Implanted satellite transmitters affect sea duck movement patterns at short and long timescales

Authors: Lamb, Juliet S., Paton, Peter W. C., Osenkowski, Jason E., Badzinski, Shannon S., Berlin, Alicia M., et al.

Source: The Condor, 122(3) : 1-16

Published By: American Ornithological Society

URL: https://doi.org/10.1093/condor/duaa029

THE CONDOR
Ornithological Applications
AmericanOrnithology.org

Volume 122, 2020, pp. 1–16
DOI: 10.1093/condor/duaa029

RESEARCH ARTICLE

Implanted satellite transmitters affect sea duck movement patterns at short and long timescales

Juliet S. Lamb,[1,2,*] Peter W. C. Paton,[1] Jason E. Osenkowski,[2] Shannon S. Badzinski,[3] Alicia M. Berlin,[4] Tim Bowman,[5] Chris Dwyer,[6] Luke J. Fara,[7,8] Scott G. Gilliland,[9] Kevin Kenow,[7] Christine Lepage,[10] Mark L. Mallory,[11] Glenn H. Olsen,[4] Matthew C. Perry,[4] Scott A. Petrie,[12] Jean-Pierre L. Savard,[13] Lucas Savoy,[14] Michael Schummer,[15] Caleb S. Spiegel,[6] and Scott R. McWilliams[1]

[1] Department of Natural Resources Science, University of Rhode Island, Kingston, Rhode Island, USA
[2] Rhode Island Department of Environmental Management, West Kingston, Rhode Island, USA
[3] Canadian Wildlife Service, Ottawa, Ontario, Canada
[4] U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland, USA
[5] U.S. Fish and Wildlife Service, Anchorage, Alaska, USA
[6] U.S. Fish and Wildlife Service, Migratory Birds Division, Hadley, Massachusetts, USA
[7] U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, Wisconsin, USA
[8] Cooperative Wildlife Research Laboratory, Department of Zoology, Southern Illinois University, Carbondale, Illinois, USA
[9] Canadian Wildlife Service, Sackville, New Brunswick, Canada
[10] Canadian Wildlife Service, Québec City, Québec, Canada
[11] Department of Biology, Acadia University, Wolfville, Nova Scotia, Canada
[12] Delta Waterfowl, Bismarck, North Dakota, USA
[13] Sciences and Technology, Environment Canada, Québec City, Québec, Canada
[14] Biodiversity Research Institute, Portland, Maine, USA
[15] Bird Studies Canada/Long Point Waterfowl and Wetlands Research Program, Port Rowan, Ontario, Canada

*Corresponding author: jslamb@uri.edu

Submission Date: January 27, 2020; Editorial Acceptance Date: May 20, 2020; Published July 30, 2020

ABSTRACT

Studies of the effects of transmitters on wildlife often focus on survival. However, sublethal behavioral changes resulting from radio-marking have the potential to affect inferences from telemetry data and may vary based on individual and environmental characteristics. We used a long-term, multi-species tracking study of sea ducks to assess behavioral patterns at multiple temporal scales following implantation of intracoelomic satellite transmitters. We applied state-space models to assess short-term behavioral patterns in 476 individuals with implanted satellite transmitters, as well as comparing breeding site attendance and migratory phenology across multiple years after capture. In the short term, our results suggest an increase in dispersive behavior immediately following capture and transmitter implantation; however, behavior returned to seasonally average patterns within ~5 days after release. Over multiple years, we found that breeding site attendance by both males and females was depressed during the first breeding season after radio-marking relative to subsequent years, with larger relative decreases in breeding site attendance among males than females. We also found that spring and breeding migrations occurred later in the first year after radio-marking than in subsequent years. Across all behavioral effects, the severity of behavioral change often varied by species, sex, age, and capture season. We conclude that, although individuals appear to adjust relatively quickly (i.e. within 1 week) to implanted satellite transmitters, changes in breeding phenology may occur over the longer term and should be considered when analyzing and reporting telemetry data.

Keywords: Black Scoter, Common Eider, Long-tailed Duck, marking, phenology, Surf Scoter, tracking, White-winged Scoter

LAY SUMMARY

- Implanted satellite transmitters are often used to study movements of waterfowl, but capture and implantation may also change individual behavior.
- Understanding these behavioral effects, and how long they last, is necessary to correctly interpret movement data from transmitters.
- We used a set of multi-year data from sea ducks with implanted satellite transmitters to examine changes in individual movement patterns over time.
- Most sea ducks appeared to resume normal day-to-day movements within a week after capture; however, they nested later and at lower rates during the year after capture compared with later years.
- While behavioral effects of transmitter implantation seem to be relatively short-term, energetics and breeding decisions may be affected over longer timescales.

Les émetteurs satellites implantés affectent les patrons de mouvements des canards de mer à des échelles temporelles courtes et longues

RÉSUMÉ

Les études sur les effets des émetteurs sur la faune se concentrent souvent sur la survie. Cependant, les changements comportementaux non létaux résultant de l'utilisation de radio émetteurs peuvent affecter les inférences des données de télémétrie et varier en fonction des caractéristiques individuelles et environnementales. Nous avons réalisé une étude de suivi à long terme et multi-espèces sur les canards de mer pour évaluer les patrons comportementaux à plusieurs échelles temporelles après l'implantation d'émetteurs satellites intracoelomiques. Nous avons appliqué des modèles d'espace d'états pour évaluer les patrons comportementaux à court terme chez les individus ayant des émetteurs satellites implantés, ainsi que pour comparer la fréquentation des sites de reproduction et la phénologie migratoire plusieurs années après la capture. À court terme, nos résultats suggèrent une augmentation du comportement de dispersion immédiatement après la capture et l'implantation de l'émetteur; cependant, le comportement est revenu à des patrons saisonniers moyens dans les 5 jours suivant la remise en liberté. Sur plusieurs années, nous avons constaté que la fréquentation des sites de reproduction par les mâles et les femelles était en baisse au cours de la première saison de reproduction après la pose de l'émetteur par rapport aux années suivantes, avec des diminutions relatives plus importantes de la fréquentation des sites de reproduction chez les mâles que chez les femelles. Nous avons également constaté que les migrations printanières et de reproduction se sont produites plus tard dans la première année suivant la pose de l'émetteur que lors des années suivantes. Parmi tous les effets comportementaux, l'importance du changement comportemental variait souvent selon les espèces, le sexe, l'âge et la saison de capture. Nous concluons que, bien que les individus semblent s'adapter relativement rapidement (c.-à-d. à l'intérieur d'une semaine) aux émetteurs satellites implantés, des changements dans la phénologie de reproduction peuvent se produire à plus long terme et devraient être pris en considération lors de l'analyse et la publication des données de télémétrie.

Mots-clés: *Clangula hyemalis*, marquage, *Melanitta americana*, *Melanitta deglandi*, *Melanitta perspicillata*, phénologie, reproduction, *Somateria mollissima*, suivi

INTRODUCTION

Many conservation decisions and predictive models require a detailed understanding of habitat associations at individual and population scales. Unlike survey or mark–recapture techniques, telemetry-based studies (Boyd et al. 2004) provide continuous data on the movements of known individuals over time, offer individual- and location-specific information on preferred habitat characteristics, and can be used to identify remote areas of particular conservation importance that might not otherwise be recognized (Tancell et al. 2013, Lamb et al. 2019). These advantages, along with advances in the accessibility and miniaturization of individual-borne telemetry devices, have contributed to the growing importance of telemetry data in wildlife ecology (Geen et al. 2019).

To ensure that telemetry studies are safe for their subjects, researchers and veterinarians generally seek to minimize mortality risks associated with radio-marking by following standard guidelines (e.g., limiting transmitter weight to less than 3–5% of an individual's body mass; Kenward 2001) and measuring survival of radio-marked birds in captive or field trials to identify factors contributing to mortalities (e.g., Hatch et al. 2000, Sexson et al. 2014, Le Net et al. 2019). However, even in cases where transmitter attachment conforms to recommendations and does not result in mortality, the energetic cost of carrying a payload can affect energetics, physiology, and life history in captive (Latty et al. 2010, 2016) and free-living birds (Calvo and Furness 1992, Barron et al. 2010, Vandenabeele et al. 2012). If the sublethal effects of radio-marking on individual behavior or fitness are not incorporated into data analysis, they may subsequently bias population-level inferences on habitat use and distribution derived from tracking data (Igual et al. 2005, Hebblewhite and Haydon 2010). Studies of sublethal transmitter effects have found that energetic consequences of transmitters may include alterations in day-to-day movements and activity budgets (e.g., individual behavior: Hamel et al. 2004, Latty et al. 2010, Enstipp et al. 2015, Kenow et al. 2018) or fitness (e.g., survival and reproduction: Fast et al. 2011, Schacter and Jones 2017, Lameris et al. 2018) and may vary across short- and long-term timescales and among species, individuals, transmitter types, and attachment techniques (Barron et al. 2010, Fast et al. 2011, Vandenabeele et al. 2012, Lameris and Kleyheeg 2017). Factors such as handling time, sex, breeding location, and timing of capture have previously been linked to variation in negative effects of capture and tagging among groups of individuals (Lamb et al. 2016, Snijders et al. 2017). Therefore, to ensure that data obtained from tracked individuals accurately represent the general population, it is important to consider sublethal impacts of capture and tagging, and their variation among individuals, in analyses and interpretation of telemetry data.

