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Shifts in Reproductive Phenology as a Response to Climate Variability
in a Population of Common Goldeneye (*Bucephala clangula*) from Interior Alaska

By

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THESIS

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Shifts in Reproductive Phenology as a Response to Climate Variability in a Population of Common Goldeneye (*Bucephala clangula*) from Interior Alaska

ABSTRACT

Effects of climatic change are observed to be rapidly increasing, particularly in northern latitudes. Some of the results of climate change include increased climatic stochasticity, which results in high interannual variability in the timing of spring onset. Migratory species that rely on these northern climates may be impacted disproportionately by these changes because they utilize networks of diverse habitats over a large area that are experiencing different rates and effects of climate variability. However, short-distance migrants like the Common Goldeneye (*Bucephala clangula*) may be better able to track phenological changes due to similarities in climate conditions on wintering and breeding grounds. I used a long-term dataset (1997-2020) of Common Goldeneye nesting records from interior Alaska, near the northern extent of the species' range, to examine the impacts of changing spring phenology on reproductive ecology. I used nesting initiation date as an indicator of breeding phenology and examined how nest initiation date varied over the 23-year study period. I then evaluated the influence of predictor variables related to spring conditions, winter conditions, female body condition, and known breeding experience on nest initiation date. Finally, I examined trends in female body condition during the study period and examined the relationship of body condition to winter conditions and known breeding experience. Across all analyses, my results indicated that nest initiation dates varied significantly with measures of spring phenology, wintering area conditions, body condition, and previous breeding. Model estimates indicate that the mean nest initiation date for this population is advancing at 0.71 days per year. Unexpectedly, poorer body condition was correlated with warmer winter conditions, which may

result in future impacts on reproductive output as climate change advances. Model results also demonstrated high repeatability of individual females as a random effect, meaning that females may consistently respond to climatic conditions independently from other females, suggesting that female personality may influence phenological responses. Though goldeneyes appear to currently track the advancement of spring conditions, my results suggest that these migratory birds rely on multiple signals to determine timing of nesting, and uncertainty remains as to how these signals may interact to influence breeding phenology in the future.

TABLE OF CONTENTS

<i>Acknowledgements</i>	<i>ii</i>
<i>Abstract</i>	<i>iii</i>
<i>Table of Figures</i>	<i>vii</i>
<i>Table of Tables</i>	<i>viii</i>
<i>Introduction</i>	<i>1</i>
Effects of climatic change on migratory birds.....	1
Effects of climatic change on waterfowl	4
Common Goldeneyes as a model study system.....	5
Biological Predictions.....	7
Short-distant migrants will be better track seasonal changes in breeding conditions.	7
Conditions on the winter grounds will influence phenology	8
Goldeneyes are bet-hedgers and respond flexibly in reproductive effort among years and conditions	9
Summary of predictions.....	9
<i>Methods</i>	<i>10</i>
Study Area	10
Data collection	12
Variables used in analysis.....	14
Data Analysis	20
<i>Results</i>	<i>22</i>
Study population.....	22

Metrics of spring conditions	25
Changes in spring conditions over time.....	27
Changes in winter conditions over time.....	28
Variation in nest initiation date over time.....	30
Factors affecting nest initiation date	31
Factors affecting female body condition	34
<i>Discussion</i>	38
Changes in climatic conditions over the study period	38
Tests of Hypotheses	39
Response to spring conditions	39
Influence of female experience.....	40
Influence of body condition	41
Influence of winter conditions	43
Changes in goldeneye breeding phenology	45
Key importance of multiple factors	45
Implications for common goldeneye nesting in Alaska.....	47
Implications for other boreal-nesting waterbird species.....	49
Management Implications.....	49
<i>Literature Cited</i>	53

