

Dynamic vegetation cover and decline in common eider breeding numbers in Nova Scotia, Canada

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Abstract

The American common eider (*Somateria mollissima dresseri*) is a colonially nesting sea duck breeding on islands in the coastal regions of Atlantic Canada. Declines in colony size have been pronounced in some parts of its range, notably in Nova Scotia, and may be attributable to a variety of interconnected factors including changes in habitat conditions. Using surveys collected two decades apart, we compared nesting habitat types, availability, and use by breeding eiders on 16 islands that supported >1600 eider nests in 1992–1993, but 830 nests in 2013. While general patterns of eider nesting habitat use remained consistent (e.g., nesting preferences exhibited for Low Shrubland and Grassland habitats, and avoidance of forest or beach habitats), overall vegetation cover declined, but relative habitat changes were inconsistent across islands. Three of the islands with the greatest change in vegetation had cormorant (*Phalacrocorax* spp.) colonies in 2013 that were not there in the earlier years. We suggest that changes in vegetation, in some cases facilitated by cormorant colony formation, influenced susceptibility of nesting females to predators, and these interconnected factors may be contributing to local population declines.

Key words: cormorant, island, population decline, habitat, sea duck

Introduction

The American common eider subspecies, *Somateria mollissima dresseri*, breeds on coastal islands of northeastern North America from approximately 41°N–54°N and 53°W–70°W (Lock 1986; Noel et al. 2021). Once harvested to near extirpation in Nova Scotia, common eider was successful in rebuilding populations such that the species became a prized game bird after the “Migratory Bird Convention Act” and its prohibitions to allow regulated hunting were passed in 1916 (Allen 2000; Rothe et al. 2015). Although numbers of American common eider have declined recently (Canadian Wildlife Service Waterfowl Committee 2020), the pattern is not uniform across the subspecies’ range, with increasing numbers of breeding birds in the north, and stable or decreasing numbers in the south (Bowman et al. 2015; Chardine 2015; Noel et al. 2021). Milton et al. (2016) hypothesized that the low survival for Nova Scotia breeding female American common eider ($S = 0.827 \pm 0.023$) and corresponding local breeding population declines were consistent with population dynamics of long-lived sea ducks (Flint 2015), and have been observed with other common eider subspecies exhibiting low adult survival (e.g., Öst et al. 2016). Moreover, Milton et al. (2016) considered that higher male eider survival rates ($S = 0.915 \pm 0.021$) and similar recovery rates with females ($f = 0.013$) in Nova Scotia suggested that lower female survival was attributable to factors other than hunting, such as predation on females at

breeding colonies (e.g., mustelids, bald eagle (*Haliaeetus leucocephalus*); Nordström et al. 2002; Waltho and Coulson 2015). Analyses of recruitment and population growth rates (Giroux et al. 2021) using capture and recapture records of breeding females across the *Somateria mollissima dresseri* range report both declining populations and low recruitment rates in Nova Scotia colonies. Among several potential drivers, low recruitment rates could reflect the effects of natural, dynamic processes of vegetation change (Clarkson et al. 2014), altering the quality of nesting habitat. Habitat change may also include effects of double-crested cormorant (*Phalacrocorax auritus*) faeces, when this species establishes a colony on a nesting island. The faeces dramatically alter overhead and ground vegetation (Milton et al. 1995; Kolb et al. 2012; Hebert et al. 2014), reducing the quality and/or amount of available breeding habitat, and thereby exposing nests, ducklings, and incubating female eiders to predators and adverse weather conditions.

Common eiders nest on the ground, breeding in colonies of a few to hundreds of pairs on offshore islands, presumably to avoid mammalian predators (Goudie et al. 2000; Chaulk et al. 2007). Numerous studies have documented eider preference for some type of cover (e.g., Gross 1944; Schamel 1977; Laurila 1989; Woolaver 1997). Even in open landscapes, breeding eiders cluster around features such as tufts of grass or rocks (Gerell 1985; Fast et al. 2007). While most studies

cite predator avoidance as a main driver of nest site selection, eiders may also choose sites with cover that affords thermoregulatory benefits to save on energetic costs (e.g., Schamel 1977; van Dijk 1986; Shutler et al. 1998; Fast et al. 2007). As the sole incubators of eggs, female common eiders take only extremely short and infrequent recesses from their nests (Bolduc and Guillemette 2003a), and may lose up to 40% of their body mass during egg laying and incubation (Korschgen 1977; Bolduc and Guillemette 2003b; Are Hanssen et al. 2003). Further, Kilpi and Lindström (1997) found that eider hens incubating in exposed habitats laid fewer eggs and lost weight at a faster rate than those incubating in sheltered areas. In a separate study, eiders protected under nesting structures were heavier at mid-incubation than those incubating at open sites (Fast et al. 2007).

Due to their high nest site fidelity and natal philopatry (Goudie et al. 2000; Öst et al. 2011; Ekroos et al. 2012), common eiders are vulnerable to ecological traps when conditions at breeding locations change (Robertson and Hutto 2006; Igual et al. 2007; Ekroos et al. 2012). Eiders may continue to return to previous nesting sites where they were once successful, even though the conditions that led to previous success have changed. Colonial bird surveys by Nova Scotia government biologists within the Eastern Shore Islands Wildlife Management Area (ESIWMA) have observed dramatic changes in the vegetation structure over three decades, as some islands progressed from being fully treed, to dead and fallen timber, to shrub- and grass-covered with little regeneration of shrubs or trees (G.R. Milton, unpublished data). This study investigates habitat change as a possible driver of change in American common eider breeding colony size and female survival 20 years after Woolaver (1997) classified and quantified the types of habitat available on islands used by nesting female eiders in the ESIWMA. We predicted that eiders breeding in the ESIWMA were increasingly nesting under suboptimal breeding conditions, leaving them exposed to predators and increased physiological stress. We compare habitat availability versus use by American common eiders in 1992–1993 and 2013 and the effect of habitat structure to moderate temperature for incubating hens through shading from the sun as the breeding season progressed.