Despite potential tag effects, the majority of researchers reporting data from movement studies do not include any assessment of how sublethal transmitter effects may influence their findings (Calvo and Furness 1992, Vandenabeele et al. 2011, Geen et al. 2019). This may be due in part to the difficulty of observing behavioral changes in free-living individuals. Since telemetry studies often target individuals or species whose life histories make them difficult to observe directly (Hussey et al. 2015, Kays et al. 2015), fully controlled observational studies comparing the behavior of radio-marked individuals with controls may not be feasible, particularly over wide areas or long timescales. However, in the absence of such systematic study, telemetry data themselves provide an opportunity to investigate long-term patterns of individual behavior following capture and radio-marking. Process models and algorithms (e.g., state-space models [Jonsen et al. 2005], hidden Markov models [Patterson et al. 2009], expectation maximization binary clustering [Garriga et al. 2016]), which treat data as discrete samples of continuous underlying movement states, are frequently used to identify and classify the behavioral processes that generate observed locations. While not as informative as a fully controlled comparative study, such models can be used to infer changes in individual post-capture behavior over time based on movement data, and subsequently compare patterns of behavioral change among individuals and species.

Rather than directly evaluating the sublethal effects of transmitters, analysis of telemetry data often assumes that immediate effects of capture and radio-marking last for a fixed amount of time in all individuals, after which effects are negligible (e.g., Nenno and Healy 1979). This practice is commonly used in movement studies of sea ducks (Tribe: Mergini), which are frequently targeted for telemetry, and, like other waterfowl, may be especially vulnerable to tag effects (Lameris and Kleyheeg 2017). Recent movement analyses of sea ducks with implanted transmitters (e.g., De La Cruz et al. 2009, Loring et al. 2014, Beuth et al. 2017, Meattey et al. 2018, Lamb et al. 2019) have censored data from the 14-day period immediately following transmitter attachment. The decision to remove the first 14 days of movement data is based on a study of Harlequin Ducks (*Histrionicus histrionicus*), in which the authors observed that most mortality of transmitter-equipped individuals occurred within 14 days of release (Esler et al. 2000). However, no assessment has yet been made to determine whether this window is also appropriate to account for sublethal behavioral effects of transmitter attachment. Previous research has suggested that waterfowl and other waterbirds with implanted transmitters may experience changes in behaviors such as foraging, migration, and reproduction that extend beyond the immediate post-capture period (e.g., Meyers et al. 1998, Hupp et al. 2003, Latty et al. 2010, Hooijmeijer et al. 2014). Thus, depending on the specific research question of interest, sublethal effects of transmitter implantation may affect inferences derived from telemetry data even after accounting for the initial post-capture adjustment period.

The objective of this study was to evaluate the effects of capture and transmitter implantation on short- and long-term behavioral and movement patterns derived from telemetry data. We used telemetry data from a long-term sea duck tracking dataset, the Atlantic and Great Lakes Sea Duck Migration Study (AGLSDMS), which includes data from hundreds of individual sea ducks with coelomically implanted satellite transmitters in eastern North America representing 5 high-priority species (Common Eider [*Somateria mollissima*], Surf Scoter [*Melanitta perspicillata*], White-winged Scoter [*M. deglandi*], Black Scoter [*M. americana*], and Long-tailed Duck [*Clangula hyemalis*]). The AGLSDMS dataset is useful for examining transmitter effects as it includes multi-year data from individuals across a variety of capture locations, capture times, species, ages, and sexes. We used state-space models to test for the presence and duration of altered behavior immediately following capture and transmitter implantation, and compared subsequent phenological parameters (breeding site attendance, breeding initiation dates, timing and duration of migration) among post-capture years to evaluate the potential effects of transmitter attachment on movement, behavior, and reproduction. We further examined relationships of behavioral responses to individual covariates including capture season, species, age, and sex. Our goal is to provide guidelines for incorporating effects of capture and transmitter implantation into analysis of movement patterns across various temporal scales, while also accounting for inter- and intraspecific variation.

METHODS

Study Area

Biologists and collaborators with the AGLSDMS project captured sea ducks in multiple areas along the Atlantic Coast and Great Lakes of North America during the molting, staging, and wintering time periods (August–March) from 2002 to 2016 (Figure 1). To maximize capture efficiency, sampling locations were selected to represent locations and time periods of particularly high nonbreeding concentrations of each species. This approach resulted in a lack of sampling efforts in less-utilized winter and staging sites; however, given the tendency of waterfowl to form large aggregations during the nonbreeding time period (Weller and Batt 1988), sampling known areas of high sea duck concentrations allowed AGLSDMS collaborators to efficiently capture individuals and deploy transmitters. Capture efforts for Long-tailed Ducks and Surf Scoters focused primarily on wintering sites where high bird concentrations are typically observed during the Atlantic Winter Sea Duck Survey (Silverman et al. 2013). Additional captures of Surf Scoter (40%) were carried out during fall migration in the St. Lawrence Estuary, Quebec,

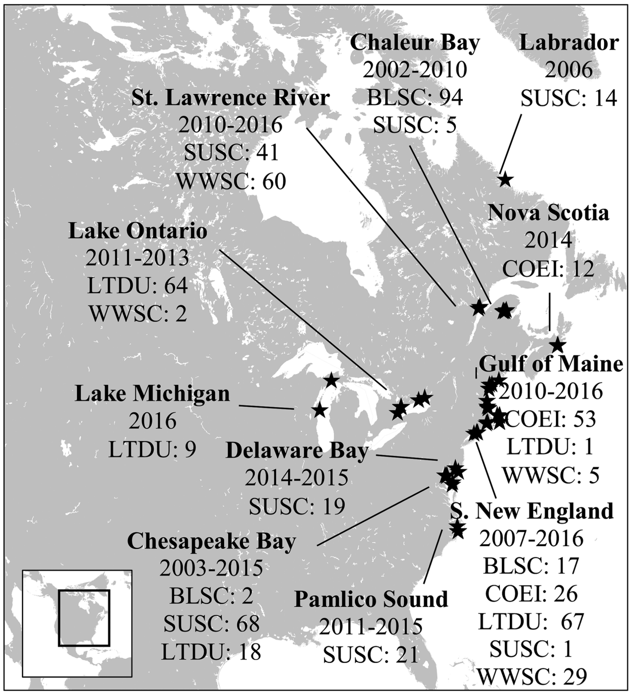

FIGURE 1. Locations, capture years, and sample sizes by species of sea duck telemetry studies used to analyze transmitter effects, eastern North America, 2002–2016 (BLSC = Black Scoter; COEI = Common Eider; LTDU = Long-tailed Duck; SUSC = Surf Scoter; WWSC = White-winged Scoter).

and additional sampling of Long-tailed Ducks wintering on Lake Michigan was added late in the project to account for areas of known use not represented by locations of individuals captured elsewhere. Capture efforts for Black Scoters focused on spring staging sites on Resticouche River and Chaleur Bay between New Brunswick and Québec, in the Gulf of St. Lawrence. Over 60% of White-winged Scoter captures were conducted on molting grounds in the St. Lawrence Estuary. Sampling of Common Eiders was limited to 1 of 3 eastern subspecies (*S. m. dresseri*) during breeding and wintering periods.

Transmitter Deployment

Biologists and collaborators with the AGLSDMS project captured subadult and adult ducks of both sexes using a combination of over-water mist nets and night-lighting (full details of capture methods in Lamb et al. 2019). We determined age by measuring bursa depth and examining external plumage characteristics. Age categories varied by species and capture timing; for the purposes of the present analyses, we simplified age to 2 mutually exclusive categories: subadult (individuals originally classified as hatch-year or second-year), or adult (individuals originally classified as third-year, after-hatch-year, after-second-year, or after-third-year). We then determined sex by cloacal examination (Sea Duck Joint Venture 2015) or external plumage characteristics and measured body mass with a Pesola spring scale (Pesola, Schindellegi, Switzerland; ±5 g) or digital hanging scale (HS-3000, Universal Weight Enterprises, Taipei, Taiwan; ±2 g). Veterinarians experienced in avian surgery implanted 26–50 g coelomic-implant Platform Transmitter Terminals (PTT) (Microwave Telemetry, Columbia, Maryland, USA; Telonics, Mesa, Arizona, USA; Geotrak, Apex, North Carolina, USA; Appendix Table 3) into the right caudal coelomic cavity following the implantation technique described by Korschgen et al. (1996). Individuals were selected for transmitter implantation based on body mass, such that transmitter mass represented <5% of overall body mass (Phillips et al. 2003; see Table 1 for overall and species-specific averages), and after being judged to be in good health and condition by the examining veterinarian. Early in the study, some Long-tailed Ducks were fitted with transmitters representing up to 7% of body weight due to the species' relatively smaller body size; however, in later study years, smaller transmitters and larger individuals were selected such that transmitter weights were <5% of body mass. Transmitters followed varying duty cycles consisting of 2–4 hr "on" periods followed by 10–120 hr "off" periods, resulting in one location every 0.5–5 days, with data acquisition frequency varying seasonally and typically less frequently during breeding (every 3–4 days on average) than during nonbreeding (every 2–3 days) (for specific duty cycles by deployment event, see Lamb et al. 2019). Argos location data were processed and disseminated through Collecte Localisation Satellites (CLS) America. PTT signals were received by equipment on polar-orbiting National Oceanic and Atmospheric Administration and MetOp satellites. Data were transferred to the CLS America processing center in Lanham, Maryland, where locations were estimated from the Doppler shift in the PTT carrier frequency.

Statistical Analyses

Data processing. Raw satellite telemetry data vary in quality of location estimates based on the configuration and number of satellites used to obtain each location. Location estimates were acquired by Argos standard service processing (CLS America, Lanham, Maryland, USA) and assigned, in decreasing order of precision, to Argos location classes (LC) 3, 2, 1, and 0 and auxiliary location processing (LC A, B, and Z). Accuracy (i.e. 1 standard deviation [SD]) for location estimates with LC 3, 2, 1, and 0 was <250, 250–500, 500–1,500, and >1,500 m, respectively (Collecte Localisation Satellites 2016). In subsequent modeling, each point was considered to represent the center of a probability distribution based on the error associated with its LC.

