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# Reproductive Strategies Of Common Eiders (Somateria Mollissima)

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# REPRODUCTIVE STRATEGIES OF COMMON EIDERS (*SOMATERIA MOLLISSIMA*)

by

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Submitted to the Graduate Faculty

of the

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in partial fulfillment of the requirements

for the degree of

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This thesis, submitted by Samuel Hervey in partial fulfillment of the requirements for the Degree of Master of Science from the University of North Dakota, has been read by the Faculty Advisory Committee under whom the work has been done and is hereby approved.

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4/29/19
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Samuel Hervey
May 2019

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To my Grandparents

# ABSTRACT

Many reproductive strategies exist all with the same goal to maximize fitness. Because reproductive strategies affect fitness directly, there is interest to understand how they are utilized within a population. The two main strategies we focus on for this work related to Common Eiders (*Somateria* mollissima) are the utilization of conspecific brood parasitism as an alternative tactic beyond simply nesting and their ability to shift timing of breeding to align young with the best opportunity for survival. To accomplish studying our two reproductive strategies we monitored the Mast and WaWao Common Eider colonies located within Wapusk National Park, Manitoba. Our first aim was understanding conspecific brood parasitism or brood parasitism, which is the act of laying ones eggs (parasitizer) in the nest of another female (host), within the same species. Our objectives were to estimate the rate of brood parasitism using microsatellite loci, identify if non-random spatial and genetic distributions exist in our colonies, and if the relatedness between hosts and parasitizers are more related on average than females nesting in the general vicinity. We estimated the overall rate of brood parasitism to be 22.7% (176 of 775 offspring) with 50.7% (104 of 205 nests) of all nests containing at least one parasitic egg. We found a correlation between pairwise distance and relatedness, but it varied by year and colony. In addition, we did observe some cases of positive local autocorrelation between a focal female and her four nearest neighbors, but we observed negative local autocorrelation as well. Therefore, evidence of kin grouping is present, but

not strong. The average pairwise relatedness of hosts and parasitizers, in 2016 (0.083), did not exceed the smallest spatial scale group's average pairwise relatedness (0.152). However, average pairwise relatedness of host-parasitizer's, in 2017 (0.308), was higher when compared to even the smallest spatial scale of 0-10 meters (-0.003). This indicates females potentially shift their preference to parasitize kin annually, which could be altered based on other environmental stressors. Our second aim was focused on the timing of breeding in Common Eiders, by understanding if weather affects the timing of breeding and if the timing of breeding was a predictor of breeding success. Our objectives were to identify weather related factors that affect timing of nest initiation and examine the effects spatial and temporal variables have on daily survival rate, one of which was date of nest initiation. We found Common Eiders date of nest initiation was correlated with the last day of snowmelt, but not other weather variables. However, date of nest initiation was not a predictor of daily survival rate in Common Eiders, but the day within the breeding season and the incubation stage of the female were, which we suggest could be consequences of the timing of predator arrival. In addition, using estimates from our top model, we found it could be more beneficial to nest later in the season versus earlier, in certain years. However, the caveat of only using daily survival rate as an index of success was we have no estimate of post-hatch success indices (brood survival or recruitment), which may be impacted by timing differently.

# CHAPTER 1

# TIMING AND REPRODUCTIVE STRATEGIES OF THE COMMON EIDER (*SOMATERIA MOLLISSIMA SENDENTARIA*)

## Reproductive Strategies in Birds

Animal behaviors are fascinating because they can come in many forms or strategies, all to serve the same purpose of maximizing fitness of the individual. In birds, many behaviors are variable within a single species such as, foraging tactics (e.g. Barta et al. 2004) or migration patterns (e.g. Ely and Meixell 2016) and selection of one strategy versus another will affect fitness. Specifically, behaviors related to reproduction are of interest because they have a direct effect on fitness of the individual.

In birds, timing of reproduction will typically dictate the success of the offspring (e.g. Elmberg et al. 2005). In most migratory bird species, the length of the breeding season is constrained due a period where resources are available, leading to wide-scale synchrony (Renfrew et al. 2013). Failure to nest within the appropriate window will lead to offspring mismatching the resources required for their survival (Lehikoinen et al. 2006).

Because birds are constrained by time each year relative to breeding, they must have some plasticity in their reproductive tactics. Sometimes nesting within the optimal time window is unfeasible for reasons such as, poor body condition or lack of nesting sites (Devries et al. 2008, Semel and Sherman 2001). If so, utilization of alternative reproductive tactics must be considered as a salvage strategy where the female will avoid having no reproductive output for a given year (Lyon and Eadie 2008). Conspecific brood parasitism is one reproductive behavior that allows female birds flexibility in how to allocate their reproductive output each year. Below we discuss the many strategies associated with conspecific brood parasitism as well as the consequences of timing in reproduction, both of which are reproductive behaviors with direct fitness consequences.

## Conspecific Brood Parasitism as an Evolutionarily Stable Strategy

Egg-laying species exhibit a wide variety of reproductive strategies and will shift strategies throughout their lifetime (Lyon and Eadie 2008). For example, many bird species utilize a behavior known as conspecific brood parasitism, hereafter brood parasitism. This behavior takes place when one individual (parasitizer) lays an egg(s) in the nest of conspecifics (hosts). Brood parasitism allows females to select one of four reproductive strategies each breeding season: Parasitize, Nest, Nest and Parasitize, or No Breeding (Lyon and Eadie 2008, Sorenson 1991). It is not understood why females choose a certain reproductive strategy, but it is hypothesized that age and resource availability are large factors (Lank et al. 1989, Tiedemann et al. 2011, Sorenson 1991).

### *Brood Parasitism not Parasitic?*

Optimal clutch size is dependent on many factors and will vary given the age and condition of the individual (Devries et al. 2008). When the clutch size of an individual is below its optimal clutch size, it could become more beneficial to increase the clutch size to increase hatching success (Andersson 2017) although biological relevancy is lacking for this hypothesis (e.g. Rockwell et al. 1987).

If young and old aged birds have average clutch sizes below the optimal clutch size for a given species, there is an opportunity to increase their clutch size by allowing others to parasitize their nest until a more optimal clutch size is achieved. However, the only scenario that this act would appear beneficial is cases where host and parasitizer are closely related. Tiedemann et al. (2011) demonstrated this in Common Eiders (*Somateria mollissima*) where young and old females had the greatest proportion of nest parasites. Although they attribute this to older females "helping out" their younger relatives, it does not explain the large proportion of young females with parasitic eggs.

Another hypothesized explanation for why females choose one of the four reproductive strategies has been attributed to the relationship between females breeding in the same area (Waldeck et al. 2007). This hypothesis proposes that females are either preferentially parasitizing or avoiding parasitism of relatives based on the benefit of the act. Negative effects from brood parasitism are more pronounced in altricial birds where offspring hatch, but require their mother to provide additional care through feeding and incubation (Yom-Tov 2001). In contrast, precocial birds have offspring that are born almost entirely independent of the mother, which has called attention to whether brood parasitism places the same level of responsibility on the host female relative to altricial birds (Andersson and Eriksson 1982). Therefore, it is plausible that the energetic cost to the host is offset by a genetic-relatedness fitness benefit (Andersson and Eriksson 1982, Lyon and Eadie 2008, Andersson 2017). Yom-Tov (2001) provided additional evidence to this argument by observing brood parasitism more commonly in precocial species compared to altricial. Although the metaanalysis provided by Yom-Tov (2001) only focused on species that are observed to have brood parasitism, it highlights an important question as to why brood parasitism is found more commonly in precocial species.

Inclusive fitness models created to describe brood parasitism behavior demonstrate how brood parasitism will always cause an inclusive fitness loss towards the host (Zink 2000), while other models illustrate certain parameters that would create an inclusive fitness gain scenario (Lopez-Sepulcre and Kokko 2002, Andersson 2017). The models that demonstrate an inclusive fitness gain required three things: 1) the host and parasitizer share some level of relatedness, 2) the parasitic eggs increase the clutch size to a more optimal size, therefore increasing hatch success, and 3) there must be strong kin recognition to avoid parasitism from non-kin (Lopez-Sepulcre and Kokko 2002, Andersson 2017).

In addition to not fully understanding the mechanisms regulating brood parasitisms persistence, the models that quantify the inclusive fitness of hosts and parasitizers have not been tested on actual populations of birds engaging in brood parasitism. The model values are based on general life history traits of different bird species, but until we test these models directly on a population, we will not understand how inclusive fitness values of hosts and parasitizers change over time and under varying environmental conditions.

### *The Role of Kin Recognition*

Kin recognition has become the hypothesized mechanism that allows brood parasitism to persist (Andersson 2001, Andersson 2017). Without kin recognition, females would choose to parasitize as their reproductive strategy rather than nest. However, when Andersson and Eriksson (1982) first proposed that there is the possibility of an inclusive fitness gain (when host and parasitizer are related), they hypothesized that the persistence of brood parasitism was due to female philopatry rather than kin recognition. They assumed that brood parasitism could persist in species with female philopatry because the result would be closely related kin groups breeding near each other while also parasitizing each other questioning the importance of kin recognition, for brood parasitism (Andersson and Eriksson 1982).

Two hypothesized mechanisms of kin recognition are visual and olfactory, in avian species (Andersson et al. 2015, Rymesova et al. 2017). Andersson et al. (2015) used camera monitoring and found interactions between host and parasitizer were “tolerant” between related individuals. The findings were attributed to, “learning phenotypes during a period of close association” (Andersson et al. 2015). However, it is unknown if the selective advantage of learning phenotypes for kin recognition is to reject non-kin from parasitizing, help maintain crêches post hatch, or form kin groups at the onset of nesting (Andersson et al. 2015). McKinnon et al. (2006) found Common Eiders arriving, nesting, and departing in groups shared higher pairwise relatedness than what would be expected by random chance. However, the average relatedness was lower between females nesting compared to arrival and departure. Kin recognition could drive the close association of females during pre and post hatching period, but nest site selection could be driven by other factors such as nest site availability, suitability, and fidelity.

Visual recognition of kin is hypothesized to occur through association (Waldeck et al. 2007). It is hypothesized visual recognition of kin take place at brood amalgamations where many broods are combined and are not kin-based (Öst et al. 2005).

This could lead to error in assignment of kin through visual association and a proposed idea for why kin recognition is imperfect (Sonsthagen et al. 2010). Additionally, if non-kin deposit brood parasites, then association between nest mates could also lead to imperfect kin discrimination.

The second form of kin recognition, which has received little attention relative to brood parasitism, is olfactory stimulus. Historically, few avian species were thought to have any useful form of olfactory senses, but recent work has provided a new perspective on a broader range of avian taxa utilizing olfactory senses (Caro et al. 2015, Rymesova et al. 2017, Leclaire et al. 2017). Specifically, it is the Major Histocompatability Complex (MHC) that is identified as the gene region responsible for birds and other vertebrates to recognize kin (Waldman 1988, Zelano and Edwards 2002). Primarily, MHC is under selection from immune response to diseases. Therefore, selecting a mate with dissimilar alleles promotes offspring with greater resilience against diseases while simultaneously maintaining genetic diversity. The result of highly polymorphic MHC loci has taken on a secondary use (i.e. pleiotropic) by allowing closely related individuals to recognize similar or dissimilar alleles through olfaction (Rymesova et al. 2017). In birds, the uropygial gland in particular is believed to secrete preening oils with chemical signals unique to that individual, which is available for detection by others through olfaction (Mardon et al. 2011).

Other hypotheses question whether there need be genetic cues for kin recognition (Lyon and Zink 2018), while others suggest there could be loci specifically for kin recognition (Holman et al. 2013). The concern is how kin recognition loci remain highly polymorphic when rare alleles have on average greater selective disadvantage against more common alleles. This is Crozier's Paradox, where individuals with common kin recognition alleles will "freeload" from non-kin, but share the same common alleles. The result is selection against rare alleles and overall low allelic richness (Crozier 1986). Pleotropic genes are one solution to Crozier's Paradox (i.e. MHC), but others have shown when individuals use disassortative mating systems to avoid inbreeding, kin recognition loci will maintain high allelic richness without being pleotropic (Holman et al. 2013). Understanding if genetic cues are used for kin recognition (visual and olfactory phenotypes) will help us determine how brood parasitism has persisted overtime and the role kin recognition plays.

### *Management Implication of Brood Parasitism*

Although the theoretical and evolutionary considerations are the central focus of brood parasitism, there are still direct applications of brood parasitism to conservation and management. For example, cavity-nesting waterfowl such as wood ducks (*Aix sponsa*) have a higher reproductive success when parasitism and population density is relatively low (Haramis and Thompson 1985). However, when population density increases, competition for nesting sites also increases and females without a nest cavity will seek out nesting females to parasitize. The result is many parasitized nests with clutch sizes well above what is feasible to incubate, leading to a crash in reproductive output (Haramis and Thompson 1985).

Further, artificially increasing the number of nest sites for wood ducks lead to an increase in brood parasitism followed by a decrease in overall nest success (Haramis and Thompson 1985). This is a direct result of considering what is assumed to be best for maximizing reproductive output (increased number of nesting sites), but ignoring the behavioral ecology of the species, which resulted in increases in brood parasitism and an overall decrease in reproductive output.

In addition, we do not typically measure the true reproductive output of a female because we only give her credit for what was laid, in her nest. However, many studies have shown that females are willing to incubate others eggs through brood parasitism and may even engage in fecundity enhancement (Sorenson 1991), which would result in a female having a much greater reproductive output than we give her credit for.

Some may argue that knowing the true reproductive capabilities of an individual female is less important at the scale of fecundity estimates for overall population trends. However, we argue that understanding each females true reproductive potential is highly understudied or even considered, and therefore our understanding of its variation in a population is also limited. Relative to life history characteristics, we know age and condition are the greatest driver of reproductive output (Andersson 2017; Devries et al. 2008 respectively), but by understanding the true variation in reproductive output in a population, we may find there are distinct groups with higher or lower reproduction, independent of condition or age.

## Consequences of Timing and Reproduction

In addition to brood parasitism, timing of reproduction is another behavioral strategy utilized by avian species for reproduction. There are two major hypotheses why nesting females time their breeding. Either females will attempt to align their hatch date with resources as they become available (mismatch hypothesis) or they will attempt to synchronize their nest with the rest of the colony surrounding them (breeding synchrony hypothesis).

The mismatch hypothesis applies directly towards migratory waterfowl, which must align their arrival to breeding grounds and initiation of nest with resources as they become available later. Typically, birds that nest earlier tend to have higher brood success compared to later nesting birds (e.g. Elmberg et al. 2005). However, age, condition, and nest site availability of the nesting females are also associated with early and late initiation making it difficult to disentangle the true relationship (Martins 1995, Devries et al. 2008, Love and Gilchrist 2010).

Another hypothesis surrounding the timing of nest initiation is colony synchrony. In lesser snow geese (*Anser caerulescens*), there is a reduction in nest success when nesting before and after the peak nest initiation date (Findlay and Cooke 1982). Aligning date of nest initiation with the rest of the colony allows females to reduce their probability of predation by over saturating the landscape with available prey for common nest predators.

## The Common Eider as a Model for studying Brood Parasitism and Timing of Reproduction

### *Brood Parasitism in Common Eiders*

Over 200 bird species engage in brood parasitism, most of which are colonial nesting species (Yom-Tov 2001). The majority of the species that engage in brood parasitism are found to belong to the order of Anseriformes. We selected Common Eiders as our study species, which engages in brood parasitism and is a colonial nesting waterfowl species.

Common Eiders are one of the most well studied sea ducks and are a model species for brood parasitism (Table 1). They have a circumpolar distribution with seven distinct subspecies. The Hudson Bay Common Eider (*Somateria mollissima* sedentaria) is the subspecies studied for this work.