Study area

The islands found along the Atlantic coast of Nova Scotia, Canada, represent a significant breeding ground for many colonial nesting marine birds, including black guillemot (*Cepphus grylle*), Arctic tern (*Sterna paradisaea*), herring gull (*Larus smithsonianus*), great black-backed gull (*Larus marinus*), Leach's storm-petrel (*Hydrobates leucorhous*), great cormorant (*Phalacrocorax carbo*), double-crested cormorant (*Phalacrocorax auritus*), and American common eider. For cormorants, they initially nested in trees on the islands, but eventually their guano killed the vegetation, and if the colony did not move, it transitioned to ground-nesting. Cormorants have nested on several of the islands over the years (e.g., Camp, Speck, Sandy, Pancake).

In 1976, a subset of islands between Sheet Harbour Passage (44.86°N, –62.47°W) and Marie Joseph (44.97°N, –62.08°W),

encompassing approximately 60 vegetated and nonvegetated islands, islets, and ledges, and thought to host 25% of the provincial breeding population of American common eider in Nova Scotia, were designated as the ESIWMA (Payne 1977). Although hunting and trapping are permitted in season, human disturbance on the islands is prohibited throughout the breeding season (April–August). This study focuses on a subset of 16 islands within the ESIWMA and immediately adjacent (Fig. 1). Because of their long history of protection and study, these islands provide the most long-term and comprehensive data sets on eider colonies and island habitats in Nova Scotia.

Methods

Nesting surveys

American common eider nesting surveys were conducted during mid-incubation and post-hatch in the spring and summer of 2013 (mid-incubation: 19 and 29 May, 5–7 June; post-hatch: 2–4 and 31 July; note that research priority shifts and then the COVID-19 pandemic has precluded comprehensive island surveys since this time). This replicated the approach undertaken in 1992 and 1993 (Woolaver 1997). Mid-incubation surveys were conducted in fair weather with large crews (≥ 5 people) to rapidly maximize coverage (i.e., complete island) and minimize incubation recesses and disturbance to the colonies. The target survey window was late in incubation to capture nests initiated later in the breeding season and to minimize nest failure due to disturbance (Bolduc and Guillemette 2003a), but before hatching to avoid exposing ducklings to predation (Keller 1991). The location of each nest was recorded with a handheld GPS unit (so we could find nests after hatch and with vegetation growth), number of eggs were counted, and surrounding habitat type was noted. When a nest was in mixed habitat or under cover of more than one habitat type, the dominant vegetation type—or the one affording the most protection to an incubating hen—was recorded. As soon as ducklings were detected on the islands, surveys were aborted and resumed only when all nests were presumed to have hatched and ducklings had left the islands. All research was carried out under appropriate permits (Canadian Wildlife Service ST2784, Acadia Animal Care Permit 03-13, CCAC approved).

Habitat types

Habitat type definitions (Table 1) are consistent with Woolaver's (1994, 1997) work on the same islands but renamed for greater conformity with current ecosystem classification standards (e.g., Neily et al. 2013; Canadian National Vegetation Classification: cnvc-cnvc.ca). To prevent disturbance to breeding eiders, ground-level delineation of habitat types occurred after the breeding season on laminated air photos (1:5000) acquired during overflights on 9 and 13 July 2013, and timed to ensure maturation of herbaceous vegetation and its visibility in the images. Although this timing did not assess habitat characteristics at the time when females may first select nest sites on the island (May), we point out that (a) we do not know if there is a specific part of the nest-

Fig. 1. The Eastern Shore Islands Wildlife Management Area and the 16 islands included in the study. Islands with an * were also used for the temperature experiment. Note that two additional islands were used exclusively for the temperature experiment due to the scarcity of forested habitats on islands with colonies. This map was constructed using ArcGIS version 10.8.1 (ESRI, Redlands, CA, USA) using a WGS84 projection and UTM coordinate system; the Wildlife Management Area boundary was provided by the Nova Scotia Department of Natural Resources and Renewables Wildlife Division; the base maps (main frame and inset) were sourced from ESRI.

