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RESEARCH ARTICLE

Identifying carry-over effects of wintering area on reproductive parameters in White-winged Scoters: An isotopic approach

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ABSTRACT

Events during one stage of the annual life cycle of migratory birds can have lasting (i.e. carry-over) effects that influence demographic parameters in subsequent seasons. We studied migratory connectivity and potential carry-over effects in a declining population of sea ducks. We measured stable isotope values of carbon (δ^{13}C) and nitrogen (δ^{15}N) in head feathers to assign breeding White-winged Scoters (*Melanitta fusca*; hereafter scoters) to either Atlantic or Pacific winter populations. The discriminant function for δ^{13}C and δ^{15}N correctly classified 93% of scoters sampled from these 2 winter areas. We then applied this classification scheme to head feathers of females breeding at Redberry Lake, Saskatchewan, and Cardinal Lake, Northwest Territories, to stratify each breeding population by winter provenance. We evaluated carry-over effects associated with winter location of females breeding in Saskatchewan by testing for differences in (1) nesting phenology, (2) clutch size, (3) mid-incubation body mass, (4) nest success, and (5) concentrations of trace elements contaminants of cadmium (Cd), mercury (Hg), selenium (Se), and lead (Pb) in blood, between strata of putative winter origin. Breeding females from the Atlantic coast had later dates of nest initiation, greater mid-incubation body mass, and also had higher concentrations of Cd (one year only), Pb, and Se, relative to birds from the Pacific. Neither nest initiation date nor mid-incubation body mass, however, were related to contaminant concentrations in blood. We found no differences in clutch size or nest success between putative winter strata. Our study detected carry-over effects in the Saskatchewan population that merit further attention.

Keywords: carbon-13, contaminants, *Melanitta fusca*, migratory connectivity, nitrogen-15, sea duck, stable isotopes, wintering grounds

Identificación de los efectos de arrastre del área de invernada sobre los parámetros reproductivos de *Melanitta fusca*: Un enfoque isotópico

RESUMEN

Los eventos durante una etapa del ciclo de vida anual de las aves migratorias pueden tener efectos duraderos (i.e. efectos de arrastre) que influencian los parámetros demográficos de estaciones subsecuentes. Estudiamos la conectividad migratoria y los potenciales efectos de arrastre en una población declinante de patos marinos. Medimos valores de isótopos estables de carbono, δ^{13}C, y nitrógeno, δ^{15}N, en las plumas de la cabeza para asignar a individuos reproductivos de *Melanitta fusca* a poblaciones ya sea del Atlántico o del Pacífico. La función discriminante para δ^{13}C y δ^{15}N clasificó correctamente 93% de los individuos muestreados de estas dos áreas de invernada. Luego aplicamos este esquema de clasificación a las plumas de la cabeza de hembras anidando en el Lago Redberry, Saskatchewan, y en el Lago Cardinal, Territorios del Noroeste, para estratificar cada población reproductiva con relación a la procedencia de invierno. Evaluamos los efectos de arrastre asociados con la localización de invierno de las hembras anidando en Saskatchewan analizando diferencias en (i) fenología de anidación, (ii) tamaño de la nidada, (iii) peso corporal a mediados de la incubación, (iv) éxito de anidación, y (v) concentraciones de trazas de elementos contaminantes (cadmio, Cd, mercurio, Hg, selenio, Se, y plomo, Pb) en la sangre, entre estratos de origen putativo de invierno. Las hembras reproductivas de la costa atlántica tuvieron fechas más tardías de iniciación del nido, mayor peso corporal a mediados de la incubación y también concentraciones más altas de Cd (solo un año), Pb y Se, con relación a las aves del Pacífico. Sin embargo, ni la fecha de iniciación del nido ni el peso corporal a mediados de la incubación se relacionaron con las concentraciones de contaminantes en la sangre. No encontramos diferencias en el tamaño de la nidada o en el éxito de anidación entre estratos putativos de invierno. Nuestro estudio detectó efectos de arrastre en la población de Saskatchewan que ameritan más atención.

Palabras clave: áreas de invernada, carbono-13, conectividad migratoria, contaminantes, isótopos estables, *Melanitta fusca*, nitrógeno-15, pato marino

INTRODUCTION

Birds, particularly migrants, may use multiple habitats that can be distributed across broad spatial scales and encompass a diverse range of environmental conditions over the annual cycle. Increasing evidence has shown that processes during one stage or season of the annual cycle can influence the success of individuals in a subsequent season or life stage (Marra et al. 1998, Norris et al. 2004, Robb et al. 2008, Duriez et al. 2012). These interactions, termed "carry-over effects" (Harrison et al. 2011), can influence demographic rates and abundances of animal populations (Juillet et al. 2012). For example, the quality of nonbreeding habitat can influence subsequent reproductive parameters; variable environmental conditions at wintering or staging areas can affect when individuals arrive at breeding areas, their physical condition, and when they breed (Norris 2005, Schamber et al. 2012). Specifically, variation in nutritional condition of adult birds during spring migration can interplay with climate on remote breeding areas to influence the subsequent production of young (Alisauskas 2002). Similarly, delays in breeding phenology can reduce recruitment (Alisauskas and Kellett 2014). Detecting carry-over effects and their influence in population dynamics could therefore be a prerequisite for informed conservation planning.

Difficulties in tracking migratory animals over the annual cycle, however, can pose challenges for detecting and assessing carry-over effects. In addition to interspecific variation in their role, magnitude of carry-over effects may change between years. Adjustments to migration rates (Marra et al. 2005) or foraging behavior during migration (Fox et al. 2012) may allow organisms to maintain consistent reproductive effort despite variable wintering conditions (Mazerolle et al. 2011). In addition, the time and distance between wintering and breeding areas may dampen potential carry-over effects from winter on breeding migrants, leading to uncertainty about their relative influences (through survival or recruitment) on population dynamics (Oppel and Powell 2009, Flint 2013).

Migratory birds often arrive on breeding areas with contaminant burdens derived from nonbreeding areas, and these burdens can potentially affect reproduction (Matz and Rocque 2007, Wayland et al. 2007). Contaminants that birds accumulate on the wintering grounds, however, may no longer be present by the time individuals arrive on the breeding grounds (Warren and Cutting 2011). Further, some studies have shown that contaminants encountered during migration do not affect reproduction (DeVink et al. 2008, Badzinski et al. 2009). Although Wayland et al. (2008a) detected no effect of heavy metal burdens on apparent survival in either White-winged Scoter (*Melanitta fusca*) or King Eider (*Somateria spectabilis*) females captured during nesting, their data did suggest a moderate, annually variable effect of blood mercury levels on capture probability, suggesting that breeding probability may have been negatively influenced. The potential for contaminants on wintering areas to mediate carry-over effects related to reproduction therefore merits further investigation, particularly in sea ducks that tend to have elevated blood concentrations of trace element contaminants.

