condition to the timing of pairing and subsequently to breeding decisions. The earlier that the eiders lay, the more likely they are to be successful (Descamps et al. 2011; Hennin et al. 2016a) and laying date is mediated by the ability of females to accrue energy stores (Hennin et al. 2015), and therefore females may need to be paired by a certain date in order for males to defend them while foraging in spring. The costs and benefits of mate-defense during either period are thus far unknown. Further studies investigating the cost–benefit tradeoffs of paired individuals should elucidate how the timing of pairing is beneficial to both male and female eiders.

Acknowledgements We extend thanks to the East Bay Island Field crews of 2015 and 2016 for data collection, AV and EL for help with stable isotope analyses, JN and JA for essential help and ensuring our safety in the field, IB for data management, MJ for coordinating fieldwork and much more, and two anonymous reviewers for helpful comments in improving this manuscript. This work was supported by the Natural Sciences and Engineering Research Council of Canada (Discovery, Northern Supplement, and Graduate Scholarship Award programs), the Canada Research Chairs Program, the Northern Scientific Training Program, and the Polar Continental Shelf Program.

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