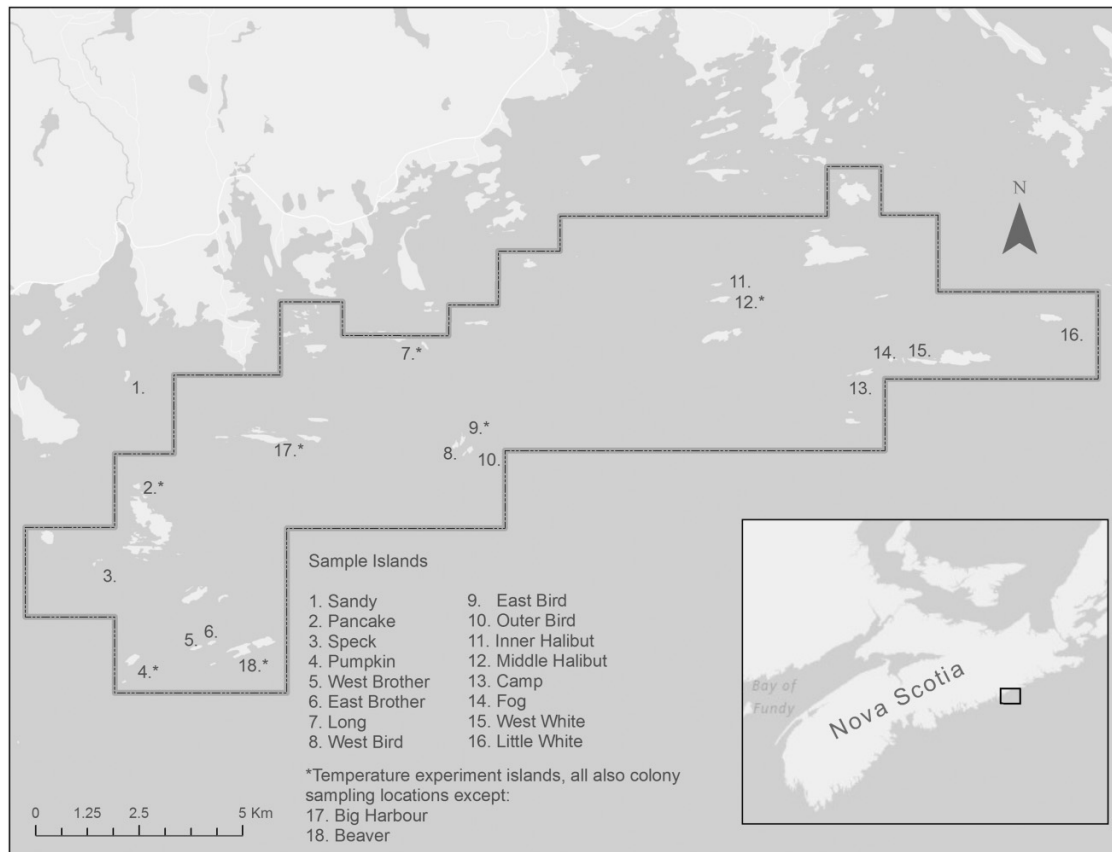


Table 1. Habitat classification used to describe the habitats used by breeding common eiders in the Eastern Shore Islands Wildlife Management Area.

Habitat type	Description (common species)
Coniferous and Mixedwood Forest	Mature stands of white spruce and balsam fir. Fir thickets near the shoreline and mixed coniferous and deciduous forest (<i>Abies balsamea</i> , <i>Picea glauca</i> , <i>Acer rubrum</i> , <i>Betula papyrifera</i>)
Coniferous Woodland	Stunted, windswept conifers, usually single or in small clumps (<i>Abies balsamea</i>)
Standing Deadwood	Standing dead trees and deadfalls
Low Shrubland	Mainly gooseberry, but includes other woody shrubs (<i>Ribes</i> spp., <i>Kalmia angustifolia</i> , <i>Myrica pensylvanica</i>)
Low Cane-Shrubland	Dense to sparse canes of raspberry or skunk-currant. Commonly associated with standing deadwood (<i>Rubus idaeus</i> , <i>Ribes gladosum</i>)
Grassland	Herbaceous growth taller than 20 cm, includes new growth as well as stems from the previous year. Tall grasses, fireweed, and ferns are all included in this category (<i>Chamerion angustifolium</i> , <i>Osmunda cinnamomea</i> , <i>Ammophila breviligulata</i>)
Herbaceous Beach Vegetation	Herbaceous growth sparse on sand, cobble, and bedrock shelves (<i>Lathyrus japonicus</i> , <i>Argentina</i> spp.)
Low Herbaceous Growth/Dwarf Heathland	Short grass, ericaceous shrubs, and herbaceous growth less than 20 cm in height. This category also includes rock outcrops and crevices, as well as areas around active cormorant colonies which lack vegetation (<i>Empetrum</i> spp., <i>Achillea</i> spp., <i>Prenanthes</i> spp.)

Note: These classifications are modified from Woolaver (1997) and are listed in order of decreasing cover afforded for incubating hens.

ing period where habitat characteristics are more important for female choice than others, given that vegetation changes through incubation and (b) female eiders have high island nest site fidelity through years (Goudie et al. 2000), so our approach standardized how we treated habitats across islands. Moreover, habitat types during the breeding season survey used remnant vegetation from previous years, and there were no significant boundary changes of habitat types between breeding surveys and the overflight imagery. Within areas of mixed habitat types, the dominant type—or the one assumed to afford the greatest protection to an incubating hen—was recorded (consistent with the nesting surveys). In large areas of mixed vegetation, the percent cover of each dominant class was estimated for the area.

The 2013 air photos were georeferenced in ArcGIS 10.1 using an average of 5 (range: 3–9) ground control points per island (total root mean square [RMS] errors < 3 m). Notes and the ground level delineations were used to create habitat polygons. Areas of mixed habitats were delineated based upon the percent cover for each habitat type present and, thus, do not match exactly their presence on the ground due to the resolution of the image and lumping of small patches within areas of mixed habitat. The area of habitat per island was obtained by totalling the area of each polygon of a given habitat type. Total vegetated area per island was obtained by merging all habitat polygons.

Woolaver's (1997) island maps and total vegetated areas were georeferenced to the 2013 aerial images using bedrock formations or prominent features unchanged in the intervening decades (i.e., consistent ground control points). The 1992–1993 habitat types could not be re-projected into Geographic Information System (GIS) polygons as Woolaver's (1997) island maps did not always distinctly delineate habitat types. However, the areas of the 14 habitat types and the total vegetated area provided in Woolaver (1994) were combined to conform to the eight types described in Table 1. Island measurements of total vegetated area (1992–1993) were corrected for small errors attributed to Woolaver's (1997) mapping technique, and then the area of each habitat type for a given island in Woolaver (1994) was adjusted with the corrected total vegetated area based on our standardization of total island size.

Net and percent change of total vegetated and habitat type areas from 1992–1993 to 2013 were calculated for the 16 study islands. In both years, rock outcrops enclosed within vegetated areas are included. Quantile–Quantile plots and the Kolmogorov–Smirnov test were used to assess normality of the distribution of change in total vegetated area. When the distribution did not approximate normality, a Wilcoxon's signed-rank test was used to determine if the change in total vegetated area was significant. A binomial test was then performed to assess whether total vegetated and habitat type area changed consistently across islands.

Habitat use versus availability

Habitat use was defined by the number of nests counted in each habitat type, while habitat availability was the total area of each habitat type. In all years, eider nests under arti-

cial shelters (generally <10 on any island) were excluded from this analysis because (a) it was not possible to compare availability in the same way and (b) shelters were deployed generally in more open areas outside of higher quality, dense nesting cover (Woolaver 1994). Individual island nest densities per area of habitat type in the ESIWMA were recorded for both 1992 and 1993 (Woolaver 1994). More islands were surveyed in 1993 than 1992 and were the focus for comparison in the present study. Of the 16 study islands, only 4 reported nesting densities from 1992 with the remaining 12 from 1993, and thus these densities from 16 islands were hereafter referred to as “1990s” nesting densities. The number of nests from the 1990s determined from Woolaver (1994) density estimates were then applied to the corrected 1992 habitat type areas for comparison with 2013 nesting densities by habitat type for a given island.