TABLE OF FIGURES

Figure 1. Map of the Chena River State Recreation Area.....	12
Figure 2. Map of band encounters between November and March of 1997-2020.....	17
Figure 3. Scatterplot representing the minimum age and known breeding experience of female goldeneyes captured by year.....	20
Figure 4. Histogram of the number of capture encounters per female.....	23
Figure 5. Scatterplot depicting the total number of nest boxes occupied by Common Goldeneye by year.....	24
Figure 6. Julian dates of ice breakup on the Tanana River from (1917-2021) plotted against the Julian date of ice breakup on the Chena River (1917-2021).....	25
Figure 7. Scatterplot of the bivariate fit between ice breakup dates on the Tanana and Chena rivers during the years of the study, 1997-2020.....	26
Figure 8. Scatterplot of the bivariate fit of the average spring temperature (F°, March-April) on the Julian Date of ice breakup of the Tanana River at Nenana (1997-2021).....	27
Figure 9. Scatterplots demonstrating ice breakup on the Tanana River.....	29
Figure 10. Graph demonstrating the mean winter (November through March) Pacific Decadal Oscillation for the winter preceding each breeding season during the study years.....	30
Figure 11. The advance in nest initiation dates among years over the study period (1997-2020)...	31
Figure 12. Line graph demonstrating the modeled linear relationships between the standardized predicted variables and nest initiation dates.....	35
Figure 13. Line graph demonstrating the modeled linear relationships between the standardized predicted variables and body condition indices.....	37

Figure 14. Variation in the body condition index of females among years over the study period (1997-2020).....37

Figure 15. Graph demonstrating mean initiation dates by individual female identification numbers.....52

TABLE OF TABLES

Table 1. A summary of biological hypotheses on the response of Common Goldeneyes to variation in spring and winter conditions.....10

Table 2. Comparison of mixed models to examine variation in nest initiation dates (Julian) as a function of standardized values of ice breakup dates on the Tanana River, mean spring temperature, breeding experience, body condition index, and preceding winter mean PDO.....32

Table 3. Results of a linear mixed model to evaluate the influence of ice breakup date, spring temperature, female breeding experience, female body condition, and winter PDO on nest initiation dates of Common Goldeneyes.....33

Table 4. Comparison of mixed models to examine variation in body condition of Common Goldeneye females as a function of breeding experience and preceding winter mean PDO.....36

Table 5. Results of a linear mixed model to evaluate the influence of winter PDO and female breeding experiences on body condition of female Common Goldeneyes.....36

INTRODUCTION

Effects of climatic change on migratory birds

While climatic changes have occurred throughout history, contemporary changes are happening much more rapidly than in the past, which may have substantial impacts on wildlife species that are unable to adapt at increasing rates of environmental change (IPCC 2012). Northern latitudes are particularly sensitive to climate change, and in the past 60 years, Alaska has warmed at more than twice the rate of the contiguous United States, which has resulted in melting permafrost, drier landscapes, and more frequent and larger wildfires (Stewart et al. 2013). Worldwide, future climatic shifts are predicted to include an increasing mean annual temperature, greater climatic stochasticity, decreasing winter harshness, earlier spring conditions, changes in precipitation and cloud cover regimes, and shifts in ocean level and pressure (IPCC 2012, Guillemain et al. 2013).

In the boreal forest found across northern North America, milder temperatures allow for overwinter survival and rapid spread of pathogens, which may result in large-scale die-off of trees and increased forest fires (Stewart et al. 1998, Price et al. 2013). While the boreal forest doesn't boast a particularly high species richness, this disturbance could be detrimental because the boreal forest is one of the most expansive biomes in North America and is a critical breeding habitat for large numbers of birds (Wells and Blancher 2011).

Additionally, migratory species, such as boreal-breeding birds, may especially be susceptible to changes in climate because they utilize a network of diverse habitats throughout their annual cycle, over large areas that are each experiencing different rates of change (Jones and Cresswell 2010, Reynolds et al. 2017, Ambrosini et al. 2019). Migrants that winter in areas far

from their breeding grounds are especially challenged to track these shifts, due to the use of spatially distant and diverse habitats. The difficulty in tracking environmental states across large areas creates a risk of decoupling optimal conditions for reproduction from the timing of migration and breeding, such that populations no longer arrive and breed in suitable conditions (Miller-Rushing et al. 2010). This phenological mismatch can lead to reduced survival and breeding success, in part resulting from reduced forage availability during key periods of incubation and brood rearing (Doiron et al. 2015).