To delineate behavioral states underlying observed locations, we used a switching state-space model (Jonsen et al. 2005). This modeling approach, which calculates the distributions of turning angles and step lengths between subsequent locations, allowed us to simultaneously account for variations in data quality (i.e. device error) and changes in the movement patterns that generated observed locations. During modeling, we interpolated tracking data to 1-day intervals based on probable paths between locations. Interpolated locations were inexact and did not account for within-day movement; however, they allowed us to use available information to determine the most likely days on which shifts in large-scale movement patterns occurred (see below). We did not interpolate over time periods of >7 days between successive locations, because longer temporal gaps produce unrealistic movement trajectories (Jonsen et al. 2005); any tracks with gaps >7 days were split into separate tracks before and after the gap. Based on the duty cycles of transmitters, the maximum programmed gap between locations for a correctly functioning unit was 5 days (120 hr), with most units sampling more frequently; thus, 90% of locations were separated by ≤4 days, and 78% of locations were separated by ≤3 days. Average sampling intervals varied among species from 2.3 (Surf Scoters) to 3.6 days (White-winged Scoters). For individuals with few locations, we found that models either failed to converge or produced results with high uncertainty. To meet the data requirements of state-space models, we removed all individuals with <50 locations in LC 1–3 (typically, individuals with 1 month or less of location data) prior to analysis.

We ran all models in the *bsam* package (Jonsen et al. 2005, Jonsen 2016) in R 3.6.2 (R Core Team 2019) using a switching first difference correlated random walk model with a 1-day time step, 5,000 burn-in samples for model training, and 5,000 posterior samples for analysis. We thinned posterior samples by selecting every fifth sample to reduce autocorrelation and computing time, and used a 0.1 smoothing parameter. While thinning is not a necessary step, it may be justified in cases where it substantially increases computational efficiency or where extensive post-processing is required (Link and Eaton 2012); in this case it was necessary to efficiently process a large number of individual tracks and locations. Model outputs included probable daily locations with 2.5, 50, and 97.5% confidence intervals, as well as a score (hereafter, *b*) which takes a value between 1 and 2, indicating the average assignment of the location to either a transient (1: long step lengths and low turning angles) or resident (2: short step lengths and high turning angles) behavioral state across all posterior samples post-thinning. Thus, a lower average value of *b* for a given location indicates more dispersive behavior, while a higher value indicates more sedentary behavior.

Post-capture behavior. To determine the duration of altered behavior following tagging, we calculated the mean value of b for resident locations (i.e. $b > 1.5$) for each individual within the season in which capture and transmitter implantation occurred. In keeping with standard practices for screening sea duck telemetry data, we considered that a bird was exhibiting “normal” seasonal behavior from 14 days after transmitter attachment (Esler 2000) until the first sustained dispersive movement (i.e. $b \leq 1.5$ for ≤3 consecutive locations) following transmitter implantation. We thus considered the mean b-value of all locations within this window to represent the “normal” mean value of b (b_{norm}). To evaluate the sensitivity of b_{norm} to the censorship window, we also calculated b_{norm} using a 30-day censorship window, which resulted in an average change of ±0.09% relative to b_{norm} values calculated using a 14-day window. We therefore considered that the substance of our results was not sensitive to the specific length of the censorship window. For each individual and day, we calculated the difference between the daily b value and the seasonal b_{norm} (b_{diff}) as a measure of daily deviation from typical seasonal behavior. To determine the duration of behavioral effects, we also calculated time-to-normal (i.e. the number of days from the date of transmitter implantation to the first date on which b_{diff} was within the 95% confidence interval of b_{norm}). We calculated both b_{diff} and time-to-normal beginning on the date of capture, and related these indices to individual covariates using mixed-effects models as described below (see Effects of individual covariates).

Breeding site attendance and phenology. In addition to assessing behavior immediately following transmitter attachment, we also compared breeding site attendance across multiple post-capture breeding seasons. We assumed that any immediate negative energetic effects of capture and tagging would result in reduced breeding site attendance during the first breeding season following capture, while the second breeding season would possibly represent a return to normal breeding site attendance. Based on nest site attendance rates by breeding sea ducks, we defined breeding site attendance as 3 or more points classified as resident ($b > 1.5$) at a terrestrial site near an inland water body during the sea duck breeding season (May–August: Johnsgard 1978). Since the length of time spent at a breeding site may include breeding and molting activities, we did not attempt to determine breeding success based on residence times. Instead, we used a binary covariate for nest site attendance (0 = did not attend breeding site; 1 = attended breeding site).

To evaluate migratory and breeding phenology, we used the state-space modeling results to identify periods of migratory movement ($b \leq 1.5$ for ≥3 consecutive locations). We defined the first of the days on which $b \leq 1.5$ as the start date of the migration period, and calculated the duration of the migratory movement as the total number of days on which $b \le 1.5$ before reaching a period of more than 3 consecutive days on which $b > 1.5$. Periods of residency within migrations (i.e. $b > 1.5$ for ≤3 consecutive days) were classified as stopovers, and periods of residency between migrations were classified as breeding, molting/fall staging, wintering, or spring staging based on their habitat characteristics and position in the annual cycle. We assigned migratory movements to one of 5 categories depending on its location within the annual cycle: spring migration (i.e. between wintering and spring staging sites), breeding migration (between spring staging and breeding sites), molt migration (between breeding and molt/fall staging sites), winter migration (between fall staging and wintering sites), and within-season dispersal (short dispersive movements between sites within a season, not considered in this analysis). Some individuals did not attend distinct breeding and/or molt sites; in these cases, we classified the entire migration between wintering and nonbreeding summer sites as a single spring migration, and the entire migration between breeding or nonbreeding summer sites and wintering grounds as a single winter migration. In addition to migratory phenology, we also determined arrival date at the breeding site, since later arrivals may experience reduced fitness through obtaining poorer breeding territories or failing to fledge chicks before the onset of poor weather. Since sea duck species differ in their overall phenology (e.g., Toft et al. 1982), we corrected for interspecific differences in timing of breeding and migration by calculating mean breeding initiation dates and migration start dates during the second year after transmitter implantation for each species. We then subtracted the species-specific second year mean value from each individual breeding initiation date or migration start date, so that negative values indicate an earlier start and positive values indicate a later start.

Effects of individual covariates.
We used mixed effects models to evaluate the relationship of behavior and phenology to individual covariates following capture and transmitter implantation. After using histograms to examine the distributions of individual response variables and determine the most appropriate distribution for each model, we fit generalized linear mixed models (GLMMs) to 11 response variables: time-to-normal (exponential distribution, log link), breeding site attendance (binomial distribution, logit link), breeding initiation date, and start dates and durations of breeding, molt, winter, and spring migrations (Gaussian distribution, identity link). Predictors included fixed effects of years post-capture, capture season (fall migration/molt, winter, or spring), transmitter manufacturer, transmitter weight as a percentage of body weight, age (subadult or adult), species, sex, and their interactions, as well as individual, capture site, and year as random factors. After testing the fit of the global model for each response variable, we dropped random terms whose variance values were close to zero, and generated candidate models using a backward stepwise selection of the remaining fixed terms. When all remaining terms were significant ($P < 0.05$), we considered this our final model.

RESULTS

Of 672 individual radio-marked sea ducks (deployed), 476 had sufficient data for our analysis (retained; Table 1). Sample sizes for each species ranged from 76 (Common Eider) to 139 (Surf Scoter), and sampling for each species included individuals of both sexes. The sample included 424 adults and 52 subadults at capture. Transmitter masses varied from 1.4 to 5.7% of body mass, with species-specific means ranging from 2.3 to 4.3%, and an overall mean of 3.6 ± 0.9% (Table 1).

Behavioral state b-values were generally below seasonal averages (i.e. more dispersive) immediately following capture, but increased to seasonally average levels within ~5 days (Figure 2). After reaching normal levels, behavioral state values for all species remained within the normal range through the rest of the 14-day post-capture period.

Our final model for time-to-normal included species, age, and capture season, with random effects of year and

TABLE 1. Sample sizes for transmitter deployments on 5 species of sea ducks in eastern North America, 2002–2017.

	Number of individuals					Transmitter weight as a percentage of body weight (mean ± SD)	Locations individual^{-1} (mean ± SD)	
Species	Deployed	Retained	Males	Females	Subadults [a]		Raw	Interpolated
Common Eider	91	76	15	61	0	2.3 ± 0.4	419 ± 361	407 ± 159
Surf Scoter	207	139	75	64	7	4.2 ± 0.5	552 ± 483	282 ± 158
White-winged Scoter	96	83	21	62	22	3.1 ± 0.4	346 ± 230	361 ± 224
Black Scoter	113	89	42	47	14	3.6 ± 0.2	611 ± 340	530 ± 311
Long-tailed Duck	165	89	30	59	9	4.3 ± 0.9	258 ± 189	229 ± 123
Total	672	476	183	293	52	3.6 ± 0.9	445 ± 377	351 ± 286

[a] Age at capture.