A chi-square goodness-of-fit test was used to determine if eiders were using habitats in proportion to their availability (Neu et al. 1974). Chi-square assumptions were met with average expected observations of 218 and 92 from 1990s and 2013, respectively, and no expected observations under 12 (Roscoe and Byars 1971). We assumed that numbers of eiders in different habitats were attributable to habitat selection, and independent of the number of other eiders in that habitat, but acknowledge that breeding site fidelity, prior breeding success, and indirect information transfer (e.g., observing successful nests) could all influence nest site choice by female eiders (Goudie et al. 2000). A Bonferroni adjusted family-wise approach of simultaneous confidence intervals was then used to determine preference or avoidance of habitat classes in the study area (Byers et al. 1984).

Habitat temperature profiles

To establish temperature regimes for each habitat class, temperature data loggers (iBCod-Z, Alpha Mach Inc., Montreal, Quebec, Canada) were placed in each of the eight habitat types. Three replicates were distributed amongst different islands for each habitat type, resulting in a total of 24 loggers on seven islands (see Fig. 1). Data loggers were synchronized to record the entire incubation period from 23 April to 17 July. Each logger recorded hourly temperatures up to a maximum of 26.4 °C (the maximum limit for this model of logger). Temperature readings were truncated to start with the earliest calculated laying dates (1 May 2013) and end with the last calculated hatch date (5 July 2013). Incubation stage was calculated based on the Vaisanen (1974) egg floatation method. This covered a period of 66 days during which at least one eider hen was known to have been incubating.

A linear mixed-effect model fit by restricted maximum likelihood was used to assess the relationship between temperature and habitat class (lme4, R version 3.5.1, R Core Team 2018). To remove variation in the temperature data due to expected seasonal increases and the correlation in temperature across consecutive days, mean daily temperature values were detrended by subtracting overall mean daily temperature from each data point. Detrended mean daily temperature was then modelled as the response variable, with habitat (categorical with eight levels) included as a fixed effect. Is-

Table 2. Change in cover of eight habitat types for 16 islands in the Eastern Shore Islands Wildlife Management Area between 1992 and 2013.

Habitat	1992 (m ²)	1992 (%)	2013 (m ²)	2013 (%)	Change (m ²)	Change (%)
Coniferous and Mixedwood Forest	4116	1.9	9601	4.7	5485	133.3
Coniferous Woodland	5021	2.3	3452	1.7	−1569	−31.2
Standing Deadwood	22 473	10.2	12 706	6.2	−9768	−43.5
Low Shrubland	17 808	8.1	10 221	5.0	−7587	−42.6
Low Cane-Shrubland	20 156	9.1	4136	2.0	−16 020	−79.5
Grassland	36 831	16.7	39 993	19.6	3162	8.6
Herbaceous Beach Vegetation	20 787	9.4	17 214	8.4	−3573	−17.2
Low Herbaceous/Dwarf Heathland	93 568	42.4	106 547	52.3	12 979	13.9
Total	220 760	100	203 870	100	−16 890	−7.7

land was included as a random effect, since data loggers were distributed unevenly amongst different islands (Detrended mean daily temperature \sim Habitat + (1|Island)); [Zuur and Ieno 2016](#); [Harrison et al. 2018](#)). Model assumptions were verified by plotting residuals. The effect of habitat in the model was examined by comparing the above model with a null model where habitat was excluded.

Results

Nest surveys

In 2013, eider colonies on the 16 study islands ranged from 1 to 238 nests. For 12 islands sampled in 1992 and again in 2013, the number of nesting eiders declined from 1602 to 820 nests (49% decline). Fifteen islands were sampled in 1993 and again in 2013, and nest counts declined from 1384 to 601 (56% decline; Supplemental Table S.1). Mean colony size for 2013 was 52 ± 61 standard deviation (SD), while 1992 and 1993 mean colony sizes were larger (133 ± 158 and 92 ± 79 , respectively). The island with the largest colony, Pumpkin, had 541 nests in 1992 and less than half this number (238) in 2013. Despite declines in breeding numbers, median clutch size was four eggs in 1992 ($n = 1414$ nests), 1993 ($n = 552$ nests), and 2013 ($n = 789$ nests; [Tomlik 2019](#)).

Habitat change

During the 21 years between 1992 and 2013, most islands experienced some decrease in vegetation cover, with a mean change of -12.3% and a significant reduction of 7.7% ($16\,890\text{ m}^2$) in total vegetated area across the 16 islands (one-tailed Wilcoxon's signed-rank test $V_{15} = 28$, $p = 0.02$; Supplemental Table S.2). Modest changes ($<10\%$) occurred on most islands although this pattern was not significant (one-tailed Binomial test, $p = 0.1$) and are likely attributable to mapping techniques. Vegetation declines $>10\%$ on Camp, Pancake, Sandy, Speck, West Bird, and West White islands are, however, too substantial to be attributed to mapping errors.

Notwithstanding the overall decrease in total vegetated area, three habitat types experienced an overall net increase while five decreased (Table 2). The greatest changes were observed in two habitat types that provide lower levels of cover for nesting eiders: Low Cane Shrubland decreased in

its proportion of cover by 7% ($16\,020\text{ m}^2$), while Low Herbaceous/Dwarf Heathland, increased by 10% ($12\,979\text{ m}^2$). Remaining cover types changed by less than $10\,000\text{ m}^2$ and Herbaceous Beach Vegetation and Coniferous Woodland, both, showed little change in their relative proportion of habitat cover.