We studied variation in timing of nesting, clutch size, mid-incubation body mass, nest success, and blood concentrations of 4 trace element contaminants for a breeding population of White-winged Scoters (hereafter scoters) in Saskatchewan, Canada. Our objective was to test 2 hypotheses related to carry-over effects: (1) variation in winter provenance, inferred from stable isotope analysis, can influence breeding performance; and (2) carry-over effects on breeding grounds are a result of variation in contaminant burdens between birds from different wintering areas. Scoters are ideal for evaluating hypotheses related to carry-over effects because they have shown long-term declines in abundance over their breeding range (Alisauskas et al. 2004) and are known to winter in marine and brackish estuarine waters along both the Pacific and Atlantic coasts (Houston and Brown 1983), as well as on fresh water in the Great Lakes, where potential exposure to contaminants is high (Godfrey 1986, Ware et al. 2011). Atlantic birds migrate farther than Pacific birds to our Saskatchewan study site, so we predicted that they would have delayed breeding due to either time constraints or reduced body condition, potentially leading to reduced nest success.

To validate the isotope approach for assignment of breeding scoters to wintering areas and assess migratory connectivity in this species, we tested whether samples from geographically distinct winter populations could be discriminated using carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values of feathers. Successful discrimination allowed us to estimate proportional winter affiliations of females from a southern (Saskatchewan) and northern (Northwest Territories) nesting population.

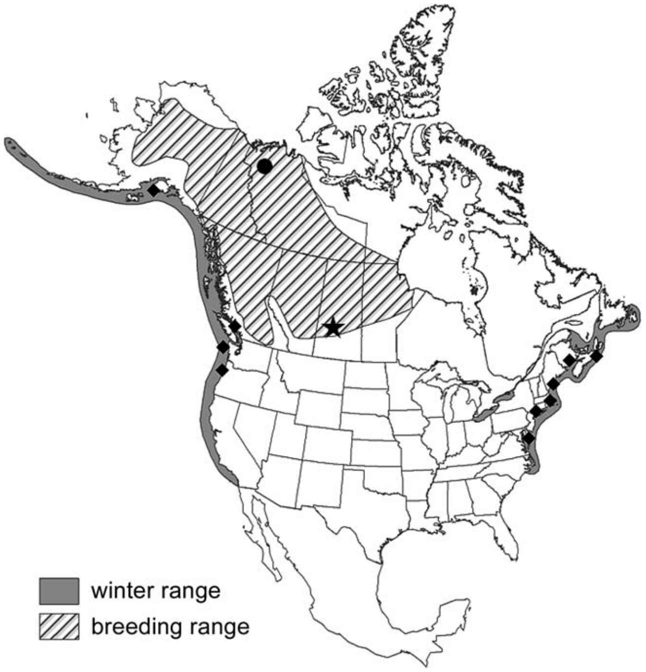

FIGURE 1. Current winter and breeding distribution of White-winged Scoters (*Melanitta fusca*) in North America. Redberry Lake study area is marked with a star; Cardinal Lake is marked with a circle. Approximate locations of winter collections are shown as diamonds.

METHODS

Study Areas

We collected contour feathers of adult scoters (males and females) from Atlantic and Pacific locations between 2001 and 2004 (Figure 1; Table 1). We also delineated wintering ground origins for 2 populations of breeding scoters: Redberry Lake (studied during 2002–2004) in southwest Saskatchewan (52.66°N, 107.17°W; Kehoe 1989) and at Cardinal Lake (studied during 2002–2006) in the Northwest Territories, southeast of Inuvik (67.61°N, 133.66°W; Gurney et al. 2011; Figure 1; Table 2).

Field Methods

Winter feather collection. To determine δ^{13}C and δ^{15}N values in feathers from known wintering locations, scoters were captured during banding operations; feathers from hunter-killed scoters were also collected during the regular hunting season and from carcasses that washed up on beaches. To determine which feather tract provided the best isotopic segregation of wintering populations, 3 feather tracts (head, back, and flank) were sampled from each individual.

Sampling on breeding areas. Two or more observers systematically searched for nests at Redberry Lake by walking line transects between mid-June and late July 2002–2004. We counted eggs, determined incubation stage by candling eggs (Weller 1956), and estimated initiation dates by back-dating, assuming a laying interval of 1.5 eggs per day (Brown and Brown 1981). Nesting females were trapped using hand-held nets after mid-incubation (~14 days incubation or later) and marked with a standard aluminum leg band. All captured females (n = 242 captures, 172 individual females) had 3–4 feathers removed from each of 3 feather tracts (head, back, and flank) for isotope analysis. In 2002 and 2003, we also collected blood (4–6 cc) from a subset of the captured females for contaminant analyses (n = 122 samples, 108

TABLE 1. To determine δ^{13}C and δ^{15}N values from feathers of wintering White-winged Scoters (*Melanitta fusca*) during 2001–2004, we collected feathers from 181 individuals (males and females) at known wintering locations on Atlantic and Pacific coasts.

Wintering area	Year	Location	n	Collection dates (range)
Atlantic	2002	Maryland	5	22 Oct to 7 Dec
		Maine	10	1 Nov to 16 Nov
		New Brunswick	2	4 Nov to 8 Nov
	2003	Massachusetts	2	30 Oct to 15 Nov
		New Brunswick	6	11 Nov to 19 Feb
		Nova Scotia	2	11 Nov
		New York	5	1 Nov to 2 Nov
Pacific	2001	Oregon	1	30 Nov
	2002	British Columbia	7	14 Dec to 16 Dec
		Oregon	1	15 Mar
		Washington	6	14 Oct to 21 Dec
	2003	British Columbia	60	9 Dec to 24 Mar
		Oregon	1	15 Jan
		Washington	24	31 Dec to 20 Jan
	2004	Alaska	3	27 Jan to 29 Jan
		British Columbia	44	23 Feb to 16 Mar
		Oregon	2	24 Jan to 28 Mar

TABLE 2. To delineate wintering ground origins for 2 distinct breeding populations of White-winged Scoters (*Melanitta fusca*), we collected feathers from 706 birds (=490 individuals) between 2002 and 2006. Only females were sampled at Redberry Lake; at Cardinal Lake, both females and males were sampled.