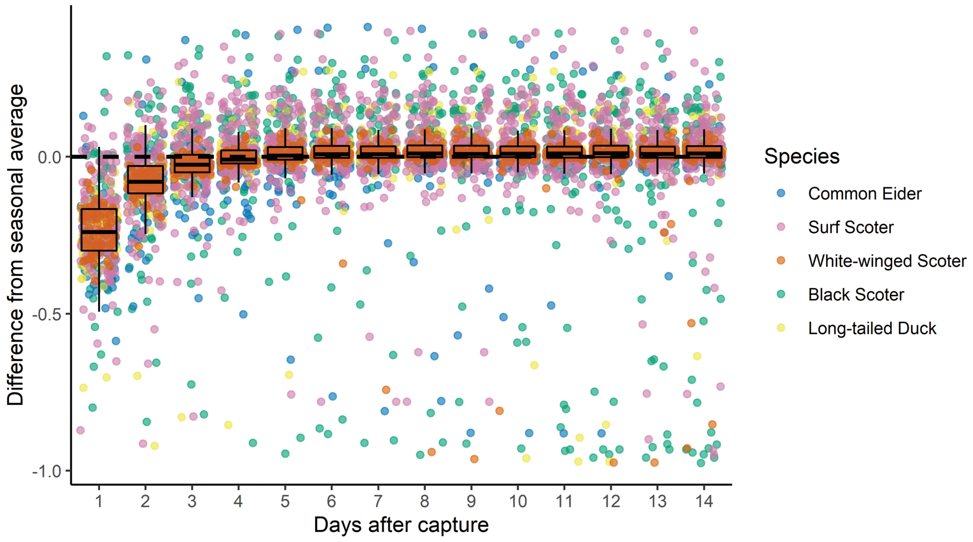

FIGURE 2. Differences in daily behavioral (movement pattern) states from seasonal averages for the first 14 days after transmitter implantation for 5 sea duck species tracked between 2002 and 2017 in eastern North America. Values below 0 indicate more dispersive behavior, while values above 0 indicate more sedentary behavior. Dots represent individual values (see Table 1 for sample sizes by species). Box plots show median (center bar), interquartile range (box), and minimum/maximum (vertical bars: ± 1.5 times interquartile range) values.

capture region (Table 2A). Median time-to-normal was highest (~6 days) and most variable for Common Eiders, intermediate (~5 days) for Long-tailed Ducks and White-winged Scoters, and lowest for Black and Surf Scoters (~4 days) (Figure 3). Common Eiders took significantly longer than the other 4 species to reach b_{norm}, while the 3 scoter species and Long-tailed Duck intervals were similar (Table 2A). Males were slightly quicker than females to return to normal behavior, although the 95% confidence interval of the coefficient estimate overlapped zero. Birds captured during winter took longer to return to normal behavior than birds captured during breeding or migration (Table 2A), with effects varying by species (Figure 3).

Our final model of breeding site attendance included years post-capture, age, species, sex, and the interaction of species and sex, with a random term for year (Table 2B). Breeding site attendance was positively correlated with the number of years post-capture, indicating lower breeding site attendance in the first breeding season after capture compared with subsequent years. Breeding site attendance also increased with age, and subadults consistently showed lower breeding site attendance than adults. Males of the 3 scoter species attended breeding sites at lower rates than females, while breeding site attendance was similar between male and female Common Eiders and Long-tailed Ducks (Figure 4).

Our final models for breeding initiation date included years post-capture, capture season, transmitter weight, and species (Figure 5A). Our final models for start date and duration of migrations included years post-capture, capture season, sex, and species (Figure 5B, C). Number of years post-capture affected breeding initiation date and the timing of spring staging and breeding migrations, with both breeding and migration dates delayed during the first year after capture relative to subsequent years (Figure 5A, B; Figure 6). Molt and wintering migrations also tended to occur later during the first year after capture compared with subsequent years, although these differences were not significant (Figure 6). Duration of winter, spring staging, and breeding migrations also increased with years post-capture, indicating quicker migrations immediately following transmitter attachment than in subsequent years (Figure 5C). Individuals captured during spring staging or breeding had delayed breeding initiation dates compared with individuals captured in fall or winter (Figure 5A). Effects of capture timing on migration start date and duration were variable (Figure 5B, C). Males had later and shorter breeding migrations than females but started fall molt and winter migrations earlier (Figure 5B, C). Birds with heavier transmitters relative to body weight began breeding slightly earlier than those with lighter transmitters (Figure 5A). Finally, after adjusting for species-specific baseline differences in phenology, species varied in their phenological parameters following transmitter implantation (Figure 5A–C).

DISCUSSION

While sea ducks resumed normal movement patterns relatively quickly following implantation of coelomic transmitters with percutaneous antenna, long-term effects

TABLE 2. Coefficient values for the best models of (**A**) time to normal movement patterns and (**B**) breeding site attendance for 5 species of sea ducks, 2002–2017. Covariates for which the 95% confidence intervals (CI) of the coefficient estimates do not overlap zero are listed in bold.

	Estimate	95% CI
A. Time to Normal		
Intercept	**1.291**	**0.888**, **1.695**
Year		
(Variance = 0.082; σ = 0.287)		
Capture region		
(Variance = 0.022; σ = 0.151)		
Species		
Common Eider (vs. Black Scoter)	**0.762**	**0.432**, **1.093**
Surf Scoter (vs. Black Scoter)	0.100	−0.212, 0.412
White-winged Scoter (vs. Black Scoter)	0.161	−0.144, 0.466
Long-tailed Duck (vs. Black Scoter)	0.034	−0.259, 0.327
Sex (male vs. female)	−0.036	−0.132, 0.061
Capture season		
Fall (vs. breeding)	0.156	−0.220, 0.531
Winter (vs. breeding)	**0.412**	**0.104**, **0.721**
Spring (vs. breeding)	0.233	−0.150, 0.615
B. Breeding site attendance		
Intercept	**0.580**	**0.363**, **0.796**
Year		
(Variance = 0.030; σ = 0.172)		
ears post-capture	**0.146**	**0.068**, **0.224**
Age (subadult vs. adult)	**−0.163**	**−0.235**, **−0.091**
Species		
Common Eider (vs. Black Scoter)	**0.207**	**0.076**, **0.338**
Surf Scoter (vs. Black Scoter)	**0.219**	**0.090**, **0.347**
White-winged Scoter (vs. Black Scoter)	0.019	−0.106, 0.144
Long-tailed Duck (vs. Black Scoter)	**0.217**	**0.091**, **0.343**
Sex (male vs. female)	**−0.528**	**−0.653**, **−0.403**
Species * Sex		
Common Eider: male (vs. female)	**0.743**	**0.173**, **1.314**
Long-tailed Duck: male (vs. female)	**0.474**	**0.243**, **0.704**
Surf Scoter: male (vs. female)	0.129	−0.105, 0.364
White-winged Scoter: male (vs. female)	−0.102	−0.314, 0.110

including reductions in breeding site attendance and delayed breeding and migration phenology occurred in the year following transmitter attachment.

Across all species, capture and transmitter attachment initially increased dispersive behavior in radio-marked individuals (n = 476), but movement patterns generally returned to normal within ~5 days of release. This period of altered movement is considerably shorter than the 14-day post-capture censorship window recommended by Esler et al. (2000) and frequently applied to sea duck movement analyses (e.g., Loring et al. 2014, Beuth et al. 2017, Meattey et al. 2019). Thus, removing data collected up to 14 days post-capture may eliminate locations unaffected by short-term effects of capture and tagging on movement. The duration of immediate capture and tagging effects was longer and more variable in Common Eiders than in the other 4 species. This accords with previous work suggesting that eiders may experience significant short- and medium-term effects that varied by individual (Latty et al. 2010, 2016, Fast et al. 2011), although none of these studies included other sea duck species for comparison. However, the difference in median values between the longest and shortest adjustment times was relatively small (2 days). This suggests that, at least in the short term, no species experienced dramatically greater effects than others of capture and tagging on movement patterns.

It is important to note that the 14-day censorship window originally proposed by Esler et al. (2000) was based on observations of elevated mortality during the period immediately following transmitter attachment, and not on any assessment of movement or behavior. By contrast, our study evaluated movement patterns but does not account for effects of transmitters on survival. Since sensor data from our transmitters were often insufficient to distinguish mortality from transmitter failure (Brodeur et al. 2008), we did not directly assess survival rates in any of the study species, and due to the requirements of our models, we did not include individuals whose transmitters failed within a month of capture. In practice, elevated mortality rates shortly after tagging have been observed in Long-tailed Ducks (Sea Duck Joint Venture 2015) and Surf Scoters (Le Net et al. 2019), possibly due to issues associated with

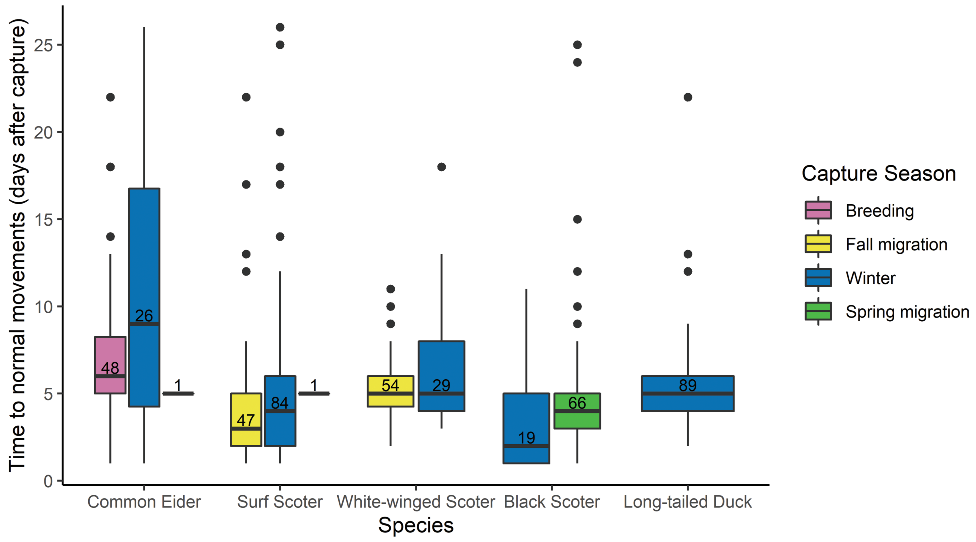

FIGURE 3. Average number of days after transmitter attachment that daily behavioral (movement pattern) state assignment probability matched the seasonal average by species and capture season for 5 sea duck species tracked between 2002 and 2017 in eastern North America. Box plots show sample size (text), median (center bar), interquartile range (shaded box), minimum/maximum (vertical bars: ± 1.5 times interquartile range), and outlier (dots) values.