The rate of parasitism in Common Eiders ranges from 2% to 55% of all nests (Waldeck et al. 2004, Waldeck et al. 2011, Waldeck and Andersson 2006, Lusignan et al. 2010, Tiedemann et al. 2011,  Hario et al. 2012, but see Table 1 for rates of brood parasitism). In addition, due to their lower reproductive value, older females willingly accept more parasitic eggs when compared to younger hosts, and there are usually high levels of relatedness between the host and parasitizer (Tiedemann et al. 2011, Waldeck et al. 2007). The rate of nests containing parasitic eggs is of interest for this specific colony of Common Eiders that have had estimates taken in 1991 (42.4%) and 2002 (31%), which identified parasitic events using different methodologies (Robertson et al. 1992, Waldeck and Andersson 2006 respectively). Revisiting the rate of parasitism will provide new estimates and a greater understanding of variation between estimates when using alternative methods.

Common Eiders nest in kin groups, but it is still unknown whether this is the result of female philopatry or selecting nest sites near relatives (Waldeck et al. 2007, Sonsthagen et al. 2010). Female Common Eiders exhibit strong philopatry with estimates of 98% of females returning to their natal grounds (Coulson 1984, Swennen 1990).

Further, it is observed that 22% of females return to nest on the same island of previous years and 70% nest within 135 meters of previous nest sites (Reed 1975).

In addition, the parental care of Common Eiders makes them interesting to study relative to brood parasitism. Common Eiders are uniparental caregivers where only the female remains to attend the nest. This not only limits the number of recess events taken throughout incubation, but also places all responsibilities of nest and brood defense on the incubating female justifying why Common Eiders engage in brood parasitism as a cooperative breeding strategy more than other waterfowl species that have biparental care where both the male and female participate in parental care.

### *Timing and Reproduction in Common Eiders*

Regardless of the strategy for nest initiation, annual weather patterns will be a constraint altering bird's ability to nest at a preferred time each year. Multiple long-term datasets on Common Eider nesting exist (e.g. Lehikoinen et al. 2006, Iles et al. 2013), making them suitable candidates for understanding the drivers of nest initiation as well as the consequences of nesting early or later in the breeding season. Previous studies associate a suite of weather variables with breeding success (Jónsson and Lúovíksson 2013, Iles et al. 2013), while others seek to understand the connection between both breeding success and time of nesting to weather variables (Lehikoinen et al. 2006, Love and Gilchrist 2010).

Pertaining to weathers impact on breeding success, Lehikoinen et al. (2006) found years with later dates of ice break up resulted in a reduction in clutch size and fledgling success and milder winters were associated with an increase in body condition. Iles et al. (2013) found a reduction in daily survival rate when early spring conditions were either wet and cold or warm and dry, while wet and warm conditions in late spring increased daily survival rate. Love and Gilchrist (2010) found increased temperature allowed additional females to nest, but the conditions of these females are unknown and assumed to be in poor condition bringing to question the true success of the nesting events. Jónsson and Lúovíksson (2013) did not find any relation between weather and apparent survival, in Common Eiders.

Summarizing previous studies, milder temperatures are associated with Common Eiders nesting earlier and having more flexibility in the date of initiation resulting in an increase in success (Lehikoinen et al. 2006, Iles et al. 2013, Love and Gilchrist 2010, but see Jónsson and Lúovíksson 2013). However, making direct comparisons between studies is difficult given multiple indices of breeding success and weather variables.

## Objectives and Major Hypotheses

### *Chapter 2 Objectives and Hypotheses*

The primary aim of chapter 2 is to understand utilization of cooperative breeding tactics in Common Eider, through brood parasitism and kin grouping. For our primary aim, we have three objectives:

1) Estimate the rate of brood parasitism in two Common Eider colonies
2) Classify the level of relatedness between nesting females at different spatial scales (kin grouping)
3) Identify if the host-parasitizer relatedness is greater than Common Eider nesting in close proximity to each other (preference to parasitize kin).

### *Primary Hypotheses*

The rate of brood parasitism is well documented in Common Eiders and is generally agreed to occur consistently across years (Table 1). We anticipate the rates of parasitism for our study should be comparable. However, the utilization of brood parasitism as a cooperative breeding strategy is still debated (Andersson 2017, but see Zink 2000). Here we define the four most plausible scenarios for both the presence of kin grouping and host's preference for parasitizing kin. We do consider the possibility of kin avoidance, but previous literature suggests it is unlikely in our study species (e.g. McKinnon et al. 2006, see Figure 1 for all possible scenarios).

*(1) Kin grouping observed and host-parasitizer relatedness is greater than what is expected due to kin grouping*

Here, we predict both kin grouping and parasitizer's preference for closely related hosts. Kin grouping is well established in other colonies of Common Eiders (McKinnon et al. 2006, Waldeck et al. 2007, Sonsthagen et al. 2010). In addition, the average relatedness between host and parasitizer was beyond what was observed between closely nesting individuals when nesting in kin groups (Waldeck et al. 2007).

*(2) Kin grouping is not observed, but host-parasitizer relatedness is beyond what is expected even in absence of kin grouping.*

Here, we predict there will be no spatial trend relative to relatedness in nesting females, while parasitizer's will still maintain a preference to parasitize kin. Interestingly, the only study of Common Eiders not found to nest in kin groups came from the same colony studied for this work (Andersson and Waldeck 2007). In addition, this study also found the average relatedness between host-parasitizers to be beyond the average relatedness observed at small spatial scales (Andersson and Waldeck 2007).

*(3) Kin grouping is observed, but host-parasitizer relatedness is not beyond what is expected by kin grouping.*

Here, we predict the presence of kin grouping, but the average relatedness between host-parasitizers is not exceedingly greater than what would be expected from kin grouping. In this scenario, Common Eiders are preferentially nesting near one another, but parasitizers are parasitizing at random rather than preferentially seeking kin to parasitize. Although this scenario is not observed for the Common Eider thus far, it is possible for Common Eiders to utilize kin grouping as a cooperative breeding strategy with no preference to parasitize kin.

*(4) Neither kin grouping nor host-parasitizer relatedness appear to be the result of kin selection.*

Here, we predict the absence of kin grouping and preference to parasitize kin. The absence of kin grouping can occur when females are selecting nest sites without consideration of distance to relatives. This scenario would demonstrate Common Eiders prioritizing other nest site characteristics over distance to relatives, while also not having a preference to parasitize kin versus non-kin. No kin preference could be caused by years with high competition for nesting sites where individuals will nest with no consideration of distance to relatives. Under these same circumstances, parasitizers would be pressured to parasitize as a “best of a bad job” scenario and will parasitize opportunistically as strategy to salvage a portion of her reproductive output (Sorenson 1991).

### *Chapter 3 Objectives and Hypotheses*

The primary aim of chapter 3 is to determine if a connection exists between environmental drivers of nest initiation and its impact on nest success using a long-term data set of the Mast River Common Eider Colony. For our primary aim, we have three objectives:

1) Use a suite of weather variables to predict when Common Eiders will initiate their nests
2) Understand if there are consequences relative to daily survival rate when initiating early versus late
3) Identify other predictors of daily survival rate in addition to date of initiation

### *Primary Hypotheses*

The impact of weather on breeding success is documented, but ambiguous, due to studies using different weather variables and indices of success (Iles et al. 2013 versus Lehikoinen et al. 2006). Here we define the most plausible scenarios for the effect temperature will have on date of initiation and the effect date of initiation will have on daily survival rate.

#### *(1) Milder spring seasons are associated with earlier date of initiation compared to less mild springs and date of initiation is a predictor of daily survival rate*

Here we predict Common Eiders will initiate their nests earlier in response to milder springs. This can occur when mild spring temperatures allow nesting sites to become available earlier for a given year and is supported in Common Eiders (Love and

Gilchrist 2010) and other bird species (Langford and Driver 1979, Drever and Clark 2007). We also hypothesize that date of initiation will have a negative relationship with daily survival rate. Weather factors known to alter timing in breeding are associated with many indices of success such as, clutch size, fledgling success, body condition, and daily survival rate (Lehikoinen et al. 2006, Iles et al. 2013). Under this hypothesis, spring conditions will have an indirect effect on daily survival rate through alteration of date of initiation.

*(2) Milder springs show an association with date of initiation compared to less mild spring, but date of initiation is not a predictor of daily survival rate*

Similar to above, we predict Common Eiders will initiate their nests earlier in response to milder springs. However, many other factors independent of date of initiation will be associated with daily survival rate (e.g. nest predators). Under this hypothesis, spring conditions will not have an indirect effect on daily survival rate through alteration of date of initiation.

*(3) Milder springs show no association with date of initiation compared to less mild springs eliminating the connection between spring condition's indirect effects on daily survival rate*

Here we predict that earlier date of initiation is not associated with milder springs. This could occur if Common Eiders are timing their nests due to other abiotic or biotic factors, which have been observed in other studies on Common Eiders (Lehikoinen et al. 2006). Under the mismatch hypothesis, Common Eiders would prioritize matching date of initiation with the availability of resources post-hatch, independent of spring conditions, which was supported in other Arctic nesting birds (Smith et al. 2010). Therefore, if Common Eider date of initiation is independent of spring conditions, then the relationship between daily survival rate and date of initiation cannot be made.

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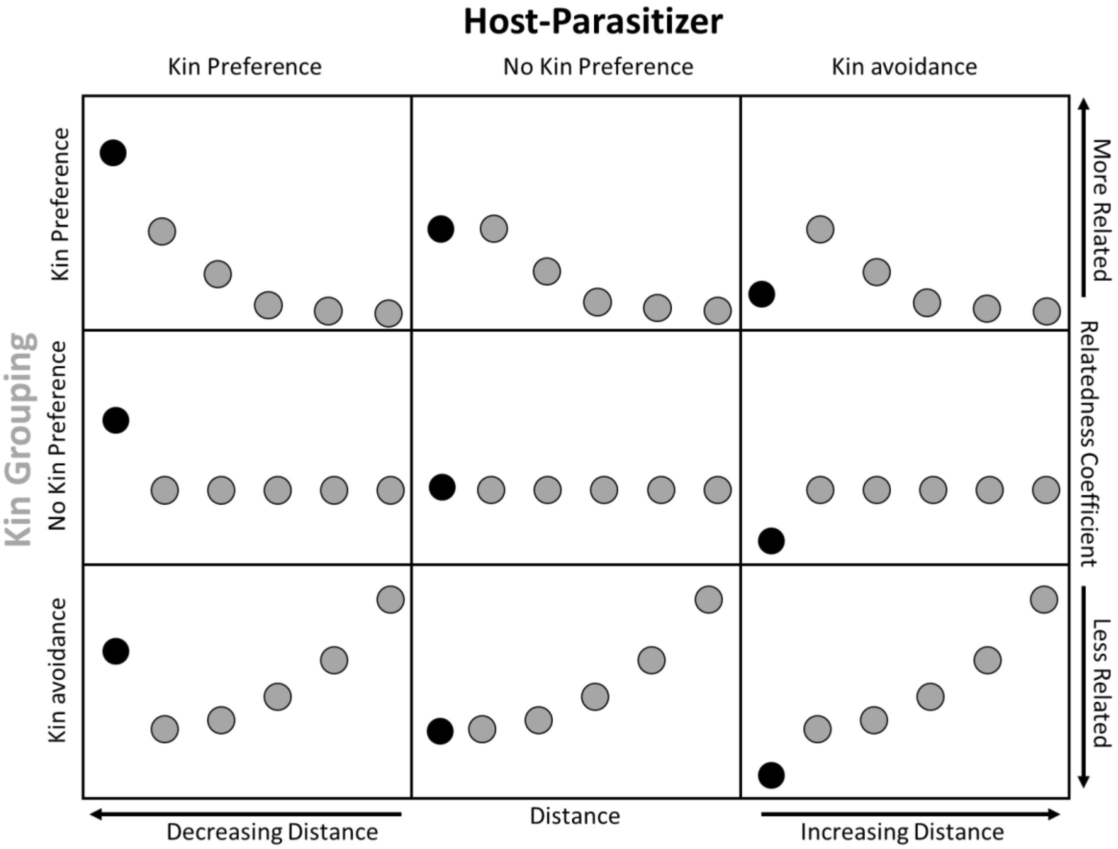

**Figure 1.** Hypothetical scenarios for relatedness at spatial scales intervals (grey) relative to the average relatedness between host and parasitizers (black), in Common Eiders (*Somateria mollissima*).

**Table 1.** Rates of conspecific brood parasitism by method, location, and year(s) of study, in Common Eiders (*Somateria mollissima*). The rate of parasitism is represented as either the percent of total eggs of parasitic origin (egg) or the percentage of nests containing at least one parasitic egg (nest). Superscript letters by location represent multiple studies from different years at the same site location.

| **Source** | **Method** | **Location** | **Rate (egg)** | **Rate (nest)** | **Year(s) of Study** |
|---|---|---|---:|---:|---|
| Robertson 1998* | Laying sequence | Canada[a] | 6-10% | 20-42% | 1991 |
| Bjorn and Eriksson 1994 | Laying Sequence | Norway[b] | 2-13% | 2-21% | 1989-1990 |
| Waldeck et al. 2004 | Protein Banding | Finland | 1-14% | 4-55% | 2001-2002 |
| Waldeck and Andersson 2006 | Protein Banding | Canada[a] | 6-10% | 22-39% | 2002 |
| Lusignan et al. 2010 | Protein Banding | Canada | 19% | 55% | 2007 |
| Andersson et al. 2015* | Protein Banding | Norway[b] | 6% | 18% | 2007-2009 |
| Hario et al. 2012 | Microsatellites | Finland | 34% | 51% | 2001-2003 |
| Tiedemann et al. 2011 | Microsatellites | Denmark | 16-17% | 30-38% | 1998-2001 |

*but see, Robertson et al. 1992

*but see, Waldeck et al. 2011

# CHAPTER 2

# COOPERATIVE BREEDING TACTICS OF THE COMMON EIDER

## Abstract

Conspecific brood parasitism or brood parasitism is the act of laying ones eggs in the nest of another female, within the same species. Brood parasitism allows females to have some flexibility in their reproductive tactics by exploiting other female's nests when nesting may not be an option or as a way to enhance reproductive output by nesting and parasitizing. Many question brood parasitism as a truly parasitic act and under the right scenario, it could be utilized as an inclusive fitness gain strategy. If the cost to incubate and brood young has a low energetic investment (e.g. precocial relative to altricial) and the individual parasitizing the host is closely related, an inclusive fitness gain scenario seems plausible. Here we seek to understand if female Common Eiders (*Somateria mollissima*) prefer to parasitize kin, non-kin, or have no preference. In addition, we re-estimated the rate of brood parasitism and extra-pair paternity for the Mast and WaWao colonies using a non-invasive molecular technique. We also discuss the efficacy of sampling different sources of genetic material. We used microsatellite loci as the molecular marker to identify parasitic eggs and their biological mother's relation to the host female. In addition, Common Eiders exhibit strong nest site fidelity. To determine that relatedness between hosts and the female laying the parasitic egg is truly from kin preference and not an artifact of nest site fidelity, we estimated the degree of relatedness at different spatial scales between nesting females in both the Mast and WaWao Common

Eider Colonies. Both feather (19.4% loss) and hatch membrane (26.6% loss) were suitable sources of genetic material, but eggshells (100% loss) did not provide any viable genotypes. The overall rate of brood parasitism was 22.7% (176 of 775 offspring) and 50.7% (104 of 205 nests) of all nests contained at least one parasitic egg. The estimate of brood parasitism is larger than previous estimates, which we propose is due to using a molecular marker with a greater probability of inclusion. We found a correlation between pairwise distance and relatedness, but it varied by year and colony. In addition, we did observe some cases of positive local autocorrelation between a focal female and her four nearest neighbors, but we observed negative local autocorrelation as well. The average pairwise relatedness of hosts and parasitizers, in 2016 (0.083), did not exceed the smallest spatial scale group's average pairwise relatedness (0.152). However, average pairwise relatedness of host-parasitizer's, in 2017 (0.308), was higher when compared to even the smallest spatial scale of 0-10 meters (-0.003). This indicates females potentially shift their preference to parasitize kin annually, which could be altered based on other environmental stressors.