Vegetation change patterns were not consistent across all islands. While most habitat types decreased their relative cover over the entire study area, some islands experienced increases in these same cover types (Fig. 2). For example, Low Cane-Shrubland showed an overall decrease in proportion of cover of 7% but increased in relative cover on three separate islands. While the increase on two islands was slight ($<5\%$), Low Cane-Shrubland increased from 0% cover to 15.7% of the vegetation on Pancake Island. Similar inconsistencies across islands were true for most habitat types. Binomial test results (Table 3) show that there was no consistent trend across islands for any habitat type, except Low Cane-Shrubland ($p = 0.046$), which decreased on 10/13 islands measured.

Habitat use versus availability

We found a significant difference between the availability of different habitat classes and their use by nesting eiders within the ESIWMA in both the 1990s and 2013 (1990s: $p < 0.001$, $\chi^2_{[7,1743]} = 3664.0$; 2013: $p < 0.001$, $\chi^2_{[7,738]} = 2485.8$). Although the total number of nests used for analysis was reduced by 58% between decades, Bonferroni simultaneous confidence intervals (summarized in Supplemental Tables S.3 and S.4 for 1990s and 2013, respectively) showed a similar use of habitats between decades. Low Shrubland was always the most used habitat type, followed by Grassland. Forests, Woodland, and Herbaceous Beach Vegetation were used infrequently or not at all.

When habitat availability is accounted for, Low Shrubland was selected as a nesting habitat far more often than its proportional availability on the landscape (Fig. 3). By contrast, Low Herbaceous Growth/Dwarf Heathland was strongly avoided; it was used infrequently but is by far the most widely available habitat type on the islands studied. Between decades, habitat preference and avoidance in the ESIWMA was remarkably consistent. Only three habitat classes saw changes in preference by nesting eiders. Use of Grassland and

Fig. 2. Island-level change in relative proportion of cover for eight habitat classes on 16 islands in the Eastern Shore Islands Wildlife Management Area between 1992 and 2013.

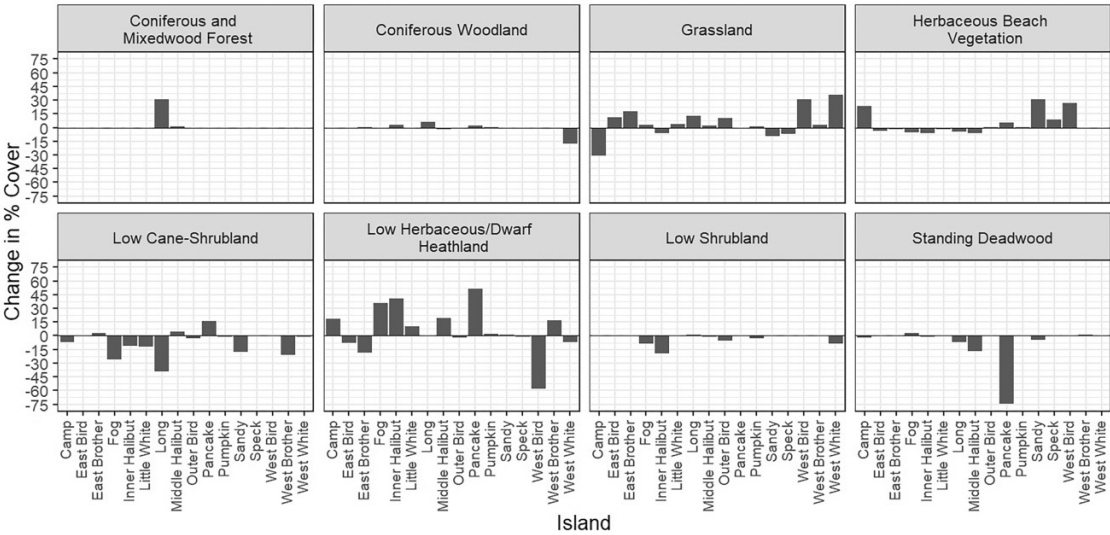


Table 3. Binomial test results for the number of islands where relative cover decreased for a given habitat class.

Habitat	Number of islands (n)	Increase	Decrease (x)	p-value (one-tailed)
Coniferous and Mixedwood Forest	2	2	0	1.000
Coniferous Woodland	10	5	5	0.623
Standing Deadwood	10	4	6	0.377
Low Shrubland	9	3	6	0.254
Low Cane-Shrubland	13	3	10	0.046*
Grassland	15	11	4	0.982
Herbaceous Beach Vegetation	16	6	10	0.227
Low Herbaceous/Dwarf Heathland	16	9	7	0.773

Note: Up to 16 islands from the Eastern Shore Islands Wildlife Management Area were included for each analysis, covering a period from 1992 to 2013. Significant results ($\alpha = 0.05$) are indicated with an asterisk (*).

Fig. 3. Preference or avoidance of habitat classes on 16 islands in the Eastern Shore Islands Wildlife Management Area in (a) 1992–1993 and (b) 2013. Habitats are preferred if they appear above the diagonal line, and avoided if they appear below the line. Habitats are used in proportion to their availability if they lie along the line.