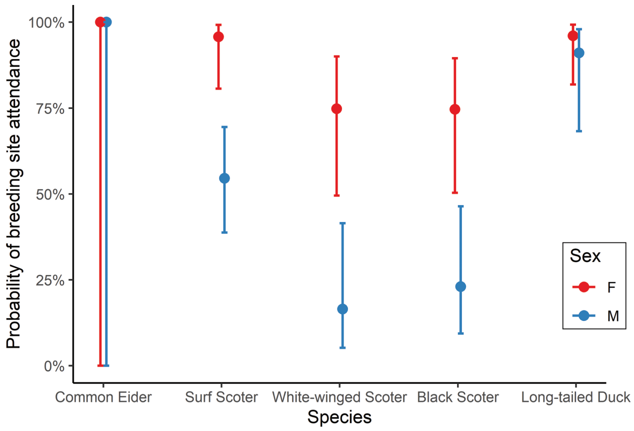

FIGURE 4. GLMM-predicted probabilities of males and females of 5 species of sea ducks attending breeding sites after capture and transmitter implantation, 2002–2017, eastern North America. Dots indicate mean probability of attendance predicted from the final models, and lines are 95% confidence intervals of predicted values.

capture and surgery (Mulcahy and Esler 1999, Iverson et al. 2006, Ford et al. 2011, Sexson et al. 2014). However, for individuals that survived the initial post-release period, we were unable to detect abnormal day-to-day movement patterns after a few days from release regardless of species. Thus, while it seems reasonable to continue excluding individuals whose transmitters go offline within a few weeks to a month of capture from further analysis, it may be necessary to censor only the first 5–6 days of data for individuals whose transmitters last months to years. Including 8–10 additional days of data may not dramatically affect conclusions at annual or multi-annual timescales; however, analyses of habitat use frequently focus on a single season (e.g., Loring et al. 2014, Beuth et al. 2017, Meattey et al. 2019). Migratory sea ducks occupy habitat areas for periods ranging from weeks (staging sites) to months (wintering areas), meaning that even a few days of additional data could potentially affect results at the focal timescales. Given that analyses of sea duck habitat use based on telemetry data have already had significant implications, including informing siting of offshore energy infrastructure (Olsen et al. 2014), incorporating all available information into such analyses is critical to ensuring the best possible conservation outcomes.

In addition to species-level effects, we also assessed whether variation in individual characteristics, capture timing, or external conditions affected the duration of change in movement patterns following capture and transmitter attachment. While sex and age differences did not contribute significantly to inter-individual variation, capture season helped to explain observed variation, as short-term changes in behavioral state lasted slightly longer during winter than during breeding and migration. However, as not all species were sampled in all seasons, it is difficult to fully separate the effects of species-specific differences in sensitivity from seasonal differences. For example, Black Scoters captured in winter exhibited normal movement patterns more quickly than Black Scoters captured during spring staging, while Surf and White-winged Scoters captured in winter showed similar adjustment times to those

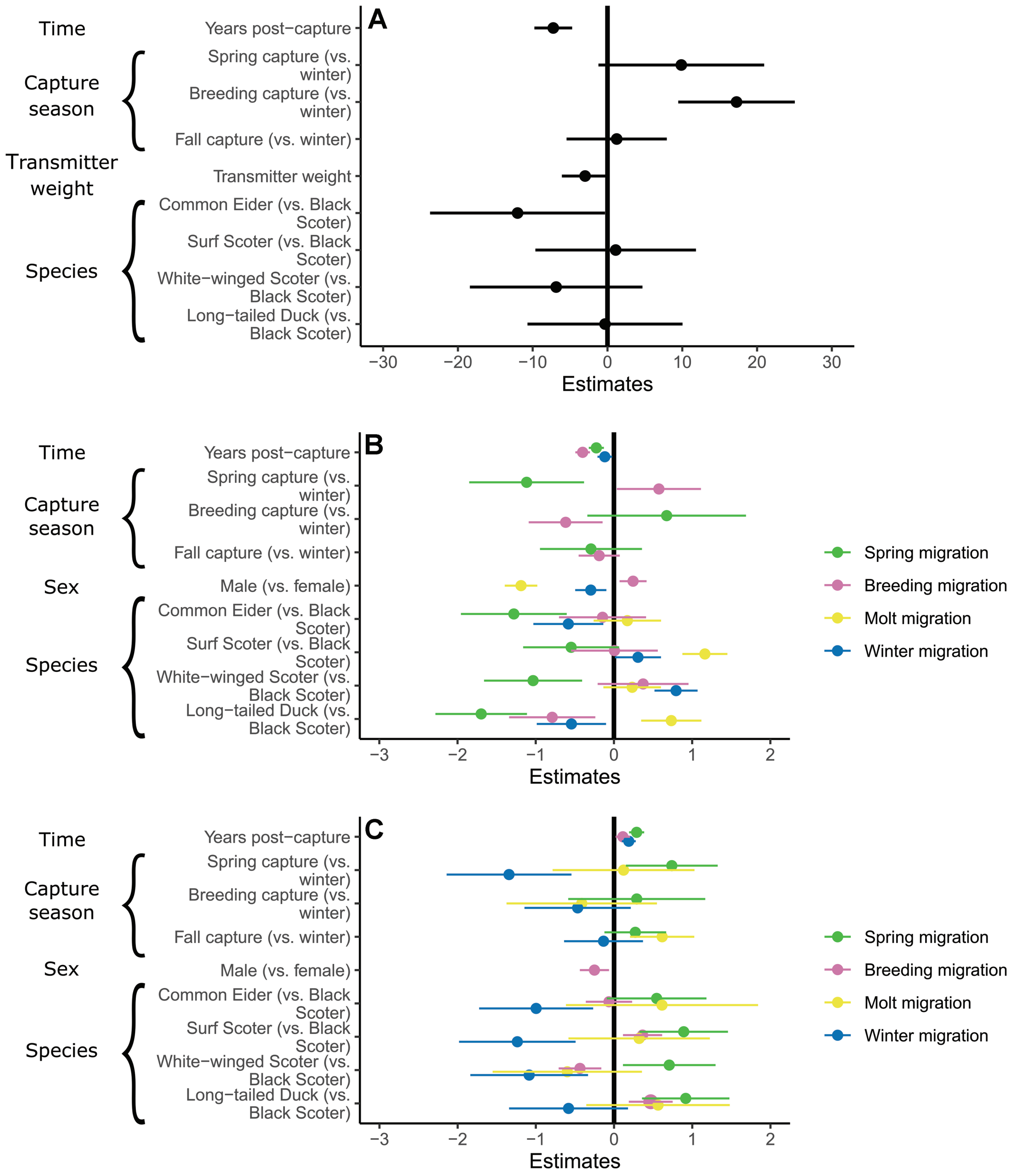

FIGURE 5. Effect sizes for fixed covariates in GLMMs of (**A**) breeding initiation date, and (**B**) start date and (**C**) duration of migration, for 5 sea duck species tracked between 2002 and 2017 in eastern North America. Dots represent coefficient estimates, and lines are 95% confidence intervals of coefficients.

captured during fall staging; as the 3 species were not all sampled during the same seasons, however, it is impossible to assess whether these differences are the result of greater sensitivity to transmitter implantation during spring staging or species-specific differences in sensitivity. Finally, we found that unmeasured among-year and among-site differences could affect the duration of short-term effects of transmitters. Previous studies of other avian taxa and transmitter types have shown that transmitter effects may vary depending on external conditions (e.g., Hamel et al. 2004, Snijders et al. 2017), and our work further supports the need to account for environmental heterogeneity in assessing the potential intensity and duration of transmitter effects.