## Introduction

Conspecific brood parasitism (also known as intraspecific nest parasitism) is the act of placing one's egg(s) in the possession of a conspecific. Conspecific brood parasitism, hereafter brood parasitism, is classified as parasitic because the individual placing eggs (parasitizer) is removing all energetic investment required for parental care and placing it upon the individual now in possession of the parasitic eggs (host). Brood parasitism allows avian species flexibility in the reproductive strategy they use in a given breeding season such as, parasitize, nest, nest and parasitize, or no breeding (Sorenson 1991). Andersson (2017) proposed a model of brood parasitism in which both host and parasite could benefit through inclusive fitness if they were sufficiently closely related to each other. However, there is debate whether brood parasitism is a realistic mechanism to gain inclusive fitness (Lopez and Kokko 2002, Andersson 2001, Andersson 2017, but see, Zink 2000). Precocial species have the potential to gain inclusive fitness from brood parasitism because their parental care is minimal compared to altricial species. However, there must be some level of relatedness shared between host and parasites, strong kin recognition, and the additional egg(s) does not exceed the host's optimal clutch size (Andersson 2001, Lopez and Kokko 2002, Andersson 2017).

Although it was assumed that strong kin recognition was required to prevent individuals from solely parasitizing rather than nesting, it is possible to have high rates of brood parasitism between related individuals as an artifact of female philopatry and strong nest site fidelity (Andersson and Erikkson 1984). There is evidence to support visual and olfactory mechanisms to discriminate between kin and non-kin in avian species (Andersson et al. 2015, Rymesova et al. 2017). However, to understand if females are preferentially parasitizing kin, we must also understand what the background genetic structure is within the colony (Waldeck et al. 2007, Andersson and Waldeck 2007).

To estimate background genetic structure, there are two mechanism that will drive a non-random geographic and genetic distribution of nests 1) strong nest site fidelity and 2) preference to nest near kin. It is near impossible to truly disentangle the two mechanism that drive a non-random distribution in nesting females. However, estimating the geographic and genetic distribution allows us to understand if parasitic acts are truly utilized as form of kin selection or are an artifact of non-random distribution of nests.

### *Historical and Current Methods of Studying Conspecific Brood Parasitism*

Methodologies in molecular ecology are constantly changing and are leading to exploiting new sources of genetic material. Originally, fresh tissue was required for studies using protein electrophoresis and resulted in the lethal removal of the organism (e.g. Lewontin 1991). With the discovery of PCR, the source of genetic material (i.e., hair, feces, hatch membranes) and its quality became less important and was the beginning of true non-invasive sampling methodologies.

Many studies that asses the efficacy of non-invasively obtained sources of genetic material, do not take into consideration the possibility of applying this methodology to a study with many samples. For example, the process to chemically and mechanically breakdown and extract DNA from genetic material is time consuming and/or expensive rendering it as an unfeasible method for large-scale datasets (Egloff et al. 2009; Stausberger and Ashley 2001). In addition, the goal of certain studies did not intend to apply their methodology to a larger scale, but their findings provide additional evidence on how to extract DNA from a certain source of genetic material (Oskam et al. 2010). Specifically, in avian species there is interest in collecting tissue samples at the nest where both maternal and offspring DNA are available. Examples of potential studies include, nest site fidelity, the spatial structure of kin grouping, or the rate of brood parasitism.

Historically, parasitic eggs were determined by studying the laying sequence of the host and identifying the eggs that did not align with the timing of the host’s natural laying cycle. In addition, the morphometrics and color of an egg that deviated significantly from the host's other eggs also were considered parasitic (Robertson et al. 1992, Bjorn and Erickstad 1994, Drugger and Blums 2001), requiring nests were visited daily forcing females from their nests potentially increasing the level of stress. Genetic based methods are currently used to identify acts of brood parasitism either through the use of protein banding or microsatellites (Waldeck and Andersson 2006, Tiedemann et al. 2011, respectively). Protein banding methods require puncturing a small hole in the egg to retrieve albumin, but this method is proven to have no effect on hatchability (Andersson and Åhlund 2001) and in most scenarios will lead to a greater sample size when compared to DNA methods. However, protein banding will have a lower probability of inclusion and gives no genetic information on the male(s) siring the clutch (Andersson and Åhlund 2001). Microsatellite methods require DNA, which has been sampled invasively by blood draws (Tiedemann et al. 2011). However, other non-invasive techniques have been developed to collect both maternal and offspring DNA from nest after completion to avoid any contact with the incubating female (Kreisinger et al. 2010).

### *Objectives*

To inform our overarching question we had three objectives: 1) estimate the rate of brood parasitism in two Common Eider colonies nesting along the western Hudson Bay, 2) classify the level of relatedness between nesting females at different spatial scales, and 3) identify if the host-parasitizer relatedness is greater than Common Eiders nesting in close proximity to each other.

As discussed in chapter 1, Common Eiders are an ideal study species for studying brood parasitism because the behavior is well documented (Chapter 1: Table 1). Further, in the Mast River Common Eider Colony the previous estimate of brood parasitism was 7.8% of all eggs were parasitic using laying sequence and morphometrics of eggs (Robertson 1998), while 8.2% of all eggs were parasitic using protein banding (Waldeck and Andersson 2006). Because we have estimates of brood parasitism using different methods on the same colony, we can observe how estimates of brood parasitism may be affected by the method used.

In addition, we will use non-invasively sampled genetic material to address the objectives above. Our final objective is to determine the methodological feasibility of three sources of genetic material (feather, eggshell, and hatch membrane).

## Methods

### *Study area*

We studied nesting Common Eiders based out of the field station, Nestor 2, located approximately 40km east of Churchill, MB. The remoteness of Nestor 2 allows researchers to study wildlife in their natural environment with little influence from anthropogenic factors. Two Common Eider colonies near Nestor 2 are located where the Mast River (58°43'38.4"N 93°28'21.2"W) and Wawao Creek (58°42'25.7"N 93°27'10.1"W) enter into La Pérouse Bay. This region consists of small islands ranging from 1 to 300$m^2$. Islands utilized by the Common Eiders have a mixture of birch (*Betula glandulosa*) and willow (*Salix* spp.) with vegetation height ranging from 0.6 to 2m (Schmutz et al. 1982).

### *Sampling Design*

Nest searches begin during the first week of incubation. Each year we attempt to locate all nests within the colony, but there are still nests that could be unaccounted for either from female Common Eiders nesting later than the average initiation date or if a nest is placed outside of the historic colony boundaries. Once nests are found, GPS coordinates are recorded, which allow us to measure distance between nests and where high, medium and low nest density areas are within the colony. We candle each egg during the first nest visit to determine the developmental stage (Weller 1956) and the date of nest initiation.

### *Sampling Genetic Material*

We collected up to four feathers lining the nest bowl during the first nest visit. Eggshell and hatch membranes were obtained from each nest bowl shortly after fate of nest (either predation or hatch). Eggshell and hatch membranes were attached to one another for a single egg and were carefully removed, cleaned, dried and stored, shortly after removing from the field.

### *DNA Extraction*

*Feather*- We removed the calamus from each feather sample and made a single cut targeting the superior umbilicus indicated by a red dot where blood commonly clots (see Hovarth et al. 2005 for detailed description; see Figure 1 for the location of superior umbilicus for Common Eider nest bowl feathers). *Eggshell*-Approximately 70mg of eggshell was removed from hatch membrane carefully to avoid cross contamination from hatch membrane. We removed any remaining membrane or debris from the inner section of the shell and placed it into a 1.5mL tube. There is not any section of the eggshell that is known to increases the probability of extracting DNA (Oskam et al. 2010) and for our study, determining the exact area an eggshell fragment originated from was not feasible. *Hatch Membrane*- We removed approximately 25mg of hatch membrane targeting chorionic vessels containing embryonic DNA (Kreisinger et al. 2010; see Figure 2 for an example of hatch membrane sample).

Once each tissue type was isolated, it was placed into a 1.5mL with 5 ceramic beads and 500µL genomic lysis buffer. We placed the 1.5mL tubes into a TissueLyserII (Qiagen Inc.) for 15 minutes at 1800 oscillations/min to simultaneously breakdown tissue mechanically and chemically. Rather than testing multiple single sample extraction protocols that ranged in the time spent on individual samples given their condition, we tested our tissue types using a high throughput DNA extraction method. The DNA extraction was performed using a 96-well silica based spin column kit (Zymo Research Corporation) following the blood and whole serum extraction protocol.

We calculated the percent loss into three categories: *Field Loss*-Sample loss during sample collection, in the field. Predation or hatch membranes being removed from the nest by an attending female caused sample loss for eggshell and hatch membranes. In addition, if a nest failed early in incubation before the attending female lined her nest bowl with down, feather samples were not collected. *Preprocessing Loss*- Sample loss while cleaning and placing into 1.5mL tubes. Closer visualization of each sample allowed us to determine if samples were unfit for DNA extraction. Either unfit samples could be from lack of necessary region for DNA extraction (superior umbilicus and chorionic vessels) or the sample was degraded to a level unsuitable for DNA extraction. *Extraction Loss*- Samples with less than six genotyped loci were considered an extraction loss.

Extraction loss can come from many sources such as, poor quality of sample (either low volume of DNA or poor quality DNA), failed DNA extraction, failed PCR (1st or 2nd round), or failed bridge amplification on the flow cell of the the Mi-Seq High-Throughput Sequencing System (Illumina, Inc.). We calculated the total sum of samples for each stage of processing samples: 1) Starting sample 2) Collected sample 3) Extracted Sample and 4) Genotyped Sample. We ran a preliminary run and determined eggshells produced no viable genotypes. Therefore, total loss for the eggshell tissue type was estimated for the extraction loss category based on 22 preliminary samples.

*Molecular Methods*

To genotype microsatellites, we first amplified (refer to Darby et al. 2016 for details on PCR amplification and library prep) and then sequenced on the Mi-Seq High-Throughput Sequencing System (Illumina, Inc.) at the University of North Dakota Medical School. Microsatellites used for analysis were Sfiμ1, Sfiμ3 (Fields and Scribner 1997), Sfiμ9 (Öst et al. 2005), Smo1, Smo4, Smo6, Smo7, Smo8, Smo9, Smo10, and Smo12 (Paulus and Tiedemann 2003, but see Table 1.a for description of each locus).

We used a two round PCR methodology (Darby et al. 2016). 1st round (Locus-specific amplification) PCR conditions: PCR was carried out in 20µL volumes per well in 96-well PCR plates, containing 1X DreamTaq™ Green Buffer (contains KCL, (NH-$_4$)SO$_4$, and 2mM MgCl$_2$), 200µM dNTP, 0.2µM for both forward and reverse primers, 0.5 U DreamTaq Hot Start Polymerase (Thermo Scientific). Amplifications were performed in Applied Biosystems SimpliAmp Thermal Cycler with the following reaction profile: one cycle 95 °C 1 min; 30 cycles 95 °C 30 sec, 55 °C 30 sec, 72 °C 30 sec; one cycle 72 °C 5 min.

2nd round (Adapter-indexing amplification) PCR conditions: Five µL from each multiplex group plate (total of 20µL) were pooled into a single plate and run through PCR clean up kit using 96-well silica based spin column kit (Zymo Research Corporation). PCR of pooled PCR product from 1st round amplification was carried out in 20µL volumes per well in 96-well PCR plates, containing 1X DreamTaq™ Green Buffer (contains KCL, $(NH_4)SO_4$, and 2mM $MgCl_2$), 200µM dNTP, 0.2µM for both forward and reverse primers, 0.5 U DreamTaq Hot Start Polymerase (Thermo Scientific). Amplification were performed in Applied Biosystems SimpliAmp Thermal Cycler with the following reaction profile: one cycle 95 °C 1 min; 20 cycles 95 °C 30 sec, 55 °C 30 sec, 72 °C 30 sec; one cycle 72 °C 5 min.

This method of genotyping microsatellites by sequencing instead of by capillary electrophoresis allowed us to submit a high number of samples in a single run (937 samples on a single MiSeq Run) and resolved a greater number of alleles (e.g. through SNPs and variable repeat motifs) than through length alone (Darby et al. 2016). Paired-end sequencing reads were merged into one read, de-replicated, and assigned to their respective locus with the - fastq_mergepairs -fastq_filter -fastx_uniques commands of USEARCH v11 (Edgar 2010). A custom Python/Biopython script was used to sort reads by locus and enumerate the frequency of each unique read for each specimen, thus providing the genotype (i.e. allele) for each specimen at each locus. We re-genotyped approximately 5% of the total sampled population to obtain estimates of marker error from allelic drop out, null alleles.

### *Parasite Assignment*

We used a conservative criterion adopted from Kreisinger et al. (2010) to identify brood parasitism. Young were considered parasites if either 1) at least one locus did not match the putative mother of the nest that could not be explained as the result of allelic drop out or null alleles (i.e., both female and young heterozygous at locus), or 2) at least two loci did not match the putative mother of the nest that could be explained as the results of allelic drop out or null alleles.

We identified cases of extra-pair paternity by taking the remaining young not attributed to brood parasitism and used their genotypes with the putative mother of the nest to reconstruct the paternal genotype. Paternal genotypes were reconstructed using GERUD 2.0 (Jones 2005). Because this type of analysis does not accept missing genotypes, we used three loci to identify cases of extra-pair paternity (Smo06, Smo07, and Smo08). Loci used to identify extra-pair paternity were selected by having a high probability of exclusion (see Table 1.b) and few missing genotypes for young and mother. Of the cases of mismatch between mother and young that could be the result of allelic dropout or null alleles (only four cases), we estimated the second allele of the mother or young by selecting the allele of the highest frequency that would eliminate the mismatch.

### *Estimate of Kin Grouping*

We estimated kin grouping by identifying if spatial autocorrelation of pairwise genetic relatedness existed at different spatial scales. To accommodate multiple loci, we used a multivariate approach calculated within GenAlEx, where the pairwise genetic distance and spatial distance pairwise comparisons are correlated with each other across predefined distance classes (Smouse and Peakall 1999). Distance classes were determined based on previous studies on Common Eiders conducting similar analyses (Andersson and Waldeck 2007). Within each distance class, a null distribution of relatedness was created through random permutations to compare against the observed average pairwise relatedness. Relatedness values above zero represent distance classes where relatedness exceeds what is expected by random chance, while values below zero represent scenarios where relatedness is lower than what is expected by random chance (Smouse and Peakall 1999). Significance of kin grouping was determined using a heterogeneity test in GenAlEx (Smouse et al. 2012). In addition, we tested for a spatial trend between relatedness and distance between nests using a non-parametric approach. To calculate pairwise relatedness, we used ML RELATE (Kalinowski et al. 2006) and tested for significance of the trend relative to pairwise distance using Spearman rank correlation $r_s$.

To measure fine-scale genetic clustering of nests, we also measured the two-dimensional spatial autocorrelation of nests relative to their genetic structure, implemented in GenAlEx as described by Double et al. (2005, but see Sonsthagen et al. 2010 for kin grouping details). We anticipate local autocorrelation under non-random distributions of nesting females due to breeding site fidelity. However, if females are faithful to a nest site rather than close association to kin, then no local autocorrelation should be observed. To estimate local autocorrelation, we took the four closest neighboring nests for each females and compared those pairwise genetic and geographic distances in GenAlEx (10,000 permutations). We used a two-tailed test detect both positive (kin grouping) and negative (kin avoidance) autocorrelation scenarios.