Breeding area	Year	*n*	Trapping dates (range)
Redberry Lake, Saskatchewan	2002	72	4 Jul to 29 Jul
	2003	97	3 Jul to 1 Aug
	2004	73	6 Jul to 30 Jul
Cardinal Lake, Northwest Territories	2002	97	10 Jun to 25 Jul
	2003	166	5 Jun to 25 Jun
	2004	78	3 Jun to 17 Jun
	2005	84	2 Jun to 17 Jun
	2006	39	8 Jun to 17 Jun

individual females). Concentrations of trace element contaminants in blood provide a suitable metric for both short-term as well as longer term exposure because blood concentrations of trace element compounds are correlated with concentrations in storage tissues (Wayland et al. 2001, Ohlendorf and Heinz 2011).

We trapped breeding pairs at Cardinal Lake during the pre-nesting period (mid-June to early July) using floating mist nets (Kaiser et al. 1995) and collected feathers from both females and males ($n = 464$ captures, 318 individuals), as described for Redberry Lake. Blood for contaminant analyses was not collected from Cardinal Lake birds. All research methods were approved by the Animal Care Committee, University of Saskatchewan, on behalf of the Canadian Council on Animal Care (Protocol 20000010).

Laboratory Methods

Stable isotope analyses. Feathers were cleansed of surface oils by rinsing with a solution of 2:1 chloroform to methanol and allowed to air dry for 24 hours. A 0.95–1.05 mg portion of each sample was enclosed in a tin cup and then combusted in a Robo Prep elemental analyzer interfaced with a Europa 20:20 continuous-flow isotope-ratio mass spectrometer at the Department of Soil Science, University of Saskatchewan. By convention, the isotope values are reported in delta notation as δ^{13}C and δ^{15}N according to:

$$\delta X = \left(\frac{R_{sample}}{R_{std}} - 1\right)‰,$$

where $X = {}^{13}C$ or ${}^{15}N$, $R = {}^{13}C{:}{}^{12}C$ or ${}^{15}N{:}{}^{14}N$, and std = Vienna PeeDee Belemnite (VPDB) for ^{13}C and atmospheric N_2 (AIR) for ^{15}N.

Two secondary isotopic reference materials (egg albumen and lyophilized bowhead whale baleen) were used as standards. Standards (in the same mass range as the test samples) were processed before and between every 5 feather samples within each analytical run (for albumen) and at the start, midpoint, and end of each run (for baleen). We used replicate standard measurements within a run to estimate analytical precision ±1 standard deviation (SD): mean δ^{13}C within runs = –22.4‰ ± 0.0%, and mean δ^{15}N within runs = 6.8‰ ± 0.1% for egg albumen; mean δ^{13}C within runs = –18.5‰ ± 0.1%, and mean δ^{15}N within runs = 14.8‰ ± 0.2% , for bowhead whale baleen. Measurement errors (±1 SD) were estimated to be ± 0.1‰ for δ^{13}C and ± 0.3‰ for δ^{15}N, based on measurements of laboratory standards across multiple runs.

Blood contaminant analyses. Following collection, blood samples from Redberry Lake females were transferred to nitric acid-washed vials, kept cool in the field, and frozen pending further processing. Mercury (Hg), Selenium (Se), and Lead (Pb) analyses were conducted at Atlantic Environment Canada's National Wildlife Research Centre according to methods described by Neugebauer et al. (2003); Cadmium (Cd) was analyzed at the Institut National de Santé Publique du Québec according to Stoeppler and Brandt (1980). Cd concentrations were expressed on a volumetric basis, whereas Hg, Se, and Pb concentrations were expressed on a wet weight basis. Blood samples used in these analyses were identical to those used by Wayland et al. (2007), who described analytical techniques in detail, including standard reference materials, percent recovery, detection limits, measurement precision, and accuracy.

Statistical Analyses

Identifying winter origins. All statistical analyses were performed using SAS Version 9.3 (SAS Institute 2009). We visually assessed bivariate plots of δ^{13}C and δ^{15}N from each feather tract to evaluate overlap between known Atlantic and Pacific winter populations. Feathers from 6 individuals (5 from Atlantic females and 1 from a Pacific female; Figure 2) showed extremely low δ^{13}C values relative to all others, suggesting a freshwater influence. These feathers may have been molted during fall migration while staging on freshwater ecosystems, and because no feathers from Redberry Lake birds had similar signatures, we excluded them from subsequent analyses.

Because isotope values were normally distributed, we used multivariate analysis of variance (MANOVA, PROC GLM) to test for effects of winter area, sex, winter area*sex interaction, and date of collection on δ^{13}C and δ^{15}N values, and to determine whether sex or date needed to be accounted for in our Discriminant Function Analysis (DFA). We then used DFA (PROC DISCRIM) to quantitatively assess which feather tract would most accurately discriminate between Atlantic and Pacific populations based on δ^{13}C and δ^{15}N. We tested for homogeneity of within-covariance matrices using a chi-square test of homogeneity (POOL = TEST option). Because the

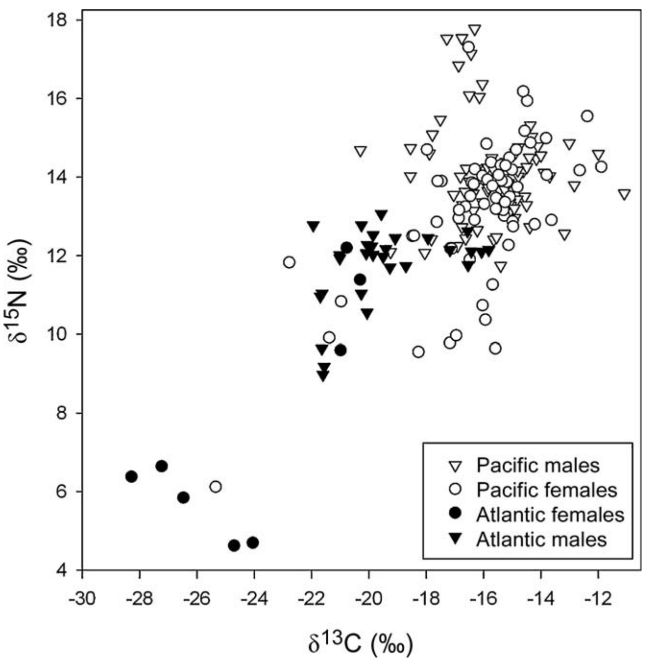

FIGURE 2. δ^{13}C and δ^{15}N values of White-winged Scoter (*Melanitta fusca*) head feathers from known wintering locations provided the best discrimination between Atlantic and Pacific wintering areas. δ^{13}C values from 6 individuals (lower left of panel) were considered to be influenced by freshwater and excluded from subsequent analyses.

variances were not different ($\alpha = 0.05$), they were pooled, and we conducted a linear DFA. Prior probabilities were set equal to sample sizes for each group, and separate DFAs were performed using δ^{13}C and δ^{15}N from all possible combinations of the 3 feather tracts, including each tract independently.