Unlike many long-distance migrants, some northern-breeding birds may be able to respond to environmental shifts by adjusting the timing of migration and reproduction to match changing breeding conditions. As spring conditions advance, many species of birds have also advanced in their timing of spring migration and breeding (Lehikoinen and Sparks 2010, Liebezeit et al. 2014, Andersson et al. 2022). This pattern is particularly notable among short-distance migrants; these species may be able to better track conditions on breeding grounds given a closer proximity to wintering areas (Miller-Rushing et al. 2008, Bitterlin and Van Buskirk 2014, Clark et al. 2014, Usui et al. 2017). As a result, mismatch may be less severe in short-distance migratory species than in long-distance migrants because timing of breeding is related to local weather conditions rather than large-scale climatic patterns (Oja and Pöysä 2007, Lehikoinen et al. 2006, Clausen and Clausen 2013). Furthermore, the life history and ecology of migratory species also influences their abilities to respond to rapid phenological shifts. For example, greater spring advancement in nesting phenology is often seen in species that are multi-brooded, require longer breeding windows, have a larger body size, and have greater endogenous reserves to allow for earlier breeding attempts (Bitterlin and Van Buskirk 2014, Usui et al. 2017).

Beyond shifts in their phenology, many migratory birds have also responded to milder winters by overwintering further north (Hitch and Leberg 2007, Maclean et al. 2008, Ambrosini et al. 2011). Consequently, migration from wintering areas to breeding areas is faster and the distances are shorter (Ambrosini et al. 2019). One explanation for these patterns is that the decreased winter harshness in northern habitats creates more, and earlier, ice and snow-free areas. This, in turn, may allow foraging throughout the winter and facilitate an enhanced ability to match breeding phenology to advancing spring conditions by arriving on breeding grounds earlier (Knudsen et al. 2011, Ambrosini et al. 2019).

Changes in overwintering locations and phenology may have negative or positive impacts on populations. On the one hand, earlier springs and northward range shifts may move populations into areas with drier, poorer conditions that can have deleterious effects on reproductive output and survival (Ambrosini et al. 2011). Such instances are often referred to as ecological traps, when a species uses cues historically associated with preferred habitat or phenology, but recent environmental shifts result in the cued response no longer being adaptive (Schlaepfer et al. 2010). In this case, shifting breeding phenology may not compensate for the detrimental impacts of climate change, as many species are experiencing population declines that appear to be related to climate change (Møller et al. 2008, Jones and Cresswell 2010, Saino et al 2011). On the other hand, some species of northern breeders may experience short-term benefits from milder winters and earlier spring conditions, such as more ice-free foraging areas, lower energetic demands for thermoregulation, and overall better body condition (Gaston et al. 2005, Knudsen et al. 2011). This improved body condition allows birds to depart for breeding grounds earlier and arrive in better condition (Guillemain et al. 2010, Fox and Walsh 2012). Milder autumn conditions may also allow for more time to complete molting in the fall before the conclusion of breeding and the beginning

of fall migrations (Bitterlin and Van Buskirk 2014). These short-term benefits may not be long-lasting, however, and populations may be impacted in the future as environmental conditions and habitats continue to change further from the conditions that species are adapted to. For example, a population of common eiders breeding in Scandinavia exhibited improved reproductive performance under warming conditions, but recent work on the same population indicated weakening of the positive trend as non-native predators dispersed into new areas due to climate warming (Lehikoinen et al. 2006, Öst et al. 2021). Clearly, climate effects may be nonlinear and shift over time.

Effects of climatic change on waterfowl

A large portion of existing research on climate-driven impacts on migratory birds has focused on migratory songbirds, due to their vulnerability, observed population declines, and international migrations. However, understanding the influence of climatic change on waterfowl is also critical because they have considerable socio-economic importance as game species, and biological significance as indicators of wetland ecosystem health (Green and Elmberg 2014). A concern for waterfowl is that continuing climatic change may reduce wetland availability, due to drought, and have detrimental effects on waterfowl breeding success (Dzus and Clark 1998, Guillemain et al. 2013).

Some species of waterfowl are exhibiting earlier and faster migrations (Møller 2008, Tøttrup et al. 2008, Fox and Walsh 2012, Andersson et al. 2022). These changes in migration are correlated with improved body condition, which may be in part driven by increased food availability and decreased thermoregulation requirements on wintering grounds and stopover areas (Gaston et al. 2005, Knudsen et al. 2011, Guillemain et al. 2010, Fox and Walsh 2012, Stirnemann et al. 2012). If breeding chronology continues to advance, it may further impact population

dynamics if greater numbers of ducks becoming flighted and migrate earlier during the fall hunting season, thereby influencing overall harvest rates (Oja and Pöysä 2005, Guillemain et al. 2013). Several species of waterfowl have also exhibited range shifts in response to rapid environmental change and appear to be wintering further north than in known history (Ward et al. 2009). While this pattern might be related to thermoregulation costs, some work suggests that increased food availability is more important in these shifts (Dalby et al. 2012). Although many effects of climatic shifts across taxa are thought to have negative impacts on populations, some species of waterfowl appear to benefit from earlier spring breakup, such as earlier nest initiation, greater reproductive success, and higher recruitment (Dickey et al. 2008, D'Alba et al. 2010).