### *Host-Parasitizer Relatedness*

Of the parasites identified, we assigned pairwise relationships with the rest of the nesting population of females using program COLONY (Wang 2004). COLONY uses a maximum likelihood method to assign inferred mothers to offspring in the sampled population with a probability of the relationship. GenAlEx was used to calculate the relatedness between hosts and parasitizer's, and was compared to the average relatedness observed at different distance classes mentioned above. If host-parasitizer relatedness exceeded the background levels of relatedness observed at all spatial scales, this would indicate parasitizers are preferentially parastizing closely related females beyond random chance.

## Results

### *Success of Non-Invasive Sampling*

Sample loss was lower in feathers (19.4% total loss) relative to hatch membrane samples (26.6% total loss). However, of the eggshells tested, none produced viable genotypes (Table 2, Figure 3). The average proportion of hatch membranes sampled from total nest failure clutches was 0.30, while successful nests (at least one egg hatched) had on average 0.81 (Figure 3). The proportion feather samples genotyped from total nest failure clutches was 0.72 (64 of 89 nests), while successful nests had 0.85 (173 of 204 nests; Figure 3).

### *Rates of Parasitism and Extra-Pair Paternity*

Of the samples we could compare nesting female to young in nest, we found an overall rate of 22.7% (176 of 775 offspring) were of parasitic origin and 50.7% (104 of 205 nests) of all nests contained at least one parasitic egg. We estimated the rate of parasitism in 2016 to be 18.8% (87 of 464 offspring) and 44.3% (54 of 122 nests) of all nests contained at least one parasitic egg. We estimated the rate of parasitism in 2017 to be 28.6% (89 of 311 offspring) and 60.2% (50 of 83 nests) of all nests contained at least one parasitic egg.

Of the 164 clutches we observed (after removing parasites and nests that we were unable to score for extra-pair paternity), we found four clutches containing offspring resulting from extra-pair paternity (2.4%). We found three of the 101 nests to have extra-pair paternity and one of the 62 nests to have extra-pair paternity in 2016 and 2017, respectively.

*Kin Grouping and Host-Parasitizer Relatedness*

We observed kin grouping, but the significance of the trend varied by year and colony (Figure 4, but see Table 3 for all Spearman's correlation combinations). In addition, we observed evidence of kin grouping relative to distance class, in 2016 ($p < 0.001$), but not in 2017 ($p = 0.048$, Figure 5). We observed both positive and negative autocorrelation of focal nests to its four nearest neighbors, which varied by year and colony (Figure 6, Table 4). However, visual observation of the location of positive and negative autocorrelation indicates autocorrelation was not held to a specific site across years.

Because parasitizers from WaWao colony were found parasitizing females in the Mast Colony in both 2016 and 2017, we combined both colonies average pairwise relatedness for different spatial scales, for both years. The average pairwise relatedness of hosts and parasitizers, in 2016 (0.083), did not exceed the smallest spatial scale group's average pairwise relatedness (0.152, Figure 5). However, average pairwise relatedness of host-parasitizer’s, in 2017 (0.308), was higher when compared to even the smallest spatial scale of 0-10 meters (-.003, Figure 5).

## Discussion

### *Considerations for Non-Invasive Sampling*

Both feather and membrane were viable sources of genetic material for this project. Previous work has shown eggshells contain nuclear DNA (Egloff et al. 2009). However, here we show when attempting to process many samples using high-throughput methods, the success rate is much lower. We strongly caution future studies using non-invasive sources of genetic material to consider the amount of time and money that will be required for a successful extraction.

We also caution that the source of genetic material could be present one year, but not in others. For example, the success of genotyping hatch membranes was much higher in successful nests versus failed. This is primarily due to predators removing the entire egg with no tissue to collect or the sample failed early into development with lack of chorionic vessels to isolate for extraction. Both 2016 and 2017 had relatively high nest success, but had this sample collection occurred during a high failure year, sample size would be greatly reduced.

### *Historical Estimates of Conspecific Brood Parasitism versus Current*

We found higher rates of brood parasitism relative to previous estimates of brood parasitism in the Mast and WaWao Common Eider Colonies (Figure 7, Robertson 1998, Waldeck and Andersson 2006). The difference in estimates could be in response to environmental conditions or variation in colony size between years (Robertson 1998).

Microsatellite markers are highly polymorphic and in general have greater probability of inclusion relative to less polymorphic molecular markers (i.e. protein banding) and non-molecular methods. It is most plausible that the higher rate of brood parasitism detected is not a change in brood parasitism across years, but instead a consequence of a more accurate method to identify parasites from biological offspring. This is further supported by the two of the three highest estimates of brood parasitism were found in studies using microsatellites (Chapter 1: Table 1, but see Tiedemann et al. 2011, Hario et al. 2012).

### *Rates of Conspecific Brood Parasitism and Extra-Pair Paternity*

The rate of brood parasitism was higher in 2017 (28.6%) when compared to 2016 (18.8%). Our overall estimate of 22.7% brood parasitism is higher than the 16–17% estimated by Tiedemann et al. (2011) and lower than the 34.2% rate of brood parasitism estimated by Hario et al. (2012) both using microsatellites to estimate brood parasitism in Common Eiders.

Factors that could cause different rates of brood parasitism between years for our study were dates of initiation and daily survival rate. However, we found similar dates of initiation between both years and the daily survival rate had similar trends relative to time within breeding season (see chapter three). This indicates there were no major temporal or nest failure based differences between years that would pressure Common Eiders to parasitize as a “best of a bad job” scenario (Lyon and Eadie 2008).

Another consideration is the age of the nesting females. Tiedemann et al. (2011) provided evidence, which suggests older females with a lower reproductive value are parasitized more often when compared to other age groups. From 2009-2015, we observed a high rate of nesting failure for the Mast River Common Eider Colony. If there was a substantial decrease in recruitment from these years of high nest failure, then we would anticipate a shift in the average age of nesting females to increase in years following. Although we lack information on the age of individuals within our Common Eider colonies, if we assume the ratio of older birds are increasing, we also should see an average increase in brood parasitism overtime supporting our finding.

Forced copulation occurs across in many waterfowl species. However, the success of these forced copulations are understudied in Common Eiders (Waltho and Coulson 2015). Here we provide estimates of low extra-pair paternity in Common Eiders in both years of our study. Male Common Eiders will aggressively pursue females on the breeding ground. These males are assumed to lack a pair-bond and will use forced copulation as a last attempt to reproduce (Waltho and Coulson 2015). However, we find that the success of late breeding forced copulations by males may be mostly unsuccessful or may not commonly occur within this colony.

### *Alternative Reproductive Tactics*

Of the 176 nest parasites we identified, 60 (34.1%) were identified to another female nesting within either the Mast or WaWao colonies supporting the idea of females enhancing their fecundity beyond their own nest (Lyon and Eadie 2008). American coots (*Fulica americana*) are also shown to engage in fecundity enhancement, but there are tradeoffs to the strategy (Lyon 1998). If the parasitizer lays eggs in conspecific's nest, she has in turn reduced her own clutch size making it available for parasitism. In Common Eiders, it is not understood if fecundity enhancement is truly the best reproductive option for females or if it the response of already being parasitized and adjusting the clutch to avoid a suboptimal size. Andersson (2017) suggests Common Eiders may benefit from parasitism even in the absence of relatedness if the parasitic act raises the clutch to a more optimal size. Further studies tracking the distribution of parasitic acts and their timing will allow us to understand if parasitism is in response to pure parasites followed by fecundity enhancers readjusting their clutch size or if fecundity enhancement truly represents females with the highest reproductive output.

Of the 294 potential nests to sample genetic material from, we obtained genotypes for 237 nests of them (80.6%, Table 2). It is plausible that the 57 nests not sampled could be biological mothers of the remaining 116 parasites not attributed to another female in the Mast or WaWao colonies. If we assume not all of 116 parasites are from other nesting females, this shows both pure parasites (non-nesting parasitizer) and fecundity enhancer (nesting parasitizer) strategies are present in Common Eiders.

In addition, we found female Common Eiders parasitizing nests over 4km from the location of their nests (Figure 4). It appears unlikely that females are seeking out nests to parasitize at such a great distance, but an alternative explanation for these scenarios are cases of nest takeover. Nest takeovers occur when a female begins nesting with a portion of her clutch laid before being removed from the nest by another female who then lays her own clutch (Waldeck and Andersson 2006). The result would still appear parasitic, but the initial incubating female now needs to seek out another nest site to lay the remainder of her clutch.

### *Management Implications*

The rate and utilization of brood parasitism is important to consider when estimating reproductive output of avian species. Clutch size is one estimate of success and an index of health for the population, but our findings demonstrate that 50% of nests will contain at least one parasitic egg. This drastically alters our understanding of what the true reproductive capabilities of nesting females are and supports others skepticism in using clutch size as an index of fecundity (Etterson et al. 2011). Additional studies will be necessary to understand what the true variation of clutch size is within a population along with the reproductive tactic of the nesting female.

### *Kin Grouping*

Our findings support the hypothesis that kin grouping is present in 2016, but not 2017 (Figure 5). This coincides with previous estimates of kin grouping observed in other colonies (McKinnon et al. 2006, Waldeck et al. 2007, Sonsthagen et al. 2010), but presence of kin grouping contradicts what other have observed for this specific colony (Andersson and Waldeck 2007, but see Robertson et al. 1995). This is interesting given other studies suggest strong nest site fidelity of Common Eiders (Franzman 1983, Bailie and Milne 1989, Swennen 1990).

When we observe the two-dimensional local autocorrelation of Common Eiders nesting, we observe cases of both positive and negative autocorrelation beyond what is expected. The location of positive and negative autocorrelation are not held constant over years, indicating females are less faithful to a specific breeding site and are possibly have greater preference to nest near kin (Figure 6). In addition, given there was an equal magnitude of negative local autocorrelation, it is hard to determine the true biological significance of the cases where positive local autocorrelation occurred (Table 4).

Andersson and Waldeck (2007) suggested the lack of kin grouping is due to Common Eiders prioritizing other attributes associated with nest site quality before considering nesting near kin. Other colonies of Common Eiders that rely on the amount of driftwood for nesting have a higher genetic clustering of nesting females on islands with greater nest site availability (Sonsthagen et al. 2010). The hypothesis that kin grouping will increase in response to increased number of nest sites is not supported here. We observed that high water levels at the onset of the breeding season reduced the number of islands available for nesting in 2016 (Rockwell personal observation), which had more support for the presence of kin grouping relative to the 2017 breeding season (Figure 5).

### *Host-Parasitizer Relatedness*

Host-parasitizer relatedness was within the range of average pairwise relatedness at the smallest spatial scale (0-10m), in 2016. This indicates that Common Eiders had no preference in who they were parasitizing. In contrast, a difference was observed between average pairwise relatedness of host-parasitizers when compared to the smallest spatial scale, in 2017 (Figure 5). This contradicts previous literature, which suggests parasitic acts occur between kin at a higher frequency than what would be expected under kin grouping (Andersson and Waldeck 2007, Waldeck et al. 2007). However, here we suggest that Common Eiders may switch preference of whom they parasitize annually given other potential stressors. For example, we mentioned 2016 experienced a flooding event where the number of available nest sites were unavailable during a part of the laying period. This environmental factor of limited nest sites could drive females to prioritize parasitism with no kin preference over kin preference in years where options for reproductive output is limited. Although full support for this hypothesis is lacking given the rate of parasitism in 2016 (18.8%) was lower than what was observed in 2017 (28.6%).

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**Figure 1.** Photograph of Common Eider (*Somateria Mollissima*) feather collected from nest bowl. Black box outlines the superior umbilicus where blood clots commonly form making them the target area for DNA isolation. Each grid cell is 1X1 inches for scale.

**Figure 2.** Photograph of Common Eider (*Somateria mollissima*) hatch membrane collected from nest post-hatch. This hatch membrane contains chorionic vessel, which are isolated for DNA extraction of embryonic DNA.

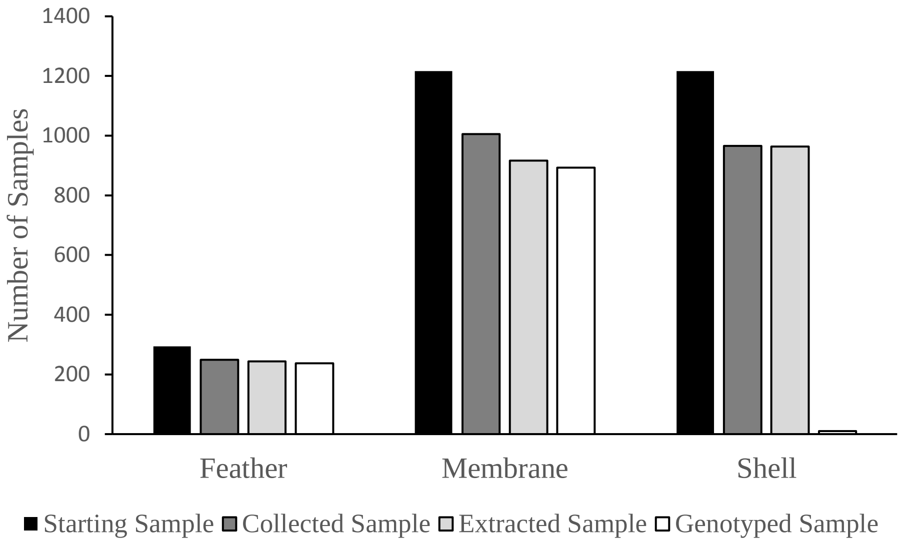

**Figure 3.** For both the Mast and WaWao Common Eider (*Somateria mollissima*) Colony (2016 & 2017), the total number of samples of feather, hatch membrane, and eggshell samples available relative to the total sample across all steps. The number of samples genotyped for eggshell samples was estimated from a preliminary run where no viable genotypes were obtained (see methods).

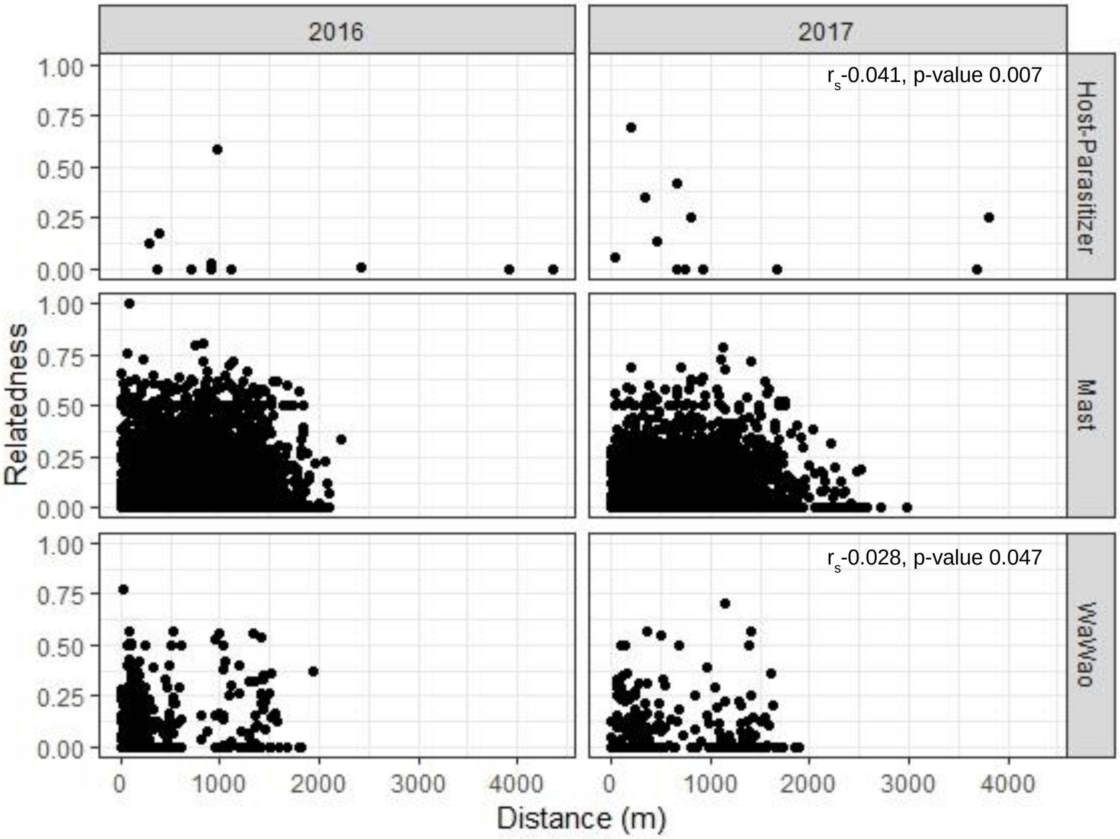

**Figure 4.** Pairwise relatedness and pairwise distance of Common Eiders (*Somateria mollissima*) by year, colony and host-parasitizer groupings. The relatedness coefficient ranges from unrelated (0) to identical (1). Significance ($p < 0.05$) is indicated by panels, which contain an $r_s$ and p-value.