The performance of each tract-specific DFA was evaluated based on the error rate from leave-one-out cross-validation, and subsequent DFA of isotopic differences between winter populations were based on feathers from the most informative tract. Feathers from breeding areas at both Redberry Lake and Cardinal Lake were assigned to either Atlantic or Pacific winter areas using linear DFA based on the discriminant function obtained from this analysis (Appendix A). To be conservative in further hypothesis testing, we considered scoters with $<$0.90 posterior probability of assignment to either winter area to be of uncertain winter provenance and excluded them from further analyses.

Effects of winter origin. We used general linear mixed models (PROC MIXED) to test for effects of putative winter area on nest initiation date, clutch size, mid-incubation body mass, and blood Hg and Pb. Generalized linear mixed models (PROC GLIMMIX) were used to evaluate effects of winter area on blood Cd and Se, which had negative binomial distributions. Mixed models allowed us to account for covariance in the response variable from dependencies among repeated measures from the same bird (a random effect) while treating winter area and other covariates as fixed effects (Littell et al. 2006). Marginal log likelihood values were computed using either the restricted maximum likelihood method (PROC MIXED) or the Laplace approximation (PROC GLIMMIX; SAS Institute 2009). We used an information-theoretic approach to model selection, with models ranked according to second-order Akaike's Information Criterion (AIC$_c$; Burnham and Anderson 2002).

Candidate models for breeding phenology included fixed effects of year, winter location, and mid-incubation body mass. Predictor variables in models of clutch size were the same as for timing of breeding but also included clutch initiation date to account for seasonal declines in clutch size, a pattern observed consistently in single-brooded birds (Krapu et al. 2004, Gurney et al. 2011). To assess whether effects of clutch initiation date and winter origin on clutch size were confounded (because Atlantic birds tended to nest later), we also ran a clutch size model that included winter origin but not clutch initiation date. Our a priori model set for mid-incubation body mass included fixed effects of year and wintering origin. We estimated probability of nest survival in relation to winter origin with the nest survival model (logit-link function) in program MARK (White and Burnham 1999) and considered 6 candidate models for nest success, selecting the best-approximating model(s) using AIC$_c$.

In addition to a constant survival model, we assessed effects of year, winter location, nest initiation date, and nest location on nest survival. We also used a time invariant null model, using data for all found nests, to calculate Mayfield (1975) estimates of nest success for comparison with previously published results. Finally, to evaluate contaminant burdens as a potential mechanistic explanation for reproductive carry-over effects of wintering location, blood concentrations of Cd, Hg, Pb, and Se were included in model sets for timing of nesting and mid-incubation body mass. Candidate model sets for contaminants included year, winter location, and mid-incubation body mass as main fixed effects. We also estimated the influence of incubation stage on blood contaminant levels (Wilson et al. 2007) by including nest initiation date in these model sets.

In all cases, following selection of the top-ranked models, inference of fixed effects was based on the degree to which included variables reduced model deviance (i.e. –2 log likelihood), as well as on the precision (85% confidence interval [CI]) of regression coefficients (β). Although the 85% CI is narrower and less commonly used than a 95% CI, criteria for model selection and for estimating influence of parameters are more similar under this approach. If confidence intervals of estimated

TABLE 3. Classification success (%) of linear discriminant function analysis based on $\delta^{15}N$ and $\delta^{13}C$ values from feathers of known-source Atlantic or Pacific coastal wintering populations of White-winged Scoters (*Melanitta fusca*) indicates that this approach classifies winter origin with a high degree of precision. Feather tract(s) are listed in order of classification success for Atlantic populations. Sexes were pooled because MANOVA showed no sex effect.

	Location				
	Atlantic		Pacific		
Feather Tract(s)	*n*	%	*n*	%	Bias[a]
Head	32	78	149	96	18
Flank	10	60	17	100	40
Back, Flank	10	60	17	82	22
Back, Head	10	60	17	88	28
Back	10	70	17	100	30
Back, Flank, Head	10	40	17	82	42
Flank, Head	10	40	17	88	48

[a] Bias = % SuccessPacific − SuccessAtlantic (represents favor toward the Pacific)

parameters included zero, effects associated with these parameters were considered to be uninformative; models containing such effects were not used for inference and were not included in final model sets (Arnold 2010).

RESULTS

Discrimination of Source Winter Areas

MANOVA for $\delta^{13}C$ and $\delta^{15}N$ values showed differences between winter areas (Wilks' $\lambda = 0.73$, $F = 33.09_{2,175}$, $P < 0.001$) but not between sexes (Wilks' $\lambda = 0.98$, $F = 1.96_{2,175}$, $P = 0.15$), no interaction between winter area and sex (Wilks' $\lambda = 1.00$, $F = 0.41_{2,175}$, $P = 0.66$), and no effect of collection date (Wilks' $\lambda = 0.99$, $F = 0.90_{2,175}$, $P = 0.41$). Therefore, we considered only 2 groups, Atlantic and Pacific, for discriminant analysis.

Scoter feathers from known Pacific wintering sites had enriched ^{13}C and, to a lesser extent, enriched ^{15}N relative to those from known Atlantic sites (Figure 2). Of the 3 feather tracts analyzed (head, back, flank), head feathers displayed the greatest difference in mean $\delta^{15}N$ and $\delta^{13}C$ values between Atlantic and Pacific coasts and therefore provided the most accurate discrimination (Table 3). The most important value for correct classification was $\delta^{13}C$; classification bias was reduced by only 3% with inclusion of $\delta^{15}N$. Feather $\delta^{13}C$ and $\delta^{15}N$ of scoters from these known wintering populations provided reference data for assigning winter provenance to breeding scoters.

Certainty of correct assignment of Redberry Lake birds was somewhat greater during 2002, with 90% (65 of 72) of all individuals having >0.90 probability of having wintered on either the Atlantic or Pacific coast, compared with 82% (80 of 97) of individuals with >0.90 probability in 2003, and 78% (57 of 73) of individuals with >0.90 probability in 2004. In both 2002 and 2003, 25% of females breeding at Redberry Lake were assigned to Atlantic and 75% to Pacific waters. In 2004, however, only 12% were assigned to Atlantic and 88% to Pacific waters (Figure 3A). The classification of breeding females for Cardinal Lake was of similar precision in all years for which feathers were available; over 5 years (2002–2006), only 3% (7 of 321) individuals (males and females) were considered to be of unknown origin. In contrast to Redberry Lake scoters, those from Cardinal Lake were almost exclusively of Pacific winter origin, with only 3 classified as Atlantic (Figure 3B).