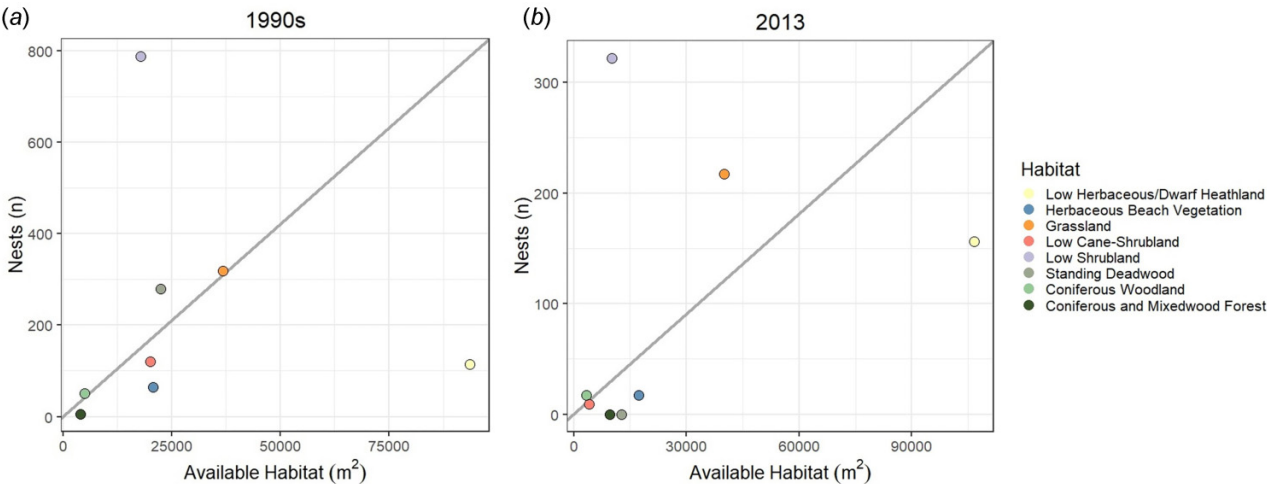


Table 4. Mean temperature for eight habitat types in the Eastern Shore Islands Wildlife Management Area for the incubation period of 1 May–5 July 2013.

Habitat	Mean temperature (°C ± SD)
Low Herbaceous/Dwarf Heathland	12.2 ± 6.0
Herbaceous Beach Vegetation	12.6 ± 5.5
Grassland	11.8 ± 5.9
Low Cane-Shrubland	12.0 ± 4.8
Low Shrubland	11.4 ± 4.7
Standing Deadwood	11.1 ± 4.5
Coniferous Woodland	11.1 ± 3.7
Coniferous and Mixedwood Forest	9.9 ± 3.2
Overall mean temperature	11.5 ± 5.0

Note: Overall mean temperature across all habitat types is also shown.

Low Cane-Shrubland increased relative to their availability, while Standing Deadwood decreased its use by eiders, going from a preferred habitat to an avoided one.

Habitat temperature profiles

Among habitat types, forest cover provided the coolest habitat while Herbaceous Beach Vegetation was the warmest when compared to the overall mean daily temperature (11.5 °C ± 5.0 °C) among all habitat types throughout the incubation period (Table 4). The number of days where the maximum recordable temperature of 26.4 °C was reached varied considerably among habitat classes (Fig. 4). Low Herbaceous Growth/Dwarf Heathland, Herbaceous Beach Vegetation, and Grassland, all reached this temperature on >25% of the days during which eiders were incubating. Low Shrubland and Coniferous Woodland rarely reached this temperature during incubation (2.9% and 0.6%, respectively), while Forest never recorded this maximum.

Habitat class was a significant factor for explaining variability in mean daily temperature among habitat types, as shown by comparing the alternative model with a null model excluding habitat ($\chi^2 = 1032.9$; $p < 0.001$; model validation supportive; Zuur and Ieno 2016). Across habitat types, as vegetation structure increased in complexity (coincident with presumed increasing protective cover value for incubating hens), mean daily temperature decreased ($p < 0.001$ for all habitat classes; Table 5). This suggests that females incubating in less exposed habitats also experience some relative temperature moderation in the form of cooling throughout the breeding season.

Island accounted for some of the observed variation in temperature (marginal-conditional $R^2 = 32.5\%$, $ICC_{\text{Island}} = 0.58$), with less variation occurring within islands than among islands ($\sigma^2 = 0.73$, $\tau_{00 \text{ Island}} = 1.02$). To assess whether the uneven distribution of habitats and temperature loggers with five out of seven islands hosting three or fewer loggers/habitats had an effect, the same analysis was performed using temperature loggers that ran for the entire incubation period from a single island with all eight habitat types. Nearly identical results were obtained as with using the full data set despite some loggers not being deployed until later in May.

Discussion

American common eider numbers in Nova Scotia have fluctuated greatly over the past century, from lows during unregulated harvest before 1916 to strong breeding numbers in the 1990s (Bowman et al. 2015; Noel et al. 2021), making it difficult to establish a value for an expected, sustainable baseline (Soga and Gaston 2018) in the province. Nonetheless, the number of nesting eiders in the ESIWMA declined by >40% over the two decades since the 1992–1993 study by Woolaver (1997), and expert opinion suggests this trend may have continued over the last decade (Noel et al. 2021). Colony size on islands varied between the periods but was mostly negative, with dramatic losses of the large colonies; six islands supported 20 or fewer nests at the last census. For example, Middle Halibut Island, which formerly supported more than 300 nests, had only 23 nests in 2013; mammalian predators were using the island regularly since 2010 (G. Parsons, personal observation). The declining island breeding numbers were consistent with expected responses to low female survival (Milton et al. 2016) and recruitment and population growth rates (Giroux et al. 2021) within the Nova Scotia population. Although breeding effort within a population can vary from year to year (Gilliland et al. 2005), and a perceived risk of reduced survival can deter breeding (Coulson 1984; Jaatinen et al. 2022), long-term data from the study site show gradual but steady declines in breeding numbers and colony sizes from the mid-1990s onwards (G.R. Milton, unpublished data). So, while a decline in breeding numbers does not necessarily mean an equivalent population decline, such a prolonged period of low reproductive effort would contribute to overall population decline. Continued monitoring could attempt to assess the propensity for nonbreeding in this population.

What was the main driver of these losses? One hypothesis was that hunting overharvest could result in the observed declines. However, this is not supported in the harvest data. Although female survival was ~10% lower than that of males, banded males and females had similar recovery rates (Milton et al. 2016). Additionally, males are actually favored in the American sport hunt for their striking plumage (Rothe et al. 2015).