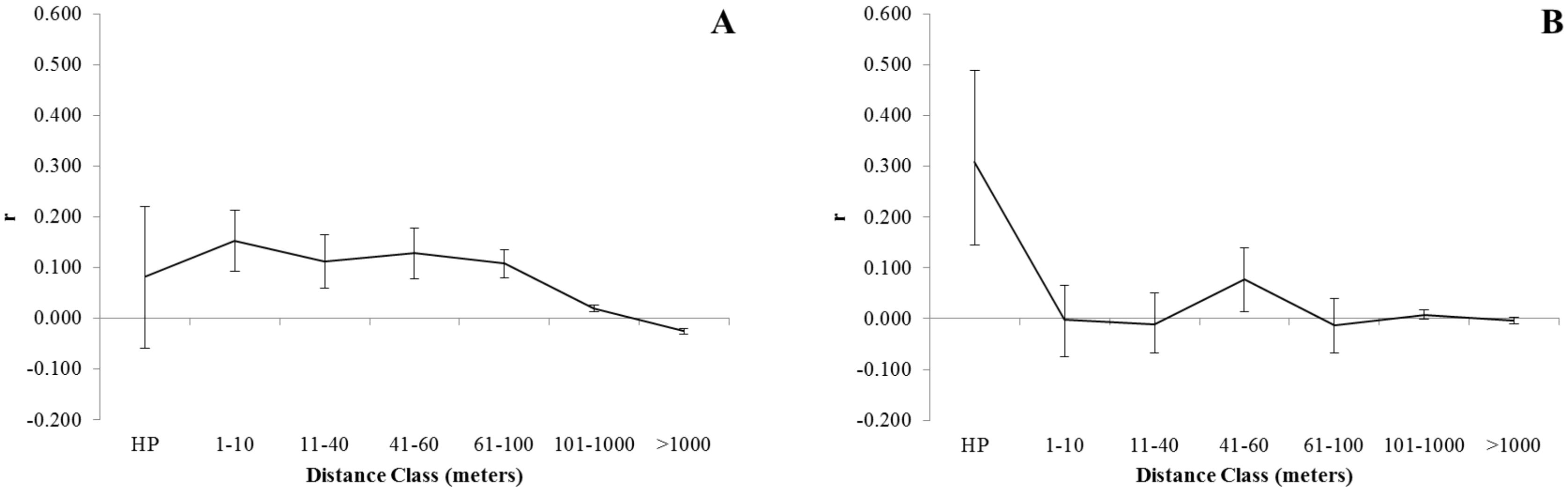

**Figure 5.** Average pairwise relatedness at different distance classes and host-parasitizer of Common Eiders (Somateria mollissima), in 2016 (A) and 2017 (B). Relatedness coefficient calculated in GenAlEx and pairwise distances are in meters. Mast and WaWao colonies were not separated for analysis because a subset of the sample contained females from one colony parasitizing females from another.

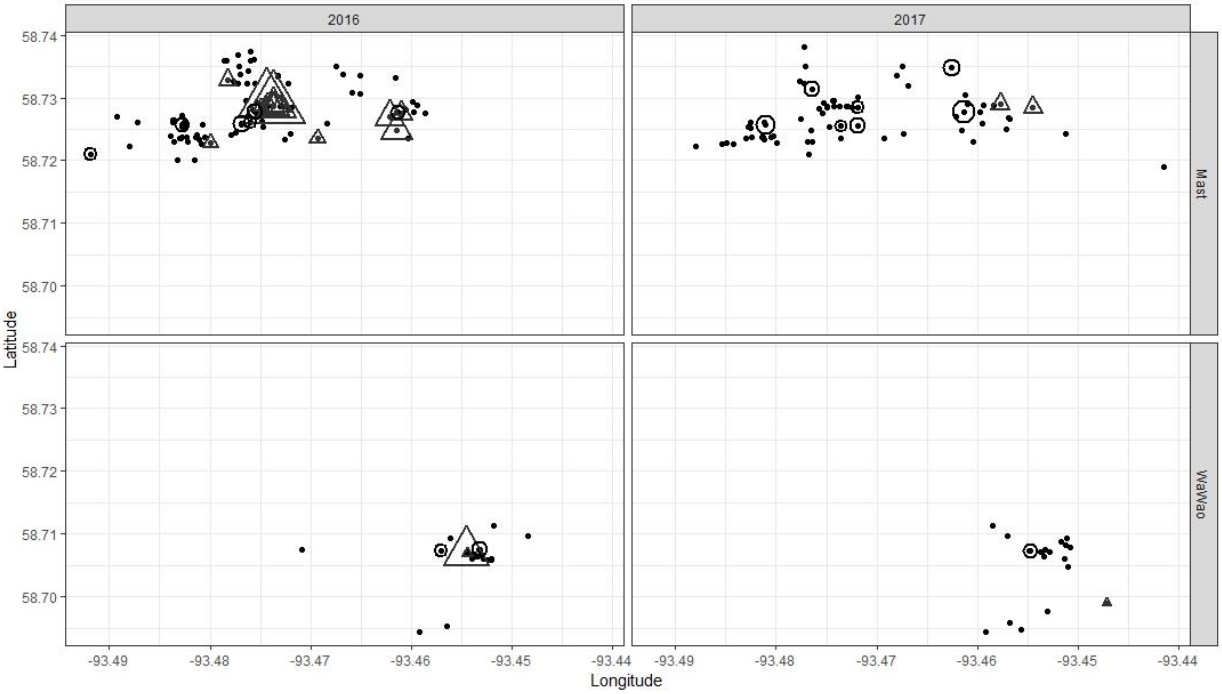

**Figure 6.** Two-dimensional local autocorrelation (lr) of Common Eiders (*Somateria mollissima*) of the Mast and WaWao Colonies in both 2016 and 2017. Small filled black dots represent each Common Eider nest. Circle (negative lr) and triangle (positive lr) size is proportional to the degree of local autocorrelation. We determined significance of positive and negative lr for values within the 5% tails of the permutated distribution, generated from a focal female and her four nearest neighbors.

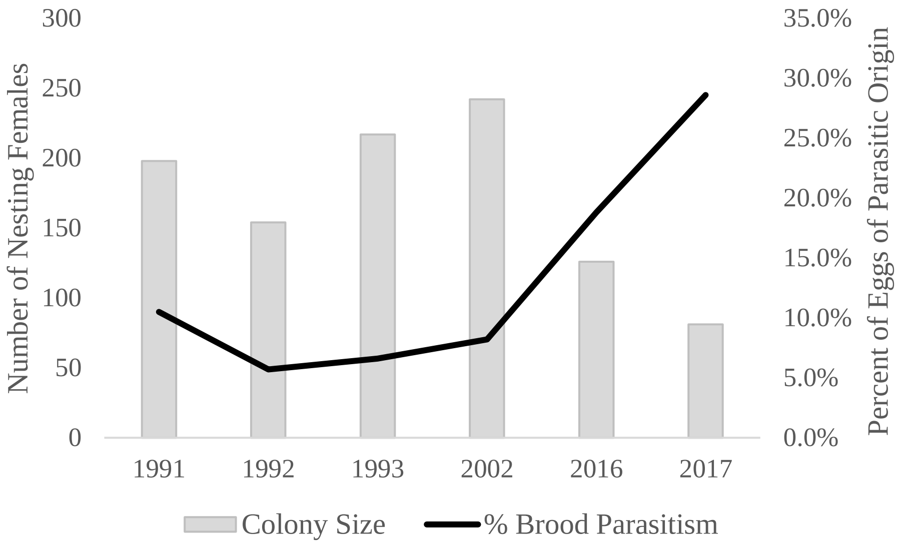

**Figure 7.** Mast River Common Eider (*Somateria mollissima*) Colony size and rate of conspecific brood parasitism by year. Conspecific brood parasitism estimated with laying sequence and morphometrics in 1991–1993, protein banding in 2002, and microsatellites in 2016-2017.

**Table 1.a.** Common Eider (*Somateria mollissima*) microsatellite loci summary table. Tandem repeat with accession number for further information and multiplex groups used for PCR.

| Name | Sequence | GenBank accession no. | Repeat sequence | Multiplex group |
|---|---|---|---|---|
| Sfi1F* | TCGTCGGCAGCGTCAGATGTGTATAAGAGACAGCACAAGGAAGCATGACCTCAGAA |  | [TA]10[CA]8 | 2 |
| R | GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAGCTCATGCCTCCTGTTAGTCATCT |  |  |  |
| Sfi3F | TCGTCGGCAGCGTCAGATGTGTATAAGAGACAGTATTCCAATATTCTGCAGGGAGG | U63682&U63683 | [GA]3N5[GA]6 | 2 |
| R | GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAGTCCAAGTTAATCAATTATCTGAT |  |  |  |
| Sfi9F | TCGTCGGCAGCGTCAGATGTGTATAAGAGACAGTTCCTTCCAACCCAAGACATTC | AF180499 | [CT]N | 4 |
| R | GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAGAAACTTCCAACCATTCTTCAAGG |  |  |  |
| Smo1F | TCGTCGGCAGCGTCAGATGTGTATAAGAGACAGCTTAAGGTATTGTGCTTTATA | AJ 427841 | [GA]17 | 1 |
| R | GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAGTGGTCCAAAGGGTGTTCTCAGAA |  |  |  |
| Smo4F* | TCGTCGGCAGCGTCAGATGTGTATAAGAGACAGACTTTCCACAGCCTCTTTCACAA |  | [AG]18A | 1 |
| R | GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAGGACAGTGTTTGTCAATGGAT |  |  |  |
| Smo6F | TCGTCGGCAGCGTCAGATGTGTATAAGAGACAGGGGGTGGGAAAGAAGCAGTTTAG | AJ 427846 | [TG]18T4 | 2 |
| R | GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAGTCCTGGGACTTTGAAAGTGGCTC |  |  |  |
| Smo7F | TCGTCGGCAGCGTCAGATGTGTATAAGAGACAGTTTTCACCCAGTTCACTTCAGCC | AJ 427847 | [GT]12 | 1 |
| R | GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAGGATTCAAATTTGCCGCAGGATTA |  |  |  |
| Smo8F | TCGTCGGCAGCGTCAGATGTGTATAAGAGACAGTGCCTTATAGGATGTCACTCTTC | AJ 427848 | [TG]11 | 4 |
| R | GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAGAAAATACTATGCTCGTTTCAAAA |  |  |  |
| Smo9F | TCGTCGGCAGCGTCAGATGTGTATAAGAGACAGTTTGGAGTTTGGAGTTCGTGGGG | AJ 427849 | [TG]11[TTTG]2 | 3 |
| R | GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAGATTTCCCTGCAAAACTTACGGCA |  |  |  |
| Smo10F | TCGTCGGCAGCGTCAGATGTGTATAAGAGACAGTCCTAGCGACAGCAATTCTAATG | AJ 427850 | [TG]31 | 4 |
| R | GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAGCATTGTTCATTGTTTCTTCTTCA |  |  |  |
| Smo12F* | TCGTCGGCAGCGTCAGATGTGTATAAGAGACAGCCTGGTGGGATAGGTTTAAAATG |  | [TG]9T11 | 3 |
| R | GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAGTGTTCATCAAAAGCAGAGAGG |  |  |  |

*****Redesigned primers

**Table 1.b.** Common Eider (*Somateria mollissima*) microsatellite loci summary table.

| Name | No.Genotyped | No. of alleles | Allele size | Same Length Alleles | $H_e$ | $H_o$ | F | PI | $Pi_{sibs}$ | PE |
|---|---|---|---|---|---|---|---|---|---|---|
| Sfi1F* R | 960 | 25 | 95-128 | 16 | 0.482 | 0.158 | 0.671 | 3.0E-01 | 5.8E-01 | 1.3E-01 |
| Sfi3F R | 1128 | 18 | 114-131 | 10 | 0.490 | 0.453 | 0.075 | 3.0E-01 | 5.8E-01 | 1.3E-01 |
| Sfi9F R | 1127 | 12 | 122-140 | 6 | 0.737 | 0.732 | 0.007 | 1.1E-01 | 4.1E-01 | 3.3E-01 |
| Smo1F R | 1058 | 8 | 116-142 | 4 | 0.696 | 0.227 | 0.674 | 1.5E-01 | 4.4E-01 | 2.7E-01 |
| Smo4F* R | 796 | 47 | 135-199 | 25 | 0.905 | 0.472 | 0.478 | 1.6E-02 | 3.0E-01 | 6.8E-01 |
| Smo6F R | 1130 | 14 | 104-130 | 3 | 0.710 | 0.751 | -0.057 | 1.2E-01 | 4.3E-01 | 3.1E-01 |
| Smo7F R | 1147 | 15 | 179-195 | 11 | 0.599 | 0.574 | 0.042 | 2.0E-01 | 5.0E-01 | 2.0E-01 |
| Smo8F R | 1143 | 12 | 92-108 | 7 | 0.680 | 0.669 | 0.016 | 1.5E-01 | 4.5E-01 | 2.8E-01 |
| Smo9F R | 1058 | 10 | 132-158 | 3 | 0.513 | 0.488 | 0.048 | 3.3E-01 | 5.8E-01 | 1.3E-01 |
| Smo12F* R | 1127 | 19 | 75-101 | 10 | 0.669 | 0.669 | 0.000 | 1.5E-01 | 4.5E-01 | 2.6E-01 |

*No. Genotyped*: Number of genotypes generated in total per locus
*No. Alleles*: Allelic richness per locus, the range of allele sizes
*Same length alleles*: detected through HTS (undetected using traditional fragment analysis by capillary electrophoresis)
($H_e$) Expected heterozygosity
($H_o$) Observed heterozygosity
*F* (fixation index): Ranges from -1 to 1 where highly positive values indicate inbreeding or undetected null alles, values close to zero indicate typical heterozygosity in a randomly mating system, highly negative values indicate an overrepresentation of heterzygous individuals under the assumption of random mating in the system.
*PI* (Probability of Inclusion): Estimate of the average probability that two independent samples will have the same identical genotype.
$PI_{sibs}$: Same as PI, but corrected for closely related sample populations.
*PE* (Probability of Exclusion): estimate of the probability of exclusion for one putative parent when the genotype of the other parent's genotype is known.