Reproductive Parameters

Of the reproductive parameters that we measured at Redberry Lake, only nest initiation date and mid-incubation body mass showed evidence of carry-over effects (Table 4). Nest initiation date was affected by wintering origin, with Atlantic birds tending to nest 3–4 days later than birds from the Pacific coast (Figure 4; $\beta_{Winter} = 3.0$, 85% CI: 1.4 to 4.6). The top-supported model also indicated annual variation in breeding phenology, with earlier nesting in 2003 relative to 2002 and 2004 (Figure 4). The best-approximating model for mid-incubation body mass also included an effect of wintering area, suggesting that during incubation Atlantic scoters were heavier than Pacific scoters ($\beta_{Winter} = 21.5$, 85% CI: 3.3 to 39.7). For both nest initiation date and mid-incubation body mass, models that included contaminant values suggested that, in all cases, these reproductive parameters were unaffected by blood contaminant levels.

We did not detect an effect of wintering area for either clutch size or nest success at Redberry Lake. Mean clutch size was 9.0 ± 0.1 (SE), and the top-supported model for this response variable included a fixed effect of clutch initiation date and a random effect of bird. This model was supported by 100% of the weight of evidence (Table 4), indicating that clutch size variability was unexplained by variables we considered. Mayfield nest success (ϕ) was also unaffected by winter location. The estimated daily survival rate of nests, however, showed considerable annual variation: $\phi_{2002} = 0.25$, 85% CI: 0.19 to 0.31, $\phi_{2003} = 0.93$, 85% CI: 0.84 to 1.01, and $\phi_{2004} = 0.73$, 85% CI: 0.60 to 0.86.

Blood Contaminants in Nesting Females

Our Redberry Lake sample of 108 unique females in 2002 and 2003 included those from which blood was sampled and for which posterior probability of assignment to either winter area was >0.90. Levels of Cd in blood samples varied between winter area and year (Table 5), with an interaction between them ($\beta_{Year*Winter} = -0.70$, 85% CI:

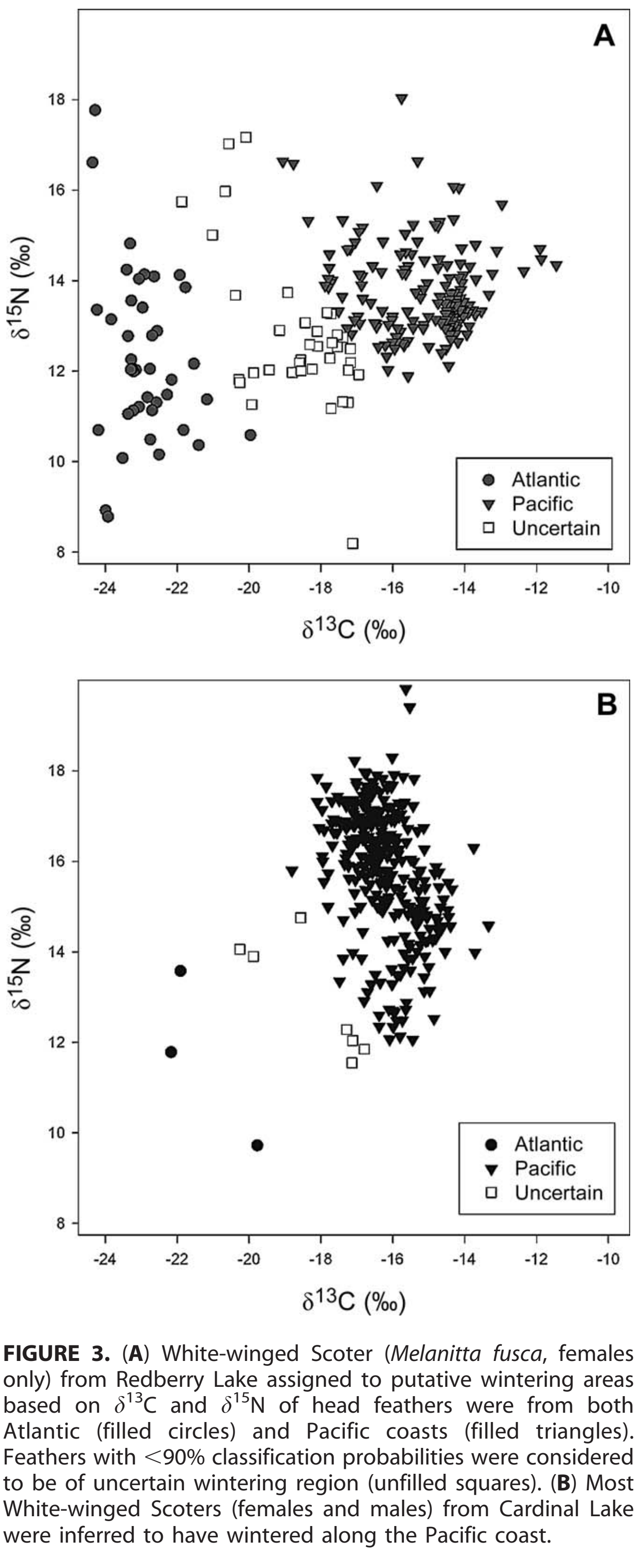

FIGURE 3. (**A**) White-winged Scoter (*Melanitta fusca*, females only) from Redberry Lake assigned to putative wintering areas based on δ^{13}C and δ^{15}N of head feathers were from both Atlantic (filled circles) and Pacific coasts (filled triangles). Feathers with <90% classification probabilities were considered to be of uncertain wintering region (unfilled squares). (**B**) Most White-winged Scoters (females and males) from Cardinal Lake were inferred to have wintered along the Pacific coast.

–1.08 to –0.32); females from the Atlantic had higher Cd levels than birds that wintered in the Pacific in 2003 only (Figure 5A). Levels of Pb were consistent across years and were higher for females from Atlantic compared to Pacific waters (Figure 5B; $\beta_{\text{Winter}} = 0.026$, 85% CI: 0.020 to 0.031). Levels of Hg did not vary between females that wintered in different areas, but values were higher in 2002 relative to 2003 (Figure 5D; $\beta_{\text{Year}} = 0.091$, 85% CI: 0.080 to 0.103). Similarly, blood Se was higher for birds from Atlantic winter areas ($\beta_{\text{Winter}} = 0.803$, 85% CI: 0.650 to 0.957) but did not vary between years (Figure 5C). Of all metals, only Se was related to body mass, and this was a positive association (Table 5; $\beta_{\text{BodyMass}} = 0.002$, 85% CI: 0.001 to 0.003).