Common Goldeneyes as a model study system

While some work has been conducted on a small number of sea ducks (tribe Mergini) of conservation interest (e.g. eiders, scoters, long-tailed ducks), there has been little research to examine climate-induced effects on life history traits of the Common Goldeneye (*Bucephala clangula*) in North America. This omission may be because Common Goldeneye have been relatively well-studied in Europe and North America, we have a good understanding of their natural history, and populations appear to be stable. However, studies of this species offer a unique opportunity to examine the effects of climatic variation because goldeneyes use a range of habitat types over a large area and are sensitive to variation in food availability (mostly invertebrate prey), and therefore water quality (Eadie et al. 1995). Goldeneyes are income breeders, which rely on exogenous food resources immediately before and during the breeding season to initiate nesting, produce eggs, and complete incubation and brood-rearing (Hobson et al. 2005). Accordingly, the timing of breeding and body condition may provide a good indication of habitat quality and serve as a proxy for habitat monitoring. Unlike other species of sea ducks that are closely associated

with coastal or tundra habitats during the breeding season, goldeneyes rely on interior boreal forest and wetland habitats that are not temperature-buffered by oceans and so may provide new insight on the influence of climatic change on a species of sea duck in a forested interior habitat. Additionally, a large portion of waterfowl breeding in North America are ground-nesting whereas goldeneyes are cavity-nesting and may exhibit different responses to variation in breeding conditions and nest-site microclimate. Understanding whether cavity-nesting boreal species are buffered from climate effects may provide insight and direction for other boreal species in adapting to the potential impacts of climatic change. In a population of Common Goldeneye in Finland, nesting phenology was correlated with advancing spring phenology, demonstrating that European goldeneye have already exhibited shifts in response to climate variability (Clark et al. 2014). However, this work did not consider the conditions that goldeneye experience on wintering grounds, and how that may influence breeding phenology.

Understanding migratory patterns and distances will be critical in understanding the response of goldeneyes to climate variability. Populations are typically classified as long or short-distance migrants based on wintering areas, migration distance, and geographic barriers that are crossed during migration (Usui et al. 2017). Using these criteria, the Alaskan population of goldeneye would be classified as short-distance migrants, since the population remains within the same state during its life cycle, and has few geographic barriers to cross during migration, a classification supported by Clark et al. (2014). Furthermore, there are increasing reports of waterfowl, including Common Goldeneye, overwintering in the Fairbanks area (Sullivan et al. 2009, Spivey 2017, eBird 2021), close to our study area.

Given the conservation concerns facing sea ducks in the north, the value of studying a species that relies more on interior forested wetlands, and indications that this species is already

responding to phenological shifts in Fennoscandia, I undertook this study to analyze the long-term phenology of the Common Goldeneye in interior Alaska in response to climatic variability. Using a long-term (1997-2020) data set for a population breeding on the Chena River State Recreation Area (SRA), my objective is to examine the influence of a rapidly-changing environment on a sea duck population which is considered to be stable across the North American Continent. In this study, I focus on the timing of breeding and examine winter and spring environmental conditions as well as female and nest-site specific influences on breeding phenology. Future studies will explore possible fitness consequences (egg size, clutch size, nest success, hatch success) of any shifts, but my goal here was to first establish if such shifts occur and if so, what factors might be driving these changes.

Biological Predictions

Short-distant migrants will be better track seasonal changes in breeding conditions

As short-distance migrants, I predict that Common Goldeneye will track shifts in phenology closely and initiate nesting attempts earlier in years of early springs and milder winters, and later in more harsh winters and later spring conditions. Additionally, goldeneye tend to nest early in relation to other waterfowl species, and so I predict that they will exhibit plasticity in nest initiation dates (Messmer et al. 2021, Miller-Rushing et al. 2010). Willie et al. (2020) reported the congeneric Barrow's Goldeneye (