**Table 2.** Total samples collected for both the Mast and WaWao Common Eider (*Somateria mollissima*) Colonies for each tissue type (2016 & 2017 combined). See methods for detailed description of each sampling step.

| **Tissue Type** | **Starting Sample** | **Collected Sample** | **Extracted Sample** | **Genotyped Sample** |
|---|---|---|---|---|
| Feather | 293 | 249 | 244 | 237 |
| Membrane | 1216 | 1005 | 916 | 893 |
| Eggshell | 1216 | 966 | 964 | 0 |

**Table 3.** Outputs of Spearman's rank correlation test for pairwise relatedness and pairwise distance in Common Eider (*Somateria mollissima*) for 2016 and 2017 in the Mast and WaWao Colonies including Host-Parasitizer groups.

| **Pairwise Group** | **Year** | **p-value** | **$r_s$** |
|---|---|---|---|
| All | Both | 0.164 | -0.012 |
| Mast | Both | 0.064 | -0.020 |
| WaWao | Both | 0.653 | -0.017 |
| Mast & WaWao | Both | 0.703 | -0.005 |
| All | 2016 | 0.158 | -0.012 |
| Mast | 2016 | 0.120 | -0.014 |
| WaWao | 2016 | 0.477 | -0.007 |
| Mast & WaWao | 2016 | 0.680 | 0.004 |
| All | 2017 | 0.139 | -0.012 |
| Mast | 2017 | 0.130 | -0.015 |
| WaWao | 2017 | 0.047 | -0.028 |
| Mast & WaWao | 2017 | 0.002 | -0.035 |
| Host-Parasitizer | Both | 0.029 | -0.412 |
| Host-Parasitizer | 2016 | 0.735 | -0.003 |
| Host-Parasitizer | 2017 | 0.007 | -0.041 |

**Table 4.** Fine scale genetic structure of Common Eiders (*Somateria mollissima*) in the Mast and WaWao Colonies for both 2016 and 2017. Positive and negative local autocorrelation (lr) and their proportions within the colony are presented with the range of distances (meters) and the median distance, in parentheses. See methods for further detail on local autocorrelation.

| | **2016** | **2017** |
|---|---|---|
| Mast | | |
| Positive lr | 0.157-0.366<br>13% (n=14/108) | 0.186-0.187<br>3% (n=2/74) |
| Distance (m) | 75-617<br>(75) | 73-435<br>(285) |
| Negative lr | -0.181 to -0.203<br>6% (n=6/108) | -0.170 to -0.248<br>9% (n=7/74) |
| Distance (m) | 8-937<br>(105) | 43-584<br>(188) |
| WaWao | | |
| Positive lr | 0.120-0.305<br>6% (n=2/33) | 0.113<br>5% (n=1/21) |
| Distance (m) | 2-30<br>(13) | 680-1057<br>(850) |
| Negative lr | -0.178 to -0.201<br>6% (n=2/33) | -0.190<br>5% (n=1/21) |
| Distance (m) | 1-287<br>(6) | 2-122<br>(60) |

# CHAPTER 3

# IMPLICATIONS OF WEATHER AND PHENOLOGY TO BREEDING SUCCESS OF COMMON EIDERS

## Abstract

The timing of bird species nesting annually are constrained by multiple factors, including variable weather patterns at the onset of the breeding season. It has been well documented that timing of nest initiation can affect breeding success, in birds. However, making the connection between spring condition's effect on timing of breeding and timing of breeding effect on nest success receives less attention. Common Eiders have a declining population at a circumpolar scale and understanding drivers of reproductive success are of upmost importance. Our objective was to identify weather related factors that affect timing of nest initiation in Common Eiders (*Somateria mollissima*). In addition, we examined the effects spatial and temporal variables have on daily survival rate, one of which was date of nest initiation. We found Common Eiders date of nest initiation was correlated with the last day of snowmelt. However, date of nest initiation was not a predictor of daily survival rate in Common Eiders. Instead, day within breeding season and the days into incubation of the nest were included in the top model as predictors of daily survival rate. These results suggest that spring snowmelt conditions influence the timing of breeding and Common Eiders become more synchronized in date of initiation in late nesting years. However, date of initiation did not appear in our top model as a predictor of daily survival rate. We found, it could be more beneficial to nest

later in the season versus earlier. However, the caveat of only using DSR as an index of success was we have no estimate of post-hatch success indices (brood survival or recruitment), which may be impacted by timing differently.

## Introduction

Interest in species' ability to match their reproduction with foraging opportunities, for themselves and offspring, in the face of climate change, is increasing. With climate change, temperatures are predicted to not only increase, but also become more variable (Hansen et al. 2012). This is concerning relative to biological systems, which 1) may lack the ability to adapt in a relatively short period of time or 2) lack the phenotypic plasticity to overcome biological constraints related to increasing and variable climate (Merilä and Hendry 2014). The inability to match timing of reproduction to resources is also known as the mismatch hypothesis and is seen in both invertebrates and vertebrates (See Dunn et al. 2011).

In avian species specifically, there is some ambiguity over the significance of the mismatch hypothesis (Dunn et al. 2011). Avian species have many factors that will disrupt their ability to match the timing of reproduction (date of egg laying) to ensure their hatch date coincides with the date of maximum resource availability. For example, avian species that migrate, must time their reproduction based on arrival to their breeding grounds (Both and Visser 2001), which is affected by variable spring conditions (Lehikoinen et al. 2006). Although avian species that migrate have the ability to adjust their arrival date between years of variable climate (Clermont et al. 2017), there is evidence that some avian species lack this flexibility (Møller et al. 2008).

The inability to adjust date of arrival to breeding grounds for avian species is concerning due to the direct consequences on reproductive success when nest initiation occurs earlier versus later in the breeding season (Dzus and Clark 1998, Guyn and Clark 1999). Although initiating early is found to be advantageous in most scenarios (Dzus and Clark 1998, Guyn and Clark 1999, but see Emery et al. 2005, Drever and Clark 2006), avian species are still limited by spring conditions potentially altering individuals' opportunity to nest at optimal times. To understand the relationship between spring conditions, date of initiation, and reproductive success, we studied the phenology of a long-lived sea duck species the Common Eider (*Somateria mollissima*), from 2009-2017.

To explore the relationship between weather and phenology of Common Eiders, we had three objectives. 1) Explore the relationship between a suite of weather variables to and timing of Common Eider's nest initiation. 2) Determine if there are consequences relative to daily survival rate when initiating early vs late in the breeding season. 3) Identify other predictors of daily survival rate in addition to date of initiation that may drive reproductive success in the species.

## Methods

### *Study area*

We studied Common Eiders at the Mast River Common Eider Colony (N 58.725388º, W -93.464288º), in Wapusk National Park located approximately 40km east of Churchill, MB. We searched for nests where the Mast River enters into La Pérouse Bay. This braided river delta includes numerous small islands ranging from 1 to 300 $m^2$. Islands utilized by Common Eiders have a mixture of birch (*Betula glandulosa*) and willow (*Salix* spp.) with vegetation height ranging from 0.6 to 2 m (For detailed study site description see Schmutz et al. 1982).

### *Sampling Design*

From 2009–2017, nest searches began during the first week of June. Each year we aimed to sample the colony in its entirety, but recognize some nests were not be detected or were outside the historic nesting area. When a nest was found, we recorded GPS coordinates, distance from the water's edge to nest, and age by candling each egg (Weller 1956). We estimated day of initiation and the date of hatch for the nest based on age and clutch size (here we assume 4 days to lay and 24 days to incubate (Iles et al. 2013)). We rechecked nests in 7-10 day intervals until it either hatched or failed determined by sign at the nest. Nests with one or more hatched eggs (presence of hatchlings or hatch membranes) were considered successful, while nests with a destroyed clutch or absence of eggs/ hatch membranes were defined as failed nests.

### *Snowmelt Model*

Many measures of weather/climate variables can be used as indices of spring conditions, which we hypothesize to be related to date of initiation in Common Eiders. With the assumption that Common Eiders cannot begin nesting until after snowmelt has ended (e.g. Lepage et al. 1996), we calculated the projected last day of snowmelt for each spring for 2009-2017. We calculated the total snow accumulation, the accumulated spring degree-days of warming (>0°C), and a combination of the two weather measures to estimate time of snowmelt for each year, within our study. To calculate weather measures each year, we obtained weather data from the Canadian Government (climate.gc.ca) for the Churchill Airport weather station, which was the closest in proximity to our study site (approximately 35km west of the colony). To calculate the total snow accumulated (mm) each spring, we summed the days with a precipitation event and a maximum temperature below freezing each winter. For accumulated spring degree-days of warming, we summed the degree days > 0°C from 1 January – 1 June each year. The total degree-days of warming each spring reflects the rate and timing of when warming occurs annually.

We calculated snowmelt using the equation (Rosa 1956):

$$M=C_M(T_a-T_b)$$

where M is snowmelt (mm/day), $C_M$ is the degree-day coefficient representing the amount of snow (mm) melted per degree day, $T_a$ is the maximum daily air temperature (°C), and $T_b$ is the base temperature of 0 °C. National Resources Conservation Service (2004) suggests using 2.74 for $C_M$ when little information about snow conditions are available, which was the case for our study. Once we determined the snowmelt for each day, the accumulation of this snowmelt was summed for each year. We classified projected last day of snowmelt for each year when the snowmelt accumulation surpassed the snow accumulation (Figure 1). This intersection represents the day where enough degree-days above freezing were achieved to melt the accumulated snow.

### *Statistical Analysis*

We conducted a Pearson's correlation test to determine if a significant correlation occurred among our weather metrics of total snow accumulation, accumulation of spring degree-days of warming, and the projected last day of snowmelt in relation to initiation date in Common Eiders. Both mean initiation date and first initiation date for each year were included, as well as the variance between initiation dates.

We calculated daily survival rate (DSR) and overall nest success for our breeding populations with Program Mark (Dinsmore et al. 2002, White and Burnham 1999). Here we define DSR as 1-(total number of failed nests/the total number of exposure days) or the probability of surviving a one-day interval. Nest success is defined as the probability of at least one egg surviving from initiation to hatch, which is the estimate of DSR to the power of 28, assuming a four-day laying period plus 24 days of incubation.

We generated five biological hypotheses to incorporate into our 13 candidate models to explain how DSR will vary relative to our covariates. 1) Constant DSR (Null): As our null model we allowed DSR to remain constant across the breeding season. 2) Year: Year was included as a grouping variable in our model to accommodate for environmental stochasticity from one year to the next that may affect DSR. 3) Spatial Characteristics: Covariates such as, nest's distance to nearest neighbor, nest's distance to water, and surrounding nest density are all predicted to make each nest more or less detectable to predators and as a result increase or decrease DSR. 4) Temporal Characteristics: Covariates such as the age of the nest, the day within the breeding season, and date of initiation are all associated with timing. However, nest age and day within breeding season allow DSR to vary across time rather than remaining constant. In addition, we hypothesized that initiation date was determined by variation in seasonal weather patterns, and we wanted to understand if date of initiation was solely a predictor of DSR. For day within breeding season, we also allowed a year specific trend to identify if the trend in DSR throughout the breeding season varied from one year to the next. 5) Global Model: We included Year, spatial, and temporal covariates to set a baseline for other models. We applied quadratic terms to all covariates after exploration of data found all trends to be nonlinear relative to DSR.

To test for goodness-of fit for our models, we first calculated each model's proportional reduction in deviance relative to the null model (Zheng 2000), or the deviance reduction measure. To do this, we calculated the ratio of deviance reduction "R", which is the deviance reduction measure of the model of interest divided by the deviance reduction measure of the fully saturated model. Our fully saturated model consisted of year specific trends for all covariates (117 parameters). R is not a true goodness-of-fit test, but allows us to measure each model's fit the data relative to the fully saturated model (see Iles et al. 2013 for detailed description).

We used Akaike's Information Criterion (AIC, Akaike 1973) with a correction for small sample size to determine which model had the highest support ($AIC_C$, Burnham and Anderson 2002). For our top models, we explored parameter estimates over a range of values to determine their impacts on DSR.

To understand what influences DSR across the breeding season, we also wanted to calculate the time and rate of nest failure. To accomplish this, we determined the availability of nests to be a function of when nests became available (day of nest initiation) and the day nests are absent either from nest success or failure. For measuring trends in the timing and rate of failure, we calculated the day of failure using the Mayfield estimator by finding the halfway interval between the day the nest was last checked with eggs present and the day the nest was fated (Mayfield 1961).

For each year, we compared the day within the breeding season where maximum nests (prey) were available to the day within the breeding season that the highest rate of failure (consumption rate by predators) occurred. We also included a one to one trend line representing a scenario where the day of highest consumption rate was matched to the day of maximum prey availability. If a year is above the one to one line then the day maximum consumption rate is occurring after the day of maximum prey availability, while if a year is below, then the day of maximum consumption rate is occurring before the day of maximum prey availability.

## Results

We located 1,735 nests over the 9 years.  The proportion of nest failure was highly variable from year to year (mean= 70%) ranging from 99% to 15%. Of the failed nests, only 1% were due to abandonment (n=17), while the remaining 99% were caused by predators (n=1,230). Length and timing of the overall breeding season also varied annually (Table 1). Year 2010 and 2015 shared the earliest date of initiation over our study (May 30), while 2009 had the latest date of initiation (June 20).

### *Snowmelt Model and Nest Initiation*

The projected last day of snowmelt was correlated (Mean Date: $R^2$=0.758, p-value=0.002. Date of First: $R^2$=0.874, p-value=<0.001) with the first and mean date of initiation for years 2009-2017 (Figure 2). In addition, the variance of initiation date was higher in years where the projected last day of snowmelt occurred earlier ($R^2$=0.461, p-value=0.044).  Lower variance was observed in years where the projected last day of snowmelt occurred later (Figure 2). Both snow accumulation and degree-days of warming were not correlated to the projected last day of snowmelt (Figures 3 & 4).

*Daily Survival Rate*

The DSR of Common Eiders for years 2009-2017 was a function of year, nest age, and the day within the breeding season (Table 2). Quadratic terms received higher support overall for nest age and day within the breeding season. Year alone improved the model substantially compared to the null model (decrease of 749.172 $AIC_c$). The addition of nest age and day within breeding season (allowing for a year specific trend) was the most supported model (Table 2). While DSR had a year specific trend in relation to day within breeding season, we observed that as nest age increased so did DSR (Figure 5). All spatial characteristics were less supported regardless of a year specific intercept.

*Timing and Rate of Nest Success/ Failure*

The parameter of initiation date did not show high support in our model and there is evidence that early and late nesting are more advantageous, dependent on year (Table 3). Estimated nest success varied across year and was highly variable when the 28-day period of incubation occurred during the early, mid, or last portion of the breeding season (Table 3).

To explore why estimated nest success is higher early in the breeding season for some but not all years, we visualized nest availability and rate of failure across the breeding season. Nest availability varied by year as well as the rate and timing of failure (Figure 6). The day of maximum prey availability consistently arrived earlier than the day of maximum consumption rate with the exception of 2016 (Figure 7).

## Discussion

We found that the date of nest initiation in Common Eiders was correlated to the projected last day of snowmelt. The projected last day of snowmelt was a combination of snow accumulation and degree-days of warming, but neither total snow accumulation or accumulated degree-days of warming alone were correlated to date of initiation, in Common Eiders. This provides evidence that snow and temperature related data alone do a poor job of determining date of initiation, in Common Eiders, but when used to inform snowmelt models, are quite accurate.

The variance of initiation date each year was also correlated to projected last day of snowmelt. This would support the idea that in years where snow melts earlier, Common Eiders have more flexibility when they initiate their nests and possibly spend more time obtaining food resources to support themselves through the incubation period when they are thought to fast (Öst and Kilpi 1999, but see Jaatinen et al. 2016). In contrast, years where snow does not melt until late in the season results in a synchronized date of initiation, within the colony, indicating there is substantial pressure on Common Eiders to nest as soon as snow is absent. In addition, the synchrony of nest initiation is absent in early nesting years suggesting that Common Eiders are not attempting to synchronize their initiation with other nesting females. It is suggested that late breeding birds will put their ducklings at higher risk through harsh fall storm exposure and increased predation (Love and Gilchrist 2010) supporting our finding of females attempting to nest as soon as nest sites become available in years where snow is late to melt. However, it was also shown that very early nesters might not maximize their duckling recruitment by having a hatch date before sea ice has left the bay (Lepage et al.