DISCUSSION

Discrimination of Atlantic and Pacific Populations

Delineation of wintering areas. Head feathers provided the best discrimination between Atlantic and Pacific scoters, likely due to their relatively small size in relation to feathers from other tracts. Small size requires less material to replace feathers, and in turn, requires a shorter period of growth (Thompson and Drobney 1996). Thus, the average isotopic input can be incorporated into the tissue over a shorter time, perhaps representing reduced variation in isotopic landscapes sampled by foraging birds over a shortened temporal sampling frame (Mehl et al. 2005). Even so, classification success (%) was much higher for Pacific than for Atlantic wintering birds (Table 3), possibly because of reduced heterogeneity in isoscapes used by Pacific scoters.

Although use of stable isotope values resulted in reasonably good discrimination between winter areas, some overlap was evident because of similarities in δ^{13}C and δ^{15}N for winter diet items (Swoboda 2007). Head and body feathers are molted twice annually, with new plumage acquired during the prealternate molt, typically in July–September and then again during the prebasic molt in March–April, before migrating to breeding areas (Brown and Fredrickson 1997). Our samples were collected throughout the fall but were largely restricted to the regular hunting season (October–January) for Atlantic samples. Thus, these samples may have included feathers grown on the breeding area, or staging areas during fall migration (i.e. before birds reached terminal winter areas).

Carbon sources influenced by freshwater inputs tend to be depleted in ^{13}C relative to carbon from marine sources; average δ^{13}C for freshwater ecosystems is about –26‰, so values below –20‰ suggest that molt occurred when birds were consuming foods from fresh or estuarine water (Fry and Sherr 1988). Depleted ^{13}C in head feathers of Atlantic birds may have resulted from increased foraging in

TABLE 4. Based on ranking of general linear mixed models (PROC MIXED), our data are consistent with an effect of wintering area on nest initiation day and mid-incubation body mass of female White-winged Scoters (*Melanitta fusca*) breeding at Redberry Lake, Saskatchewan. Response variables are listed in the first column, and for each variable, the ✓ indicates which predictor variables were included in the models as fixed effects. For all models, bird identity is included as a random effect, and in each case, models with no ✓ are the null model. Models are ranked by differences in Akaike's Information Criterion, corrected for sample size (ΔAIC_c). Winter = wintering area, as determined by discriminant function analysis; w_i = Akaike weight.

	Predictor variables			Model selection criteria		
	Year	Winter	Nest initiation day	Deviance	ΔAIC_c	w_i
Nest initiation day	✓	✓		1259.6	0.0	0.98
(n = 195 nests)	✓			1268.7	8.0	0.02
				1277.0	14.1	0.00
Clutch size			✓	627.3	0.0	1.00
(n = 195 nests)				681.2	52.8	0.00
Mid-incubation body mass		✓		2169.4	0.0	0.99
(n = 195 measurements)				2179.0	8.5	0.01

brackish estuarine habitats (Savard et al. 1999) relative to those from Pacific waters.

Atlantic scoters also may have staged in freshwater habitats for prolonged periods during fall before continuing to coastal wintering areas. Females banded at Redberry Lake have been recovered on the Great Lakes in the fall (Houston and Brown 1983), highlighting their use as freshwater staging areas and potential wintering habitat for these scoters. Increased use of the Great Lakes by both diving and sea ducks has been documented following invasion of these habitats by zebra mussels (*Dreissena polymorpha*) in the late 1980s, and prolonged staging there has occurred in recent years as a result of longer ice-free periods during the winter (Petrie and Knapton 1999, Schummer 2005).

Assignment of wintering origin to breeding populations. Using isotopic analyses, we have developed a molecular tool that will assist in conservation efforts for scoters by connecting breeding birds to known wintering areas. This study emphasizes the value of an isotopic approach for identifying connectivity between breeding and wintering locations, but we note that future research into migratory connectivity will also benefit from attached logging devices that use light-level archival technology (i.e. geolocators) to infer location (Solovyeva et al. 2012), particularly in species with substantial body mass, such as scoters. Whereas banding data for the Redberry Lake population suggest that it is composed of nearly equal ratios of Atlantic and Pacific wintering scoters, our isotopic approach showed that Pacific females comprised at least 75% of breeding individuals. In addition, ours is the first published study to document wintering ground origins for a northern-breeding population of scoters, showing that these birds winter almost exclusively on the Pacific coast.

Taken together, these results confirm the importance of Pacific wintering areas for scoters, an important first step in understanding environmental factors that may be limiting their populations (Sea Duck Joint Venture 2003). We suggest that further studies of carry-over effects in this species would be valuable. From a conservation perspective, assessing annual variation in reproduction and survival relative to environmental changes on wintering and staging habitats would be particularly insightful. For example, scoters wintering and migrating along the Pacific coast seem to rely heavily on herring (*Clupea pallasi*) spawn for restoring depleted nutrient reserves (Anderson et al. 2009). Declining herring stocks could thus result in carry-over effects related to reduced reproductive investment. This may be especially relevant at Cardinal Lake because scoters breeding at northern latitudes rely in part

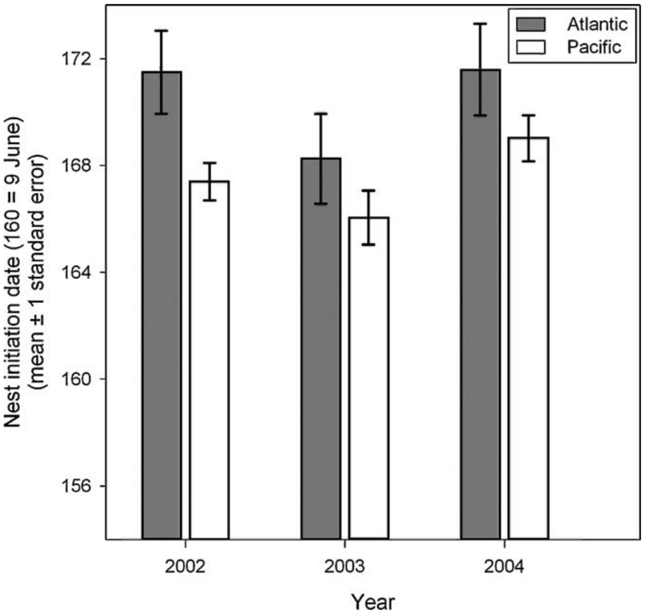

FIGURE 4. Timing of nesting by White-winged Scoters (*Melanitta fusca*) at Redberry Lake, Saskatchewan, was earlier for birds that wintered on the Pacific coast and earlier in 2003 relative to other years.