Another hypothesis for the declining breeding population and elevated mortality rate of females was that they may have been exposed to disease and contaminants. While Ballard et al. (2017) found that Wellfleet Bay virus antibodies were present in 3.4% of birds sampled in Nova Scotia, these rates were equivalent to prevalence in Québec, where populations were not thought to be declining (Bowman et al. 2015; Chardine 2015; Noel et al. 2021). There were also no observed large-scale die-offs that one might expect during a disease outbreak at a breeding colony (Descamps et al. 2009; Ballard et al. 2017). Moreover, contaminants were not thought to be contributing to the overall population decline observed in the ESIWMA, at least for toxic, nonessential trace elements, because observed concentrations in eggs were generally lower than that for most other eider populations in Canada (Pratte et al. 2015).

Instead, an alternative hypothesis for lower breeding numbers was that altered physical characteristics of breeding

Fig. 4. The proportion of days where the maximum recordable temperature of 26.4 °C was reached for eight habitat classes in the Eastern Shore Islands Wildlife Management Area. Temperatures were recorded for the incubation period of 1 May–5 July 2013.

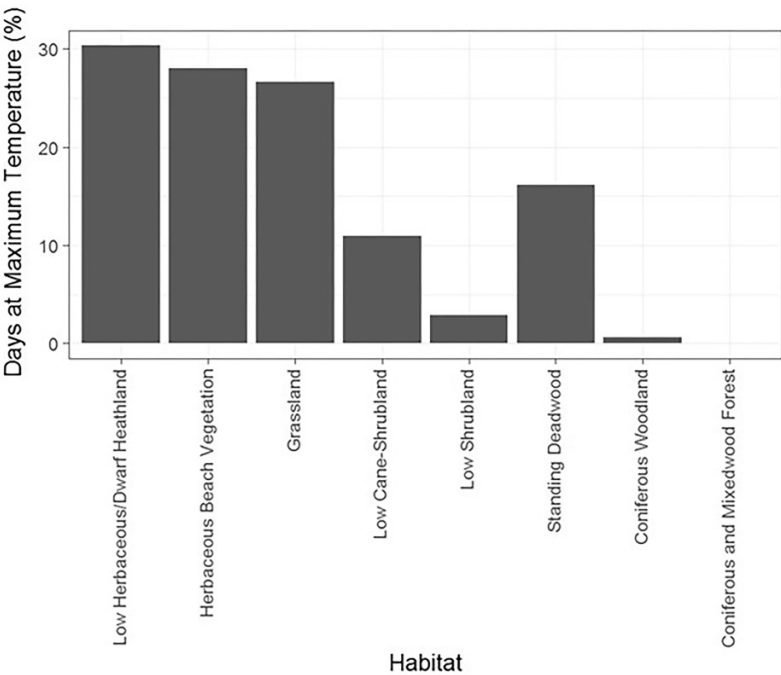


Table 5. Results for linear mixed-effect model predicting detrended mean daily temperature ($n = 1391$) for eight habitat classes with increasing structural complexity in the Eastern Shore Islands Wildlife Management Area for the incubation period of 1 May–5 July 2013.

Predictor	Detrended mean daily temperature (°C)		
	Estimates	CI	<i>p</i>
(Intercept)	1.57	0.80 to 2.33	<0.001*
Herbaceous Beach Vegetation	− 0.84	− 1.03 to − 0.64	<0.001*
Grassland	− 0.43	− 0.60 to − 0.26	<0.001*
Low Cane-Shrubland	− 1.30	− 1.49 to − 1.11	<0.001*
Low Shrubland	− 1.41	− 1.62 to − 1.21	<0.001*
Standing Deadwood	− 2.15	− 2.34 to − 1.96	<0.001*
Coniferous Woodland	− 2.43	− 2.63 to − 2.23	<0.001*
Coniferous and Mixedwood Forest	− 3.98	− 4.21 to − 3.75	<0.001*
Random effects			
σ^2	0.73		
τ_{00} Island	1.02		
ICC _{Island}	0.58		
Observations	1391		
Marginal R^2 /Conditional R^2	0.443/0.768		

Note: Daily mean temperature was detrended by subtracting overall mean daily temperature from each data point, with the resulting difference in degrees included as the response variable in the model. (Note: Low Herbaceous/Dwarf Heathland is not included as it is the reference for other habitat types.)

sites, such as availability of cover, may be contributing to the breeding population decline in the ESIWMA. Both vegetation change, predation, and their interaction have been identified as contributing to dramatic declines in common eider populations in Europe (e.g., Ekroos et al. 2012). Like the European situation, in eastern North America north to coastal Green-

land, increases in eagle abundance, and concomitant predation on eiders, is thought to influence eider numbers and behavior in recent years (Merkel and Mosbech 2008; Milton et al. 2016; Allen et al. 2019), including at the ESIWMA (R. Milton, personal observation). While some of the variability in total vegetated area detected on all islands measured in 1992

and 2013 was likely attributable to measurement error (i.e., islands with <10% change), we observed some clear and dramatic changes. Overall reduction in vegetated cover across the archipelago was slight at 7.7%, but some islands experienced reductions of 17%, 32%, or even 79%. Three of the six islands that experienced >10% reduction in total vegetation had active cormorant colonies in 2013 (Camp, Sandy, and Speck Islands), and another was a former colony (Pancake Island). Cormorant guano deposited at these sites killed off vegetation, leaving bare, exposed ground, and standing or fallen deadwood at various stages of decomposition, as has been found in studies elsewhere (Cuthbert et al. 2002; Hebert et al. 2014). However, not all islands with cormorant colonies experienced declines. Cormorants nesting on the exposed bedrock on the periphery of the island (e.g., Little White and Outer Bird Islands) did not significantly reduce vegetative cover. Thus, the presence of cormorants alone is not necessarily a causal factor in habitat change; interactions with the type of habitat at the time of cormorant colonization (notably tree presence and use by nesting and roosting birds) appears key for determining influence on eider nesting.