2000). In early nesting years, we observed females nesting across a wider range of time, which supports the idea that females could be aligning their hatch date with optimal foraging opportunities for their young.

Although the projected date of last snowmelt was accurate at predicting the date of initiation, each year the difference in date of the projected last snowmelt and date of first or mean initiation did not match one another. This could be due to varying snow conditions where snowpack is denser than what was predicted using the standard snowmelt coefficient ($C_M$). In addition, Common Eiders in this colony were found nesting within shrub-like vegetation, which is taller relative to surrounding vegetation (salt and freshwater marshes). The taller and denser vegetation could hold snow more efficiently than the surrounding area and lead to prolonged unavailability of nest sites. Although the snowmelt model did well to predict the date of initiation, in Common Eiders, there are additional variables such as snow condition, snow depth at specific locations, and albedo that could be incorporated in the future to increase overall prediction accuracy. In addition, the Mast River experiences wide fluctuations in water levels during spring melt, which will also delay nesting in years of extreme flooding. Other non-abiotic factors such as the physiology of the Common Eider must also be considered. Common Eiders are primarily capital breeders (Jaatinen et al. 2016). Therefore, females arriving to the breeding grounds in different body conditions will have different strategies related to the timing of initiation (Hennin et al. 2019).

Year, nest age, and day within breeding season were all included in the top model for DSR, in Common Eiders. Initiation date was not found in the top model for DSR and suggests that although it is correlated to annual weather patterns it is not a predictor of

DSR, in Common Eiders. This becomes more apparent when calculating nest success for an early, mid, and late-season nesting female for each year of the study based on the estimated DSR values (Table 3).

It is suggested that the best strategy of waterfowl species is to begin initiation of their nest to match offspring's hatch date with resources as they become available (Dzus and Clark 1998, Love and Gilchrist 2010). However, when only using DSR as index of success here we find there are certain years where it could be more beneficial to nest later in the season versus earlier. The caveat of only using DSR as an index of success is we have no estimate of post-hatch success indices (brood survival or recruitment), which could be impacted differently depending on when hatch date occurs (Etterson et al. 2010, Spear and Nur 1994). Further, considerations such as, sea ice conditions (post-hatch foraging) and timing of predators, may better predict overall (post-hatch or nest) success. Studies using estimates of nest success have found similar conclusions to this study (Emery et al. 2005, Drever and Clark 2006), while others using brood survival and recruitment as their index of success contrast this finding by stating an earlier initiation date will result in higher success (Dzus and Clark 1998, Guyn and Clark 1999). This reaffirms the importance of understanding the limitations in one index of reproductive success over another and should be interpreted with caution (Etterson et al. 2010).

Because day within breeding season was allowed to have a year specific trend, years 2017, 2016, and 2014 had a high DSR at the beginning of the season, and DSR decreased towards the end of the season. In contrast, all other years observed a different trend where DSR "dipped" at some point during the breeding season. The severity of this "dipping" in DSR varied from one year to the next and in how many days it spanned. In addition to the varying trends in DSR relative to day within breeding season, we found that DSR increased as the nest was farther into incubation. However, the overall biological significance in the change of DSR relative to nest age appear negligible. There could be behavioral changes such as decreased number of recess events later in incubation, in nesting females that are causing DSR to increase later in incubation. However, this was unlikely given females typically increase the number of recess events late in incubation when their body fat reserves are depleted (Wiebe and Martins 1997). Most likely, it is an artifact of predator arrival and the rate they consume nests.

We suggested a biological connection between temporal factors (day within breeding season and nest age) and DSR by identifying the days nests were available and at what point during the season failures occurred (Figure 6). Assuming nest failures are the result of nest predation (excluding abandoned nests); it becomes apparent that the timing and rate of predation vary across years. The rate of predation, in most years, increases rapidly across a 3–4 day interval, which usually comes after the day of maximum prey availability (Figure 7). The timing of maximum prey consumption always occurred after the day of maximum prey availability and could be the result of imperfect detection in day of failure used by the Mayfield estimator. Imperfect failure date detection is the result of many nests checked on the same day and biasing multiple nests to have an estimated fail date of the same day. However, with the exception of our lowest nest failure year (2016), a biological explanation for this trend could be in most years when predation is relatively high, predators time their foraging pressure to align directly on the day of maximum nest availability or shortly after. In years with low failure such as

2016, nest predators could be switching prey away from Common Eiders and matching foraging pressure with alternative prey (Iles et al. 2013).

Future studies should seek to understand how predator communities are also impacted by annual weather patterns and if they are not impacted in a similar fashion to colonial nesting waterfowl, what affect will this have on the overall success of waterfowl nesting? Having multiple predator species arriving asynchronously to one another in one year, but potentially having multiple predator species overlapping in others may increase the overall nest predation pressure within a colony.

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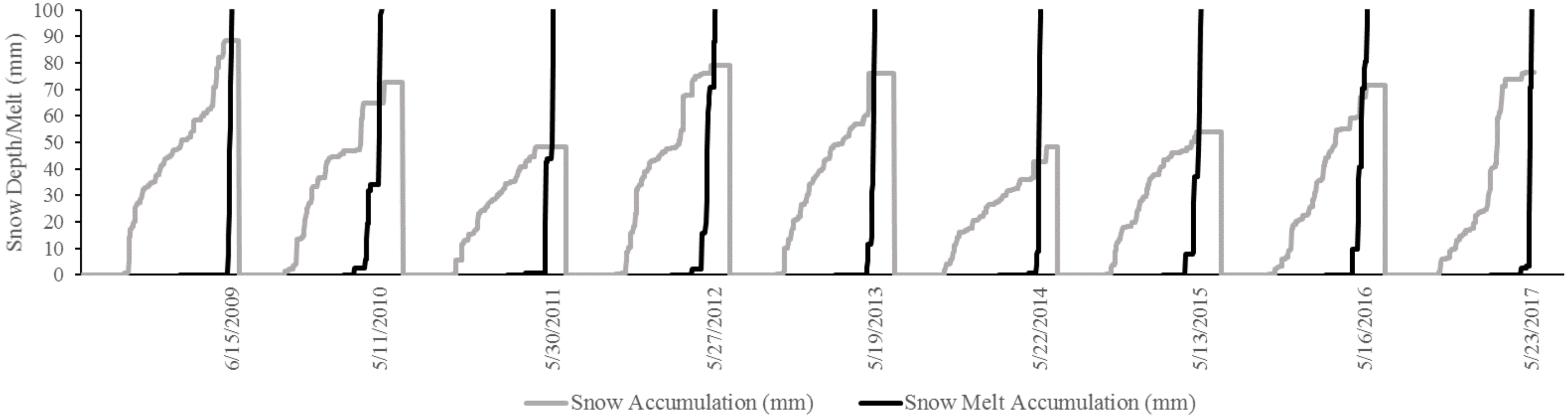

**Figure 1.** Visual representation of the intersection in snow accumulation (gray line) and snow melt (black line) of the Mast River Common Eider (*Somateria mollissima*) Colony Region. Snow accumulation is the sum total of days with a maximum daily temperature below freezing and with a precipitation even (mm). For snowmelt accumulation, refer to the subsection Snowmelt model under methods.

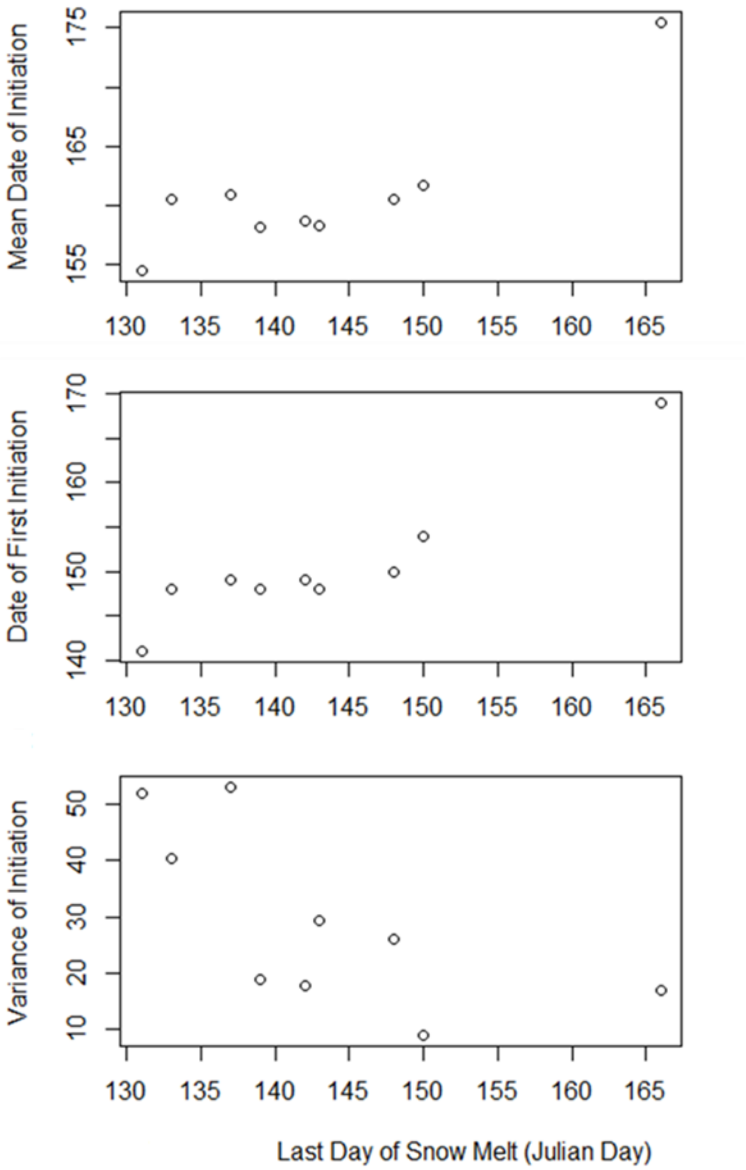

**Figure 2**. Correlation between measures of initiation date in Common Eiders (*Somateria mollissima*) and the projected last day of snowmelt. Mean date of Common Eider initiation date (top), first date of initiation (middle), and variance in date of initiation (bottom) for 2009-2017 relative to the last day of snowmelt (Pearson's correlation test: Mean Date: $R^2=0.758$, $t=4.679$, p-value=0.002. Date of First: $R^2=0.874$, $t=6.976$, p-value=<0.001. Variance of Initiation: $R^2=0.461$, $t=-2.447$, p-value=0.044).

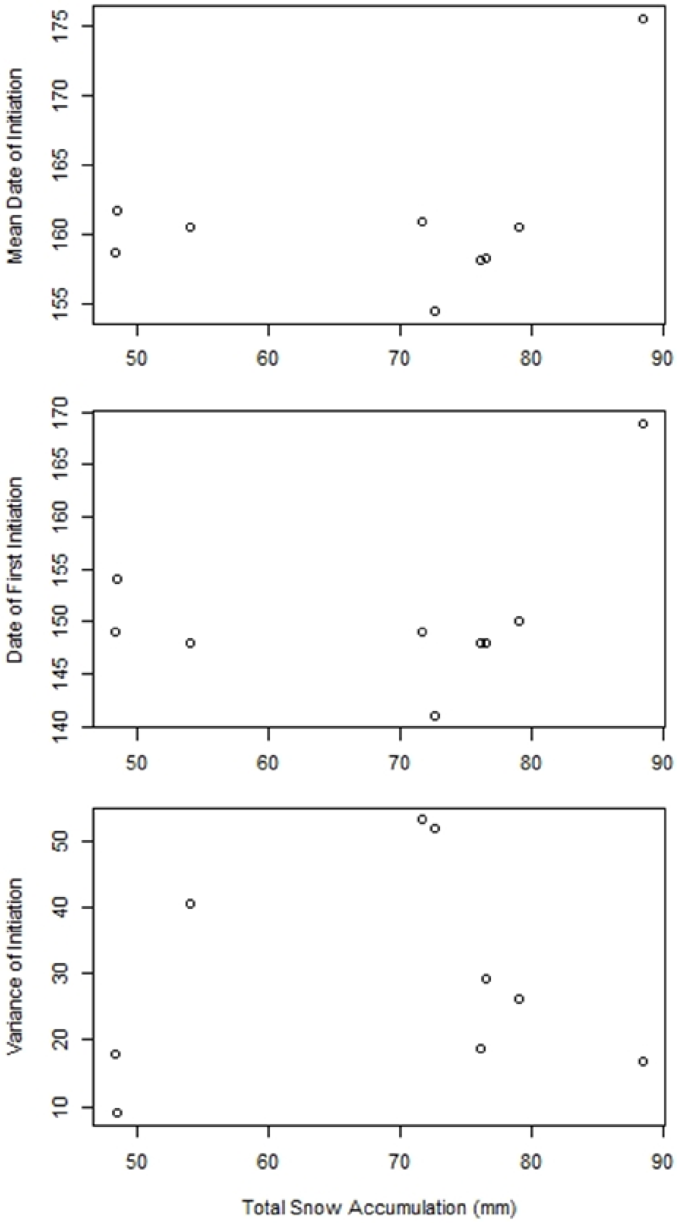

**Figure 3**. Correlation between measures of initiation date in Common Eiders (*Somateria mollissima*) and the total snow accumulation for 2009-2017. Mean date of Common Eider initiation date (top), first date of initiation (middle), and variance in date of initiation (bottom) for 2009-2017 relative to the total snow accumulation (Pearson's correlation test: Mean Date: $R^2$=0.139, t=1.061, p-value=0.324. Date of First: $R^2$=0.098, t=0.872, p-value=0.412. Variance of Initiation: $R^2$=0.024, t=0.416, p-value=0.690).

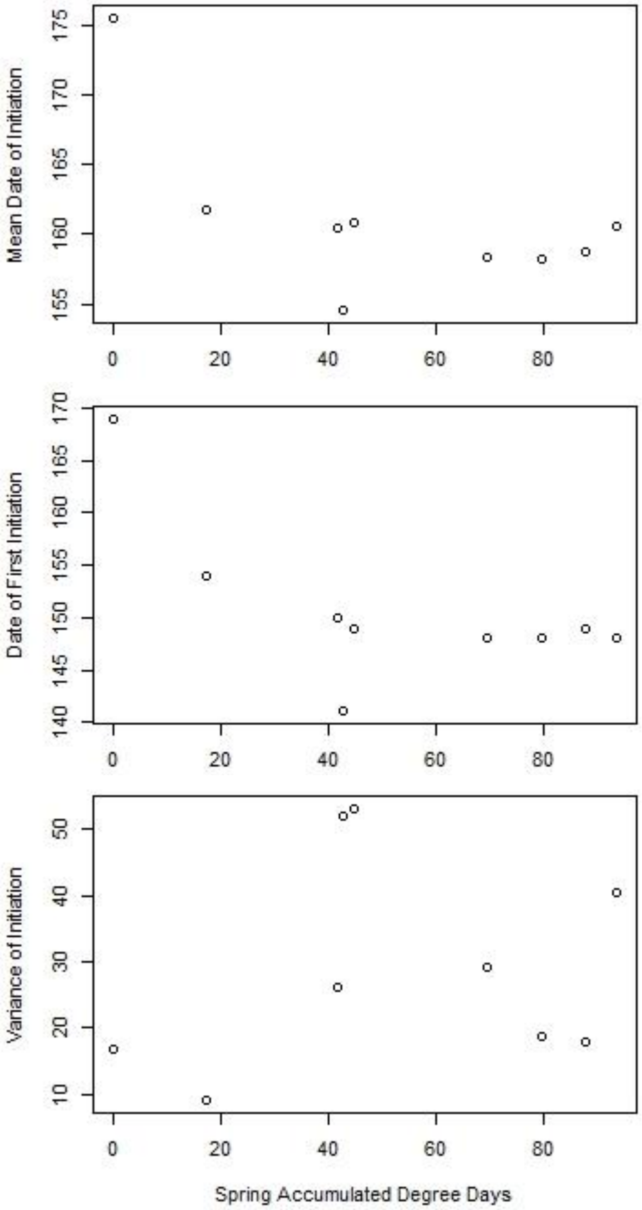

**Figure 4**. Correlation between measures of initiation date in Common Eiders (*Somateria mollissima*) and the accumulated degree days (above 0°C) each Spring. Mean date of Common Eider initiation date (top), first date of initiation (middle), and variance in date of initiation (bottom) for 2009-2017 relative to the accumulated degree days each spring (Pearson's correlation test: Mean Date: $R^2$=0.387, t=-2.103, p-value=0.074. Date of First: $R^2$=0.405, t=-2.183, p-value=0.065. Variance of Initiation: $R^2$=0.034, t=0.499, p-value=0.633).