TABLE 5. Based on ranking of general linear mixed models (PROC MIXED; lead, mercury) and generalized linear mixed models (PROC GLIMMIX; cadmium, selenium), our data are consistent with an effect of wintering area on levels of blood contaminants (cadmium, lead, selenium) in female White-winged Scoters (*Melanitta fusca*) breeding at Redberry Lake, Saskatchewan. Response variables are listed in the first column, and for each variable the ✓ indicates which predictor variables were included in the models as fixed effects, and the * denotes an interaction. For all models, bird identity is included as a random effect; in each case, models with no ✓ are the null model. Models are ranked by differences in Akaike's Information Criterion, corrected for sample size (ΔAIC_c). Winter = wintering area, as determined by discriminant function analysis, Mass = mid-incubation body mass, w_i = Akaike weight.

	Predictor variables				Model selection criteria		
	Year	Winter	Year*Winter	Mass	Deviance	ΔAIC_c	w_i
Cadmium	✓	✓	✓		472.8	0.0	1.0
(n = 132 samples)	✓				494.0	18.9	0.0
	✓	✓			498.3	24.3	0.0
					627.1	149.7	0.0
Lead		✓			−647.1	0.0	1.0
(n = 135 samples)		✓		✓	−632.9	15.3	0.0
					−620.0	26.0	0.0
Mercury	✓				−426.3	0.0	1.0
(n = 135 samples)	✓	✓			−418.8	8.6	0.0
	✓	✓	✓		−413.0	15.6	0.0
					−345.2	81.1	0.0
Selenium		✓		✓	536.0	0.0	1.0
(n = 135 samples)		✓			545.7	8.6	0.0
					598.4	61.2	0.0

upon endogenous reserves for egg production (DeVink et al. 2011).

Carry-over Effects Related to Wintering Origin

We found that scoters from Atlantic wintering areas nested later, were of higher body mass during mid-incubation, and tended to have higher blood levels of Cd, Pb, and Se than sympatrically nesting scoters from Pacific wintering areas; however, we found no direct negative associations between any trace elements in the blood and the reproductive parameters that we measured. Thus, Pacific scoters had an advantage in sympatric breeding phenology over Atlantic scoters, but this was not clearly a result of reduced blood contaminants. Other factors, including differences between winter populations with respect to diet, migration distance and duration, or use of staging areas likely have a greater influence on breeding parameters than do levels of trace element contaminants.

It seems unlikely that Atlantic scoters that nested in Saskatchewan were nutritionally compromised because they had superior mid-incubation body mass compared to Pacific scoters. Delays in migration or breeding were therefore not likely the result of difficulties in accumulation of nutrient stores for migration and reproduction, as has been suggested elsewhere (Bêty et al. 2003, Schaub et al. 2008). Instead, the inverse relationship between nesting phenology and mid-incubation body mass between winter populations may represent a trade-off. That is, even though the greater migration distance to Saskatchewan for Atlantic scoters (compared to those from Pacific winter areas) may have prolonged spring migration and resulted in nesting delays, it may also have permitted greater nutrient storage that resulted in higher body mass for these individuals. Additionally, differences in weather patterns between Atlantic and Pacific coasts (Rockwell et al. 2012), variation in the age structures of wintering populations (Goutte et al. 2010), or differences in predation risk (Jonker et al. 2010) could further influence or confound timing of migration and arrival on breeding grounds by scoters and other migratory species.

Nesting by Atlantic scoters at Redberry Lake was delayed only by about 3 days, but relative to other species scoters are relatively late nesters with slow-maturing broods (Brown and Brown 1981, Brown and Fredrickson 1997), and there is strong evidence that survival of scoter ducklings declines with advancing hatch date (Traylor and Alisauskas 2006). Thus, for scoters and other species with similar life-histories, the demographic consequences of even minor delays in breeding could be substantial and certainly can influence recruitment probability (Alisauskas and Kellett 2014). Because timing of breeding is closely linked to reproductive success and recruitment in many species (Blums et al. 2002, Gurney et al. 2012), the observed effect of wintering area on timing of breeding emphasizes that carry-over effects can potentially influence individual fitness and recruitment dynamics of migratory birds (Harrison et al. 2011). Our findings suggest that carry-over effects of this nature may affect migratory populations to a greater extent than is currently recognized.

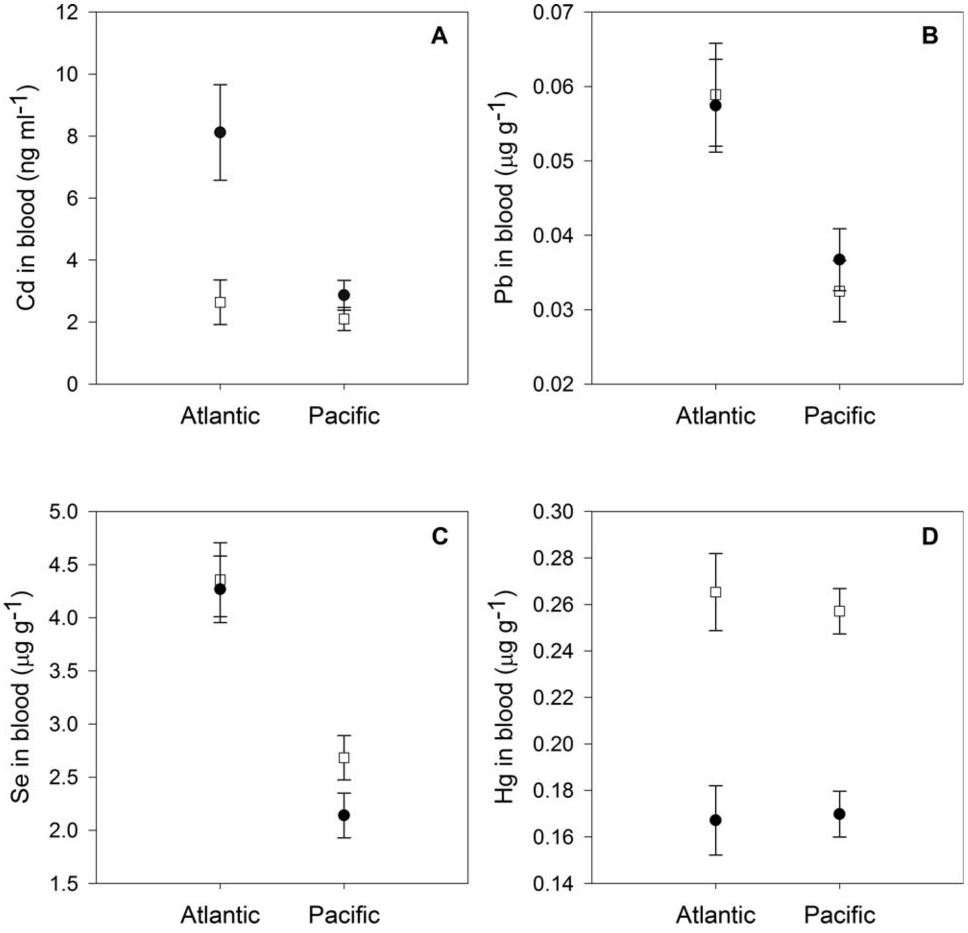

FIGURE 5. In 2002 (unfilled squares) and 2003 (filled circles), concentrations of (**A**) cadmium (Cd), (**B**) lead (Pb), and (**C**) selenium (Se) in blood of White-winged Scoters (*Melanitta fusca*) breeding at Redberry Lake, Saskatchewan, were higher for birds that wintered in Atlantic regions, with the exception of (**D**) mercury (Hg, in both years) and Cd (in 2002). In all panels, values are least squares means (85% confidence interval).