Certain physical structures and geological make-up of each island may also be a factor in vegetation change, as three of the islands with dramatic changes were relatively small and low lying, increasing the proportion of vegetation edge exposed to the erosive forces of wind and waves (Pancake, Sandy, and Speck Islands). Islands with narrow strips or small, isolated patches of vegetation near the periphery were more susceptible to vegetation loss (Sandy, Speck, and West White Islands). For example, while Sandy Island supported nesting pairs of cormorants in 2013, it was also the only site that comprised principally deposited till and/or accumulated sediment, rather than bedrock, and thus appears to have been more susceptible to erosive forces with vegetation loss. Erwin et al. (2011) also noted that habitat change, notably erosion and vegetation loss, contributed to substantial shifts in waterbird numbers in Chesapeake Bay, USA. With increased storm frequency and sea level rise projections predicted by climate change modelling for the region, islands along Nova Scotia's Atlantic coast are likely to experience more erosion and loss of vegetation (Molnar et al. 2021).

Changes in the coverage provided by the eight habitat types used by breeding eider in the ESIWMA clearly varied over approximately two decades. At least some of the changes may have been attributable to the establishment, occupation, and then abandonment of cormorant colonies, and subsequent habitat succession. Milton et al. (1995) and Woolaver (1997) posited that cormorant colonies may actually be beneficial to nesting American common eiders by destroying forest cover, which eiders seem to avoid, creating standing and fallen deadwood, and encouraging regeneration of Low Cane-Shrubland. This may have been the situation when cormorants were commonly nesting in softwood forests in the 1990s. However, by 2013, all cormorant colonies were on the ground, creating open barren areas or exposed rock covered in guano. Nonetheless, vegetation changes across islands were not consistent, with some islands experiencing local increases or decreases at odds with the overall trend for the archipelago. Areas initially covered in Low Cane-Shrubland

and Standing (and fallen) Deadwood favored by nesting eiders in the 1990s (Woolaver 1997) were largely converted to Low Herbaceous/Dwarf Heathland with some sparse raspberry cane growth and fallen deadwood by 2013. Some regeneration of forest cover had occurred at some sites where it was not completely lost to nesting cormorants. While Low Cane-Shrubland decreased consistently across islands (10/13 islands), at least two islands with recent cormorant colonies experienced increases in this cover type. Collectively, these findings suggest that after cormorants abandon colonies in forested areas, initial vegetation succession may provide favorable breeding habitat for nesting American common eiders, but this may be island-specific. However, the long-term data presented in this study indicate that later stages of succession, or succession in nonforested cover types, do not favor breeding eiders, but increase the area of cover types that breeding eiders tend to avoid.

Despite the overall decline in vegetation and the changes in overall availability of most cover types, breeding eider habitat selection was remarkably consistent between the 1990s and 2013. Observed changes in habitat selection may be attributed to overall changes in the relative availability of those same habitat types. Hens continued to heavily favor Low Shrubland, and strongly avoid Low Herbaceous/Dwarf Heathland. They rarely nested in Coniferous and Mixedwood Forest and Herbaceous Beach Vegetation, and used the relatively rare Coniferous Woodland in proportion to its availability. Low Cane-Shrubland was a relatively common habitat type in the 1990s but quite rare in 2013. Eiders continued to use this now scarce habitat type, resulting in an increase in nest density and the relative preference for this habitat type in 2013. With a decrease in availability of preferred Standing Deadwood and Low Shrubland from the 1990s and an increase in Low Herbaceous/Dwarf Heathland, eiders increased their relative use of Grassland in 2013.

The most favored habitat type, Low Shrubland, presumably offers concealment and thus reduced risk of predation, notably from avian predators (e.g., Öst et al. 2008), but also appears to offer some protection from less favorable weather conditions in terms of temperature moderation, with very few days reaching the maximum recorded temperature of 26.4 °C during the breeding season. This cover type also remained close to the overall mean temperature for all habitat types throughout the breeding season but warmed at a slower rate than the overall mean, offering some temperature moderation as the ambient temperature increased later in the season. This temperature moderation may reduce incubation costs associated with thermoregulation at the southern extent of this species' range, and reduce risks of eggs overheating if the female is flushed from the nest (Choate 1967).

Older and more experienced eider females are thought to breed earlier (Korschgen 1977; Schamel 1977) and to choose higher quality habitats (Are Hanssen et al. 2003). Predation rates (Woolaver 1997; Ekroos et al. 2012) and incubation costs (Kilpi and Lindström 1997; Fast et al. 2007) differ based on cover type, with both predation pressure and incubation cost increasing in open habitats. Higher quality, experienced females are, therefore, expected to choose sites offering the best cover for maximizing fitness in the form of short- and

long-term survival and reproductive success. Numerous studies have corroborated our findings that eiders prefer low shrub habitats despite their ability to nest in a variety of cover types (e.g., Gross 1944; Gerell 1985; van Dijk 1986), suggesting that these habitats offer maximum benefits to breeding females in terms of both survival and reproduction.

Consequently, we suggest that long-term conservation and management of sustainable eider colonies needs to consider dynamic habitat succession and availability, and the way these interact with threats like predation and disturbance, at least in forested island habitats like those in coastal Nova Scotia. Because island features may change through time, habitat managers should target protection and management of whole archipelagos, enacting regulations to minimize access and disturbance of nesting eiders (Bolduc and Guillemette 2003a), and may want to consider deploying nest shelters (Lusignan et al. 2010) to augment or sustain local colonies. Control of avian and mammalian predators may need to be considered (Mawhinney et al. 1999; Jaatinen et al. 2022), particularly if those predator populations are being subsidized by human industrial food sources (which may require direction management action as well; Gutowsky et al. 2021). In some cases, management of eider harvest may also be required (Rothe et al. 2015), although we note that human harvest is likely not a major factor in declining colony numbers in Nova Scotia (Milton et al. 2016). Collectively, wildlife and habitat managers have a suite of options to help support local eider populations; the complexity of regional and local drivers of recent eider colony declines (Noel et al. 2021) suggest that management solutions will likely require multiple actions.

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tion in any medium, provided the original author(s) and source are credited.

Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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Competing interests

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Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/facets-2022-0232>.

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