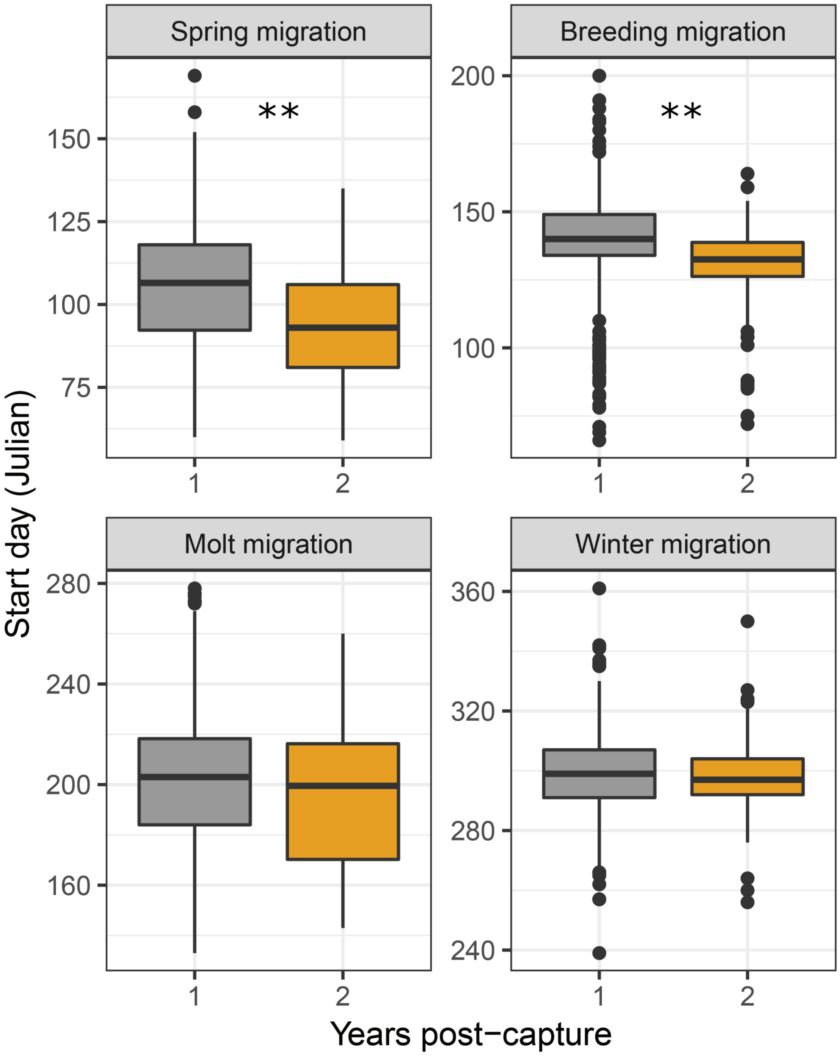

FIGURE 6. Differences between migration start dates during the first (gray) and second (orange) years after capture for 5 sea duck species (Common Eider, Surf Scoter, White-winged Scoter, Black Scoter, and Long-tailed Duck) tracked between 2002 and 2017 in eastern North America. Pairs marked with asterisks (**) indicate periods for which migration start date varied significantly with years post-capture. Box plots show median (center bar), interquartile range (shaded box), minimum/maximum (bars: ± 1.5 times interquartile range), and outlier (dots) values.

Despite the fact that sea ducks appeared to resume normal day-to-day movement patterns within less than a week after radio-marking, we observed longer-term effects on migration patterns and breeding site attendance. Probability of breeding site attendance in the first breeding season following transmitter attachment was significantly reduced compared with the subsequent season across all individuals. Moreover, individuals fitted with transmitters migrated later and more quickly between winter, staging, and breeding sites during the first year after transmitter implantation compared with subsequent years, while the timing and duration of migrations between breeding, molt, and wintering sites were not affected. Prolonged migration chronology due to tagging could introduce biases into habitat-use analysis. Delayed breeding migration was most evident in individuals captured during spring staging, followed by those captured in winter, while individuals captured during the previous fall or breeding season showed little to no delay. Later breeding migrations immediately following transmitter implantation could result from spending additional time at nonbreeding sites to augment energy reserves, possibly to compensate for decreases in foraging efficiency while adjusting to transmitters (Latty et al. 2010), and individuals may have migrated more quickly to reduce the resulting delays in breeding initiation. However, the increased speed of migration did not fully outweigh the later onset of migration, resulting in later arrival at breeding sites during the first year after implantation. As nest success in sea ducks and other migratory birds is often negatively correlated with nest initiation date (Grand and Flint 1997, Blums et al. 2002, Morrison et al. 2019), this further suggests a potential reduction in reproductive output in the season following implantation compared with subsequent years. Since breeding site attendance and phenology alone do not provide definitive information on whether individuals succeeded in raising young, additional measures of breeding success would be necessary to fully quantify the effects of transmitters on reproduction. Direct observations have suggested that reduced breeding success immediately after transmitter implantation in Common Eiders may be followed by successful breeding in subsequent seasons (Fast et al. 2011); however, further observational study is needed to assess whether the same is true across other species and sites.

We also found evidence that interannual effects of capture and transmitter implantation varied among species and between sexes. This variation did not appear to result from species- or sex-specific differences in body size, since transmitter weight as a percentage of body weight was relatively consistent among individuals and was not a strong predictor of breeding site attendance or most aspects of annual-cycle phenology, aside from a slight association between heavier transmitters and earlier breeding initiation. No individual species showed consistently greater phenological change across all migrations; however, Black Scoters tended to migrate later and more quickly in spring relative to the other 4 species. This could indicate an interannual effect of differences in capture timing, as Black Scoters were the only species captured during spring staging; it may also be related to baseline differences in phenology among species at the sampled sites.

Overall, radio-marked males attended breeding sites less frequently than females and experienced greater delays in breeding migration. While underlying differences in migration timing between males and females likely account for our observations of earlier molt and winter migrations in males, previous studies suggest that unmarked males and females typically arrive at breeding sites at similar times (e.g., Savard et al. 2007), suggesting that breeding migration chronology may be particularly affected in males following transmitter implantation. Sex-specific breeding attendance also varied by species: while male Common Eiders and Long-tailed Ducks attended breeding sites at similar rates to females, males of the 3 scoter species showed markedly lower attendance rates. This may result in part from an underlying male bias in waterfowl populations (Bellrose et al. 1961), which may be especially pronounced in scoters (Rodway et al. 2015). Depending on the timing of capture relative to pair formation, delays in migration and breeding phenology resulting from capture and implantation could further decrease the probability that a male will successfully find a breeding partner or may disrupt pair bonds that have already formed, whereas radio-marked females might be able to find breeding opportunities among the surplus males regardless of any phenological delays associated with the transmitter. Our ability to detect sex-specific trends was limited by high levels of breeding site attendance in both years for Common Eider, as well as relatively small sample sizes for males of some species (Common Eider, White-winged Scoter), meaning that further tracking of males may be needed to fully assess sex-specific variation in breeding responses for these species.

It is important to note that there were no true controls in our study; thus, our assessment of transmitter effects was limited to information available from marked individuals and may not represent population-wide norms if marked and unmarked individuals differ systematically. In particular, while the multi-year duration of transmitters provided opportunities to examine intra-individual differences in behaviors over time, these effects are necessarily confounded with age. Since age at capture could not be precisely determined for after-hatch-year individuals, we were unable to account for any potential underlying variation in parameters (e.g., phenology, breeding site attendance) with age beyond the first year. Hatch-year and after-hatch-year sea ducks did not appear to differ in any of our measured parameters for sensitivity to transmitter implantation except for breeding site attendance, which may be related to underlying differences in movement patterns between adult and subadult sea ducks (e.g., Bentzen and Powell 2015). Observational studies at breeding sites could potentially be used to compare individuals with implanted transmitters with unmarked individuals in order to remove the confounding effect of time and directly compare phenology, attendance, and breeding success between sea ducks with and without transmitters. In addition, our ability to detect behavioral change was limited by the spatiotemporal scale of data collection, which would not have identified fine-scale changes such as altered dive behavior (such as those observed in captive birds by Latty et al. [2010]) or diurnal patterns of marine habitat use (e.g., Lewis et al. 2005, Merkel and Mosbech 2008). Given the rapid increases currently occurring in both the accuracy and frequency of data from bird-borne telemetry, our approach could be used in future studies to analyze behavioral effects at finer scales.

Despite these limitations, our analysis allows us to identify several potential species- and individual-level correlates of sensitivity to tagging effects, and to provide more rigorous guidelines for future tracking studies. In particular, our results suggest that a data censorship window of 5–6 days, rather than the commonly used 14-day period, is likely sufficient to eliminate most short-term changes in movement patterns resulting from capture and tagging at the timescale of our data. We also demonstrate that tagging can affect the phenology of migration and breeding propensity, although such effects were more likely when birds were captured at spring staging sites just before their migration to breeding areas. This suggests that potential effects of capture and tagging on reproductive output could be minimized by timing captures during fall molt or winter and emphasizes the importance of collecting data across multiple years for comparison.

ACKNOWLEDGMENTS

We thank Andrew Gilbert, who served as a primary data manager for much of the data used in this study. Logistical and field assistance were provided by the University of Rhode Island (P. Loring, J. Beuth, D. Meattey), Bird Studies Canada/Long Point Waterfowl (T. Barney, J. Palframan, C. Moore, M. Illes, S. Gan, D. Okines), Canadian Wildlife Service (S. Meyer, C. Sharp, B. Campbell, J. Vanos, F. St. Pierre), Toronto Zoo (G. Crawshaw, D. Mihailovic), U.S. Geological Survey (USGS: C. Caldwell), and Western University (P. Wilson). Data, field, and lab support, insight into project design, and other resources were provided by Memorial University (B. Montevecchi, C. Burke), Biodiversity Research Institute (I. Stenhouse, W. Goodale), University of Maine (C. Gray), Cornell Lab of Ornithology (J. Fiely), USGS Patuxent Wildlife Research Center (C. Kilchenstein), Avian Specialty Veterinary Services (S. Ford), Bureau of Ocean Energy Management (J. Woehr, retired), North Carolina Wildlife Resources Commission (D. Howell), and Swansea University (S. Vandenabeele).

Funding statement: Funding and in-kind support was provided by Sea Duck Joint Venture, U.S. Fish and Wildlife Service (USFWS), Environment and Climate Change Canada/Canadian Wildlife Service, Toronto Zoo, USGS Patuxent Wildlife Research Center, Bird Studies Canada/Long Point Waterfowl, Bluff's Hunting Club, Ducks Unlimited Inc., Ontario Federation of Anglers and Hunters, Natural Sciences and Engineering Research Council of Canada, Ontario Ministry of Natural Resources, Wildlife Habitat Canada, TD Friends of the Environment Foundation, and Western University. For the Bureau of Ocean Energy Management (BOEM) diving bird captures, funding was provided by BOEM through Intra-Agency Agreement M12PG00005 with USFWS, and by the U.S. Department of Energy, the Sea Duck Joint Venture, the Bailey Foundation, and USFWS. Southern New England captures received funding and support from the Sea Duck Joint Venture, Wildlife Restoration, Rhode Island Department of Environmental Management, and the University of Rhode Island. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Ethics statement: All handling and radio-marking of sea ducks was conducted under applicable institutional and agency permits, including Insitutional Animal Care and Use Committee, Bird Banding Lab, U.S. Fish and Wildlife Service, Canadian Wildlife Service, and state agency permits. Transmitters were only implanted in individuals determined to be in good health and for which the transmitter weight was less than 3–5% of body weight, as per accepted best practices. All stages of captures (capture, handling, surgery, recovery, and release) were supervised by qualified veterinarians.