Differences in Blood Contaminants Between Wintering Areas

Although breeding parameters were unrelated to concentrations of trace elements in the blood, our study did detect significant differences in 3 of 4 contaminants for birds from different wintering areas. Blood samples for this study were collected during mid-incubation (close to the end of June), when scoters had potentially been absent from wintering areas for up to 6 weeks (Brown and Fredrickson 1989, Traylor 2003). Trace elements Cd, Pb, and Se all have relatively short half-lives in avian blood (Anders et al. 1982, Heinz et al. 1990, Wayland and Scheuhammer 2011); however, their concentrations in blood are usually well-correlated with concentrations in storage tissues, such as bone and kidney (García-Fernández et al. 1997, Wayland et al. 2001), and can indicate differences in longer-term exposure (i.e. on nonbreeding areas; Wayland et al. 2008b).

In addition, the pattern we observed in blood contaminants is consistent with previously demonstrated coastal differences in environmental contamination (i.e. Atlantic > Pacific; Daskalakis and O'Connor 1995, O'Connor 2002). Pacific-wintering scoters likely consume large quantities of herring spawn during spring migration (Lewis et al. 2007, Anderson et al. 2009), whereas those on Atlantic coasts may depend more on filter-feeding mussels, which bioaccumulate several trace elements, including Cd (Di Giulo and Scanlon 1984, Bendell 2009). Spring staging on the Great Lakes by scoters after departing from the Atlantic coast may also contribute to elevated metals in blood. Exotic zebra mussels introduced to the Great Lakes bioaccumulate contaminants at higher concentrations than native bivalve species and may be replacing scoter invertebrate prey such as amphipods and gastropods, which do not filter feed (De Kock and Bowmer 1993, Ross et al. 2005).

Current evidence thus suggests that observed differences in blood contaminants were likely the result of variable exposure to contaminants during winter or spring migration. Alternatively, exposure might be similar between wintering areas; however, if Atlantic wintering scoters deplete endogenous reserves during their longer migration route and Pacific scoters do not, metabolic changes might lead to greater mobilization of contaminants from storage tissues in birds from the Atlantic coast. Although the differences in contaminant burdens observed in our study might have been caused by events on sympatric nesting areas, this explanation seems unlikely because individuals of Atlantic and Pacific winter origin use the same habitats and have similar diets (Traylor 2003, Swoboda 2007). If Atlantic-origin scoters rely more on exogenous reserves for reproduction than Pacific-origin birds, however, it is conceivable that they may feed more locally during nesting and incubation, thereby being exposed to higher levels of local contaminants.

In general, the interplay among contaminants, wintering areas, migration strategies, and local conditions on reproductive parameters were somewhat confounded in our study. Further research designed to attribute variation in breeding ecology to specific carry-over effects in this species might benefit from detailed studies of spring migration phenology for each winter population of scoters. In particular, the use of multi-season geolocators or satellite telemetry could be used to assess differences in migration phenology, stop-over site locations and duration, and overall distances travelled from different wintering areas to common nesting areas. Additional studies to evaluate the causes and possible consequences of elevated contaminants in Atlantic wintering scoters also seem warranted. Data describing concentrations of contaminants in wintering and staging birds from both Atlantic and Pacific locations would be particularly useful in distinguishing patterns of nonbreeding area exposure, and long-term capture–mark–recapture data would provide key information concerning biological implications of winter provenance and variable contaminant exposure. Assessing environmental levels of trace element contaminants at Redberry Lake would help clarify the role of local exposure, as would details concerning differences in breeding season nutrient allocation strategies between Atlantic and Pacific birds.

Conclusion

By identifying clear differences in breeding chronology between sympatrically breeding scoters from different winter populations, our study highlights the importance of carry-over effects for migratory animals. Specifically, variation in breeding phenology constitutes an important carry-over effect with strong links to recruitment probability in many species of birds. Stratification of breeding populations by winter provenance will likely provide a much-improved understanding of variation in breeding biology in other bird species and will help clarify the extent to which carry-over effects influence bird populations.

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APPENDIX A

Predictive equations for delineating between Atlantic and Pacific winter populations of White-winged Scoters

The basic form of the linear discriminant function of belonging to a particular group can be expressed as $\boldsymbol{D_{group}} = \mathbf{a} + \mathbf{b_1}{*}\mathbf{x_1} + \mathbf{b_2}{*}\mathbf{x_2} + \ldots + \mathbf{b_m}{*}\mathbf{x_m}$, where a is a constant and b_1 through b_m are the discriminant coefficients and x_1 through x_m are the discriminating variables. Below is the linear discriminant function equation based on isotopic values from White-winged Scoter head feathers collected on both the Atlantic ($n = 32$) and Pacific ($n = 149$) coasts. The linear classification equation using carbon and nitrogen isotopic ratios was:

$$D_{Atlantic} = -142.65 + [9.07 - 8.98]{*}\left[{}^{15}N_i{}^{13}C_i\right] \qquad (A.1)$$

$$D_{Pacific} = -128.30 + [9.72 - 7.79]{*}\left[{}^{15}N_i{}^{13}C_i\right] \qquad (A.2)$$

where ${}^{15}\mathrm{N_i}$ and ${}^{13}\mathrm{C_i}$ = δ^{15}N and δ^{13}C values for observation *i*, respectively. An individual was classified as wintering in the Atlantic if $\mathrm{D_{Atlantic}} > \mathrm{D_{Pacific}}$, or in the Pacific if $\mathrm{D_{Pacific}} > \mathrm{D_{Atlantic}}$.

To calculate the probability of belonging to each population, the following equations (from Mehl et al. 2005) were used:

$$\text{Denominator} = \exp(\mathrm{D_{Atlantic}}) + \exp(\mathrm{D_{Pacific}})$$

$$\text{Probablility}_{\text{Atlantic}} = \exp(\mathrm{D_{Atlantic}})/\text{denominator}$$

$$\text{Probability}_{\text{Pacific}} = \exp(\mathrm{D_{Pacific}})/\text{denominator}$$