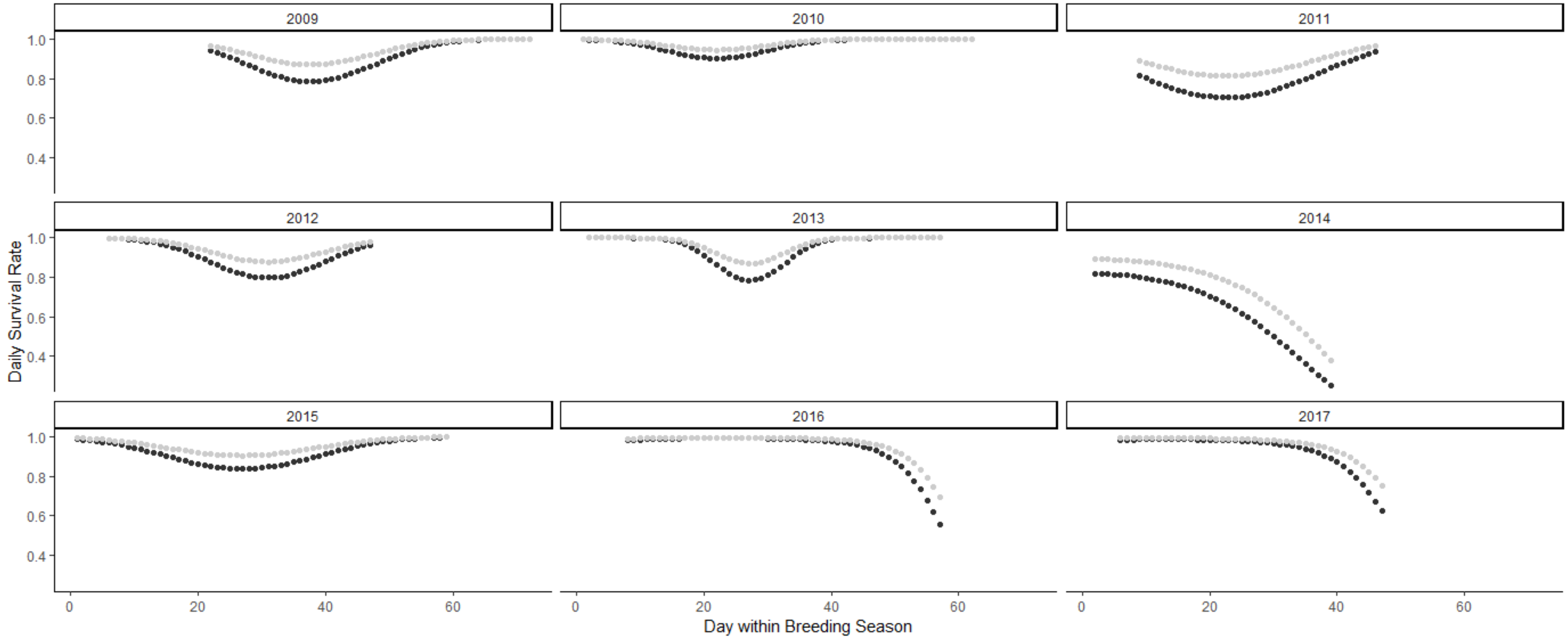

**Figure 5.** Daily survival rate of Common Eiders (*Somateria mollissima*) across the breeding season (Day 1=May 30, Day 60= July 29), as a function of year, day within breeding season, and nest age (black dot = nest age 1, grey dot = nest age 15).

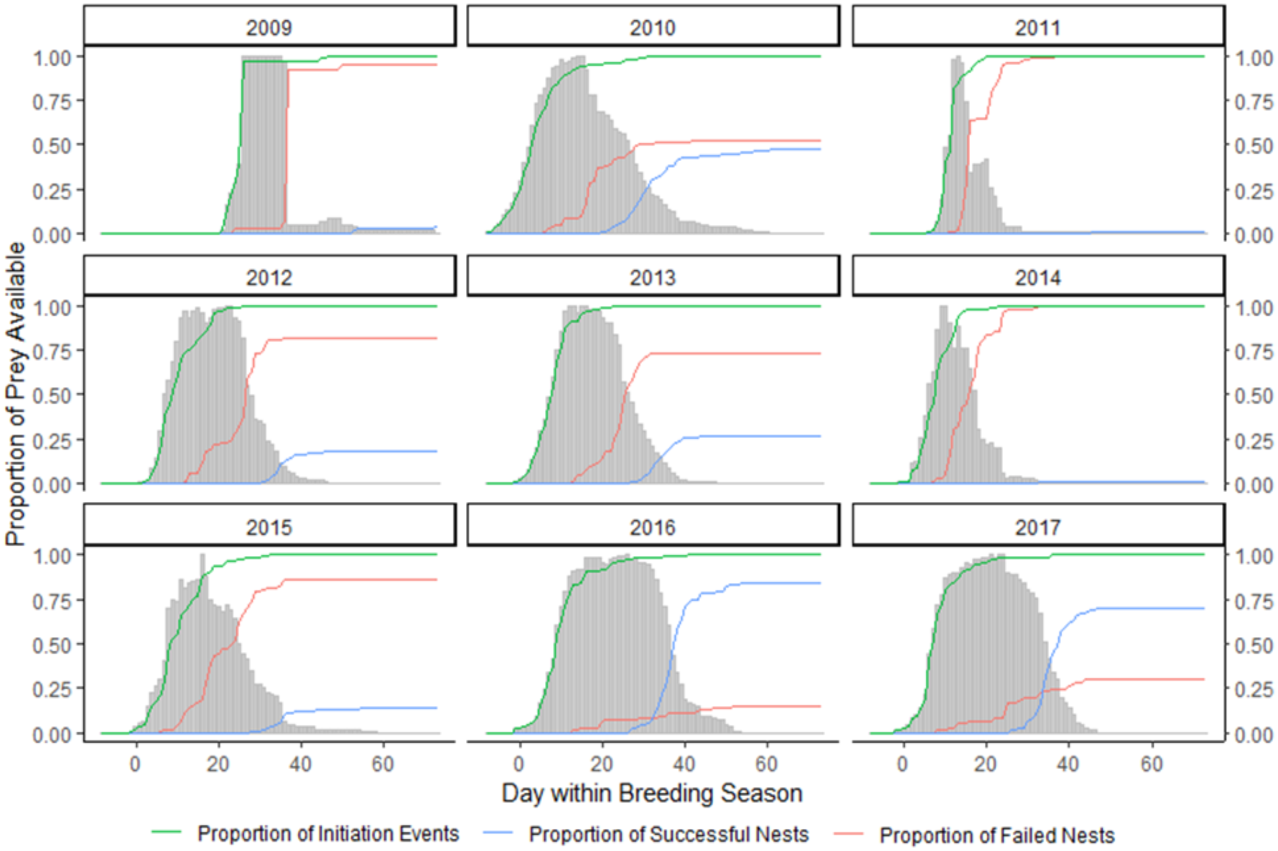

**Figure 6.** The proportion of available prey (grey bars) on each day within the breeding season as a function of when Common Eiders (*Somateria mollissima*) initiate their nests for the beginning of prey availability and when nests either succeed or fail for the loss of prey availability. Accumulation of initiation (green), successful nests (blue), and failed nests (red) across 2009-2017. Day 1=May 30, Day 60= July 29.

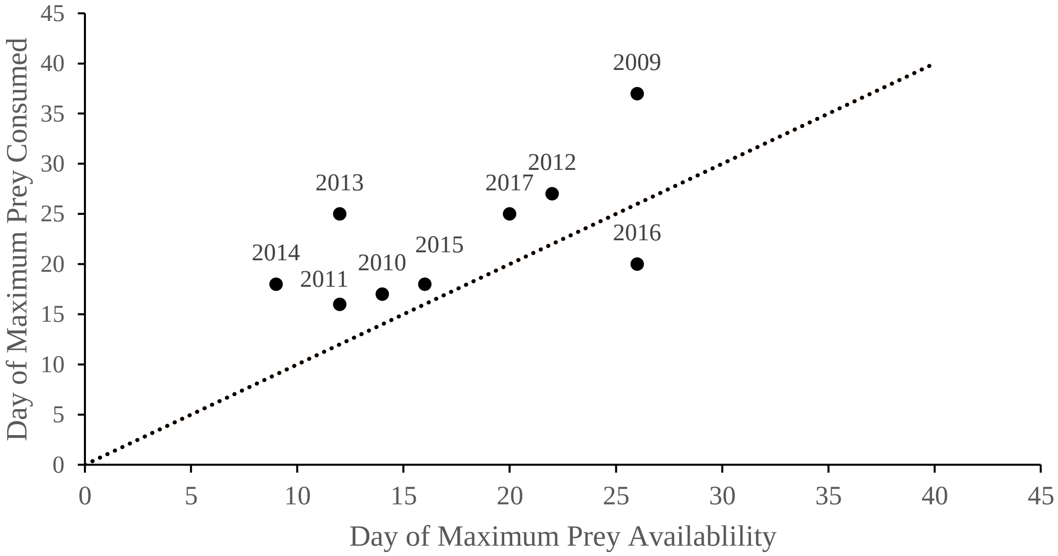

**Figure 7.** Maximum prey availability and prey consumed for 2009–2017. Prey availability was calculated from Common Eider (*Somateria mollissima*) date of initiation and when nests became absent either from failure or success. Day of maximum prey consumed was the day of highest rate of failure for each year. Multiple years had more than one day where maximum prey availability was present and the first of those days were selected. Dashed line represents the hypothesis where predators should match their highest rate of consumption on the same day as when maximum prey are available. Day 1=May 30, Day 45= July 14.

**Table 1**. Proportion of nest failure and length of breeding season for Common Eiders (*Somateria mollissima*) from 2009-2017. First and last days of the breeding season are based on Day 1 = May 30, which was the earliest nest initiation date in our 9-year dataset.

| Year | Proportion of Nest Failures | Number of Nests | First Day of Nest Initiation | Last Day of Nesting | Season Length (days) |
|---|---|---|---|---|---|
| 2009 | 0.951 | 61 | 22 | 73 | 51 |
| 2010 | 0.525 | 322 | 1 | 62 | 61 |
| 2011 | 0.994 | 177 | 9 | 46 | 37 |
| 2012 | 0.818 | 286 | 6 | 47 | 41 |
| 2013 | 0.734 | 387 | 2 | 57 | 55 |
| 2014 | 0.994 | 154 | 2 | 39 | 37 |
| 2015 | 0.857 | 154 | 1 | 59 | 58 |
| 2016 | 0.154 | 117 | 8 | 57 | 49 |
| 2017 | 0.299 | 77 | 6 | 47 | 41 |

**Table 2.** Summary of model selection results ranked using AICc for the daily survival rate of Common Eiders (*Somateria mollissima*) from 2009-2017. $w_i$ is the model weight, K is the number of parameters, Dev is model deviance, and R is the relative model reduction in deviance when compared to the fully saturated model (not included in this table). $S_{Global}$ incorporates all covariates into a single model while also maintaining biological relevancy. $S_{(.)}$ only assumes a constant DSR throughout the breeding season and is our null model. All spatial and temporal predictors were given quadratic terms.

| **Model** | **AICc** | **Δ AICc** | **$w_i$** | **K** | **Dev.** | **R** |
|---|---|---|---|---|---|---|
| $S_{\text{Year+Age+Age\^{}2+T+T*Year+T\^{}2+T\^{}2*Year}}$ | 3858.25 | 0.00 | 1 | 29 | 3800.16 | 0.86 |
| $S_{\text{Year+Age+Age\^{}2+T+T\^{}2}}$ | 4029.91 | 171.67 | 0 | 13 | 4003.89 | 0.70 |
| $S_{\text{Year+Init+Init\^{}2+Age+Age\^{}2+T+T\^{}2}}$ | 4033.23 | 174.99 | 0 | 15 | 4003.21 | 0.70 |
| $S_{\text{Global}}$ | 4040.25 | 182.00 | 0 | 21 | 3998.20 | 0.71 |
| $S_{\text{Year+T+T\^{}2}}$ | 4054.98 | 196.73 | 0 | 11 | 4032.96 | 0.68 |
| $S_{\text{Year+Init+Init\^{}2}}$ | 4142.96 | 284.71 | 0 | 11 | 4120.95 | 0.62 |
| $S_{\text{Year+Age+Age\^{}2}}$ | 4161.70 | 303.46 | 0 | 11 | 4139.69 | 0.60 |
| $S_{\text{Year}}$ | 4182.93 | 324.68 | 0 | 9 | 4164.92 | 0.58 |
| $S_{\text{Year+Water+Water\^{}2}}$ | 4183.51 | 325.26 | 0 | 11 | 4161.49 | 0.58 |
| $S_{\text{Year+NN+NN\^{}2}}$ | 4184.69 | 326.45 | 0 | 11 | 4162.68 | 0.58 |
| $S_{\text{Year+Density+Density\^{}2}}$ | 4186.74 | 328.49 | 0 | 11 | 4164.73 | 0.58 |
| $S_{\text{Year+SpatialPredictors\^{}2}}$ | 4189.72 | 331.47 | 0 | 15 | 4159.69 | 0.59 |
| $S_{(.)}$ | 4932.10 | 1073.85 | 0 | 1 | 4930.10 | 0.00 |

*Predictors in model: *Temporal*- Nest Age (Age), Day within breeding season (T), Date of nest initiation (Init). *Spatial*- Nest's distance to water (Water), Nest density of surrounding area (Density), Nest's distance to nearest neighbor (NN).

**Table 3**. Probability of nest success of Common Eiders (*Somateria mollissima*) calculated from estimates of DSR for each year (assumes a 28 day period including both laying and incubation). Column headers indicate if a Common Eider were to initiate nesting on the first day possible (First), median value between first and last day possible to initiate (Middle), and the last day possible to initiate a nest (Last) for each given year.

| **Year** | **First** | **Middle** | **Last** |
|---|---|---|---|
| 2009 | 0.008 | 0.023 | 0.266 |
| 2010 | 0.209 | 0.243 | 0.903 |
| 2011 | <0.001 | <0.001 | 0.001 |
| 2012 | 0.051 | 0.016 | 0.014 |
| 2013 | 0.123 | 0.045 | 0.357 |
| 2014 | <0.001 | <0.001 | <0.001 |
| 2015 | 0.064 | 0.022 | 0.180 |
| 2016 | 0.747 | 0.604 | 0.040 |
| 2017 | 0.554 | 0.324 | 0.045 |