Author contributions: JSL, PWCP, and SRM conceived the idea and formulated questions. All authors participated in collection of field data. JSL designed methods, analyzed data, and wrote the manuscript. PWCP, LJF, SGG, KK, CL, MLM, GHO, and SRM substantially edited the manuscript. All authors contributed substantial materials, resources, or funding. All authors approved the final manuscript.

Data availability: The data used in our analysis is archived on Zenodo: DOI: 10.5281/zenodo.3819396.

LITERATURE CITED

Barron, D. G., J. D. Brawn, and P. J. Weatherhead (2010). Meta-analysis of transmitter effects on avian behavior and ecology. Methods in Ecology and Evolution 1:180–187.

Bellrose, F. C., T. G. Scott, A. S. Hawkins, and J. B. Low (1961). Sex ratios and age ratios in North American ducks. Illinois Natural History Survey Bulletin 27:391–486.

Bentzen, R. L., and A. N. Powell (2015). Dispersal, movements and site fidelity of post-fledging King Eiders *Somateria spectabilis* and their attendant females. Ibis 157:133–146.

Beuth, J. M., S. R. McWilliams, P. W. Paton, and J. E. Osenkowski (2017). Habitat use and movements of Common Eiders wintering in southern New England. The Journal of Wildlife Management 81:1276–1286.

Blums, P., R. G. Clark, and A. Mednis (2002). Patterns of reproductive effort and success in birds: Path analyses of long-term data from European ducks. Journal of Animal Ecology 71:280–295.

Boyd, I. L., A. Kato, and Y. Roper-Coudert (2004). Bio-logging science: Sensing beyond the boundaries. Memoirs of the National Institute for Polar Research 58:1–14.

Brodeur, S., J. P. L. Savard, M. Robert, R. D. Titman, and G. Fitzgerald (2008). Failure time and fate of Harlequin ducks implanted with satellite transmitters. Waterbirds 31:183–187.

Calvo, B., and R. W. Furness (1992). A review of the use and the effects of marks and devices on birds. Ringing & Migration 13:129–151.

Collecte Localisation Satellites (2016). Argos User's Manual. CLS, Ramonville-Saint-Agne, France. http://www.argos-system.org/wp-content/uploads/2016/08/r363_9_argos_users_manual-v1.6.6.pdf.

De La Cruz, S. E. W., J. Y. Takekawa, M. T. Wilson, D. R. Nysewander, J. R. Evenson, W. S. Boyd, and D. H. Ward (2009). Spring migration routes and chronology of Surf Scoters (*Melanitta perspicillata*): A synthesis of Pacific coast studies. Canadian Journal of Zoology 87:1069–1086.

Enstipp, M. R., J. Frost, T. E. Hollmén, R. D. Andrews, and C. Frost (2015). Two methods of radio transmitter attachment and their effects on the behavior and energetics of captive Long-tailed Ducks (*Clangula hyemalis*) during winter. Animal Biotelemetry 3:36.

Esler, D., D. M. Mulcahy, and R. L. Jarvis (2000). Testing assumptions for unbiased estimation of survival of radio-marked harlequin ducks. Journal of Wildlife Management 64:591–598.

Fast, P. L. F., M. Fast, A. Mosbech, C. Sonne, H. G. Gilcrist, and S. Descamps (2011). Effects of implanted satellite transmitters on behavior and survival of female Common Eiders. The Journal of Wildlife Management 75:1553–1557.

Ford, S., G. Olsen, and M. Perry (2011). Update on satellite transmitter techniques in sea ducks. In Proceedings of the Association of Avian Veterinarians, 32nd Annual Conference (E. Bergman, Editor). Association of American Veterinarians, Denver, CO, USA. pp. 251–252.

Garriga, J., J. R. B. Palmer, A. Oltra, and F. Bartumeus (2016). Expectation-maximization binary clustering for behavioural annotation. PLoS One 11:1–26.

Geen, G. R., R. A. Robinson, and S. R. Baille (2019). Effects of tracking devices on individual birds–a review of the evidence. Journal of Avian Biology 50:e01823.

Grand, J. B., and P. L. Flint (1997). Productivity of nesting Spectacled Eiders on the lower Kashunuk River, Alaska. The Condor 99:926–932.

Hamel, N. J., J. K. Parrish, and L. L. Conquest (2004). Effects of tagging on behavior, provisioning, and reproduction in the Common Murre (*Uria aalge*), a diving seabird. The Auk 121:1161–1171.

Hatch, S. A., P. M. Meyers, D. M. Mulcahy, and D. C. Douglas (2000). Performance of implantable satellite transmitters in diving seabirds. Waterbirds 23:84–94.

Hebblewhite, M., and D. T. Haydon (2010). Distinguishing technology from biology: A critical review of the use of GPS telemetry data in ecology. Philosophical Transactions of the Royal Society B 365:2303–2312.

Hooijmeijer, J. C., R. E. Gill, D. M. Mulcahy, T. L. Tibbitts, R. Kentie, G. J. Gerritsen, L. W. Bruinzeel, D. C. Tijssen, C. M. Harwood, and T. Piersma (2014). Abdominally implanted satellite transmitters affect reproduction and survival rather than migration of large shorebirds. Journal of Ornithology 155:447–457.

Hupp, J. W., G. A. Ruhl, J. M. Pearce, D. M. Mulcahy, and M. A. Tomeo (2003). Effects of implanted radio transmitters with percutaneous antennas on the behavior of Canada Geese. Journal of Field Ornithology 74:250–256.

Hussey, N. E., S. T. Kessel, K. Aarestrup, S. J. Cooke, P. D. Cowley, A. T. Fisk, R. G. Harcourt, K. N. Holland, S. J. Iverson, J. F. Kocik, and J. E. M. Flemming (2015). Aquatic animal telemetry: A panoramic window into the underwater world. Science 348:1255642.

Igual, J. M., M. G. Ferrero, G. Taveccia, J. Gonzalez-Solis, A. Martinez-Abrain, K. A. Hobson, X. Ruiz, and D. Oro (2005). Short-term effects of data loggers on Cory's Shearwater (*Calonectris diomedia*). Marine Biology 146:619–624.

Iverson, S. A., W. S. Boyd, D. Esler, D. M. Mulcahy, and T. D. Bowman (2006). Comparison of the effects and performance of four types of radiotransmitters for use with scoters. Wildlife Society Bulletin 34:656–663.

Johnsgard, P. A. (1978). Ducks, Geese, and Swans of the World. University of Nebraska Press, Lincoln, NE, USA.

Jonsen, I. D. (2016). Joint estimation over multiple individuals improves behavioural state inference from animal movement data. Scientific Reports 6:20625.

Jonsen, I. D., J. M. Flemming, and R. A. Myers (2005). Robust state–space modeling of animal movement data. Ecology 86:2874–2880.

Kays, R., M. C. Crofoot, W. Jetz, and M. Wikelski (2015). Terrestrial animal tracking as an eye on life and planet. Science 348:aaa2478.

Kenow, K. P., S. C. Houdek, L. J. Fara, B. R. Gray, B. R. Lubinski, D. J. Heard, M. W. Meyer, T. J. Fox, and R. J. Kratt (2018). Distribution and foraging patterns of Common Loons on Lake Michigan with implications for exposure to type E avian botulism. Journal of Great Lakes Research 44:497–513.

Kenward, R. E. (2001). A Manual for Wildlife Radio Tagging. Academic Press, London, UK.

Korschgen, C. E., K. P. Kenow, A. Gendron-Fitzpatrick, W. L. Green, and F. J. Dein (1996). Implanting intra-abdominal radio transmitters with external whip antennas in ducks. The Journal of Wildlife Management 60:132–137.

Lamb, J. S., Y. G. Satgé, C. V. Fiorello, and P. G. R. Jodice (2016). Behavioral and reproductive effects of GPS transmitter attachment on Brown Pelicans (*Pelecanus occidentalis*) on three temporal scales. Journal of Ornithology 158:617–627

Lamb, J. S., P. W. C. Paton, J. E. Osenkowski, S. S. Badzinski, A. M. Berlin, T. Bowman, C. Dwyer, L. J. Fara, S. G. Gilliland, K. Kenow, et al. (2019). Spatially- explicit network analysis reveals multi-species annual-cycle movement patterns of sea ducks. Ecological Applications 29:e01919.

Lameris, T. K., and E. Kleyheeg (2017). Reduction in adverse effects of tracking devices on waterfowl requires better measuring and reporting. Animal Biotelemetry 5:24.

Lameris, T. K., G. J. Müskens, A. Kölzsch, A. M. Dokter, H. P. Van der Jeugd, and B. A. Nolet (2018). Effects of harness-attached tracking devices on survival, migration, and reproduction in three species of migratory waterfowl. Animal Biotelemetry 6:7.

Latty, C. J., T. E. Hollmén, M. R. Petersen, A. N. Powell, and R. D. Andrews (2010). Abdominally implanted transmitters with percutaneous antennas affect the dive performance of Common Eiders. The Condor 112:314–322.

Latty, C. J., T. E. Hollmén, M. R. Petersen, A. N. Powell, and R. D. Andrews (2016). Biochemical and clinical responses of common eiders to implanted satellite transmitters. The Condor: Ornithological Applications 118:489–501.

Le Net, R., D. M. Mulcahy, A. Santamaria-Bouvier, S. G. Gilliland, T. D. Bowman, C. Lepage, and S. Lair (2019). Intranasal administration of midazolam hydrochloride improves survival in female Surf Scoters (*Melanitta perspicillata*) surgically implanted with intracoelomic transmitters. Journal of Zoo and Wildlife Medicine 50:167–175.

Lewis, T. L., D. Esler, W. S. Boyd, and R. Zydelis (2005). Nocturnal foraging behavior of wintering Surf Scoters and White-winged Scoters. The Condor 107:637–647.

Link, W. A., and M. J. Eaton (2012). On thinning of chains in MCMC. Methods in Ecology and Evolution 3:112–115.

Loring, P. H., P. W. Paton, J. E. Osenkowski, S. G. Gilliland, J.-P. L. Savard, and S. R. McWilliams (2014). Habitat use and selection of Black Scoters in southern New England and siting of offshore wind energy facilities. The Journal of Wildlife Management 78:645–656.

Meattey, D. E., S. R. McWilliams, P. W. C. Paton, C. Lepage, S. G. Gilliland, L. Savoy, G. H. Olsen, and J. E. Osenkowski (2018). Annual cycle of White-winged Scoters (*Melanitta fusca*) in eastern North America: Migratory phenology, population delineation, and connectivity. Canadian Journal of Zoology 96:1353–1365.

Meattey, D. E., S. R. McWilliams, P. W. C. Paton, C. Lepage, S. G. Gilliland, L. Savoy, G. H. Olsen, and J. E. Osenkowski (2019). Resource selection and wintering phenology of White-winged Scoters in southern New England: Implications for offshore wind energy development. The Condor: Ornithological Applications 121:1–18.

Merkel, F. R., and A. Mosbech (2008). Diurnal and nocturnal feeding strategies in Common Eiders. Waterbirds 31:580–586.

Meyers, P. M., S. A. Hatch, and D. M. Mulcahy (1998). Effect of implanted satellite transmitters on the nesting behavior of murres. The Condor 100:172–174.

Morrison, C. A., J. A. Alves, T. G. Gunnarsson, B. Þórisson, and J. A. Gill (2019). Why do earlier-arriving migratory birds have better breeding success? Ecology and Evolution 9:8856–8864.

Mulcahy, D. M., and D. Esler (1999). Surgical and immediate post-release mortality of Harlequin Ducks (*Histrionicus histrionicus*) implanted with abdominal radio transmitters with percutaneous antennae. Journal of Zoo and Wildlife Medicine 30:397–401.

Nenno, E. S., and W. M. Healy (1979). Effects of radio packages on behavior of wild turkey hens. The Journal of Wildlife Management 43:760–765.

Olsen, S. B., J. H. McCann, and G. Fugate (2014). The State of Rhode Island's pioneering marine spatial plan. Marine Policy 45:26–38.

Patterson, T. A., M. Basson, M. V. Bravington, and J. S. Gunn (2009). Classifying movement behavior in relation to environmental conditions using hidden Markov models. Journal of Animal Ecology 78:1113–1123.

Phillips, R. A., J. C. Xavier, and J. P. Croxall (2003). Effects of satellite transmitters on albatrosses and petrels. The Auk 120:1082–1090.

R Core Team (2019). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rodway, M. S., H. M. Regeher, W. S. Boyd, and S. A. Iverson (2015). Age and sex ratios of sea ducks wintering in the Strait of Georgia, British Columbia: Implications for monitoring. Marine Ornithology 43:141–150.

Savard, J. P. L., A. Reed, and L. Lesage (2007). Chronology of breeding and molt migration in Surf Scoters (*Melanitta perspicillata*). Waterbirds 30:223–229.

Schacter, C. R., and I. L. Jones (2017). Effects of geolocation tracking devices on behavior, reproductive success, and return rate of *Aethia* auklets: An evaluation of tag mass guidelines. The Wilson Journal of Ornithology 129:459–468.

Sea Duck Joint Venture (2015). Atlantic and Great Lakes Sea Duck Migration Study: Progress Report June 2015. http//seaduckjv.org/science-resources/atlantic-and-great-lakes-sea-duck-migration-study/.

Sexson, M. G., D. M. Mulcahy, M. Spriggs, and G. E. Myers (2014). Factors influencing immediate post-release survival of Spectacled Eiders following surgical implantation of transmitters with percutaneous antennae. The Journal of Wildlife Management 78:550–560.

Silverman, E. D., D. T. Saalfeld, J. B. Leirness, and M. D. Koneff (2013). Wintering sea duck distribution along the Atlantic Coast of the United States. Journal of Fish and Wildlife Management 4:178–198.

Snijders, L., L. E. N. Weme, P. de Goede, J. L. Savage, K. van Oers, and M. Naguib (2017). Context-dependent effects of radio transmitter attachment on a small passerine. Journal of Avian Biology 48:650–659.

Tancell, C., R. A. Phillips, J. C. Xavier, G. A. Tarling, and W. J. Sutherland (2013). Comparison of methods for determining key marine areas from tracking data. Marine Biology 160:15–26.

Toft, C. A., D. L. Trauger, and H. W. Murdy (1982). Tests for species interactions: Breeding phenology and habitat use in subarctic ducks. The American Naturalist 120:586–613.

Vandenabeele, S. P., R. P. Wilson, and A. Grogan (2011). Tags on seabirds: How seriously are instrument-induced behaviors considered? Animal Welfare 20:559–571.

Vandenabeele, S. P., E. L. Shepard, A. Grogan, and R. P. Wilson (2012). When three per cent may not be three percent; device-equipped seabirds experience variable flight constraints. Marine Biology 159:1–14.

Weller, M. W., and B. Batt (1988). Waterfowl in winter: Past, present, and future. In Waterfowl in Winter (M. W. Weller, Editor). University of Minnesota Press, Minneapolis, MN, USA. pp. 3–8.

APPENDIX TABLE 3. Coefficient values and 95% confidence estimates (CI) for GLMMs of (**A**) start day and (**B**) duration of migration for 5 species of sea ducks, 2002–2017

	Winter migration			Spring migration			Molt migration			Breeding migration		
	Estimate	95% CI		Estimate	95% CI		Estimate	95% CI		Estimate	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper
(A) Start day												
Intercept	272.63	248.22	297.04	112.58	100.09	125.07	207.36	186.29	228.42	147.39	139.92	154.86
Species (relative to Black Scoter)												
Common Eider	15.77	−3.89	35.42	**−15.84**	**−27.97**	**−23.90**	−23.91	−52.21	4.40	**−34.03**	**−41.57**	**−26.49**
Long-tailed Duck	19.15	−1.48	39.77	−5.79	−16.43	27.01	**27.04**	**5.68**	**48.40**	−0.82	−8.28	6.65
Surf Scoter	**20.93**	**0.19**	**41.67**	**6.19**	**−4.99**	**−3.05**	−2.75	−24.01	18.51	2.29	−5.16	9.74
White-winged Scoter	13.98	−6.24	34.20	**13.67**	**2.65**	**12.18**	11.75	−10.07	33.56	**9.07**	**1.43**	**16.70**
Sex (relative to F)	**−8.05**	**−13.88**	**−2.22**	**−1.85**	**−5.57**	**−37.30**	**−37.87**	**−44.94**	**−30.81**	**3.37**	**1.02**	**5.71**
Age (relative to subadult)	−6.87	−17.05	3.31	**6.20**	**−0.92**	**−1.55**	−2.24	−17.98	13.51	1.74	−2.78	6.27
Capture season												
Fall molt (vs. winter)	**25.46**	**6.20**	**44.73**	−5.49	−16.76	1.40	5.43	−3.98	14.83	−2.09	−5.51	1.34
Spring staging (vs. winter)	**36.50**	**11.45**	**61.56**	**−16.00**	**−29.03**	**−8.90**	14.39	−6.59	35.37	**8.90**	**1.70**	**16.10**
Years post-capture	−0.95	−5.26	3.36	**−6.65**	**−9.61**	**−4.51**	−0.65	−4.91	3.61	**−8.42**	**−10.21**	**−6.62**
(B) Duration												
Intercept	20.16	3.93	36.39	2.31	−1.57	6.19	7.39	−0.56	15.34	16.66	9.21	24.12
Species (relative to Black Scoter)												
Common Eider	−9.39	−24.32	5.55	0.12	−4.16	4.40	2.22	−8.50	12.94	**−11.94**	**−19.51**	**−4.37**
Long-tailed Duck	0.99	−14.61	16.59	−0.37	−4.17	3.43	1.02	−7.09	9.13	7.26	−0.23	14.75
Surf Scoter	−13.80	−29.40	1.80	−0.70	−4.52	3.12	1.16	−6.90	9.23	−7.10	−14.55	0.35
White-winged Scoter	−14.78	−29.78	0.21	0.41	−3.46	4.28	4.65	−3.63	12.92	−1.59	−9.21	6.04
Sex (relative to F)	**5.16**	**0.56**	**9.75**	−0.67	−2.02	0.67	−0.35	−3.03	2.32	**−3.31**	**−5.65**	**−0.97**
Age (relative to subadult)	4.72	−3.26	12.70	−0.77	−3.44	1.90	1.43	−4.55	7.40	−0.84	−5.38	3.69
Capture season												
Fall molt (vs. winter)	−2.78	−14.23	8.68	1.77	−0.56	4.10	**4.88**	**1.27**	**8.48**	0.70	−2.70	4.10
Spring staging (vs. winter)	−14.30	−31.62	3.02	**4.56**	**0.73**	**8.39**	1.68	−6.31	9.67	−2.36	−9.55	4.82
Years post-capture	**2.18**	**0.53**	**3.82**	**3.42**	**2.29**	**4.55**	−0.65	−2.08	0.79	**2.17**	**0.47**	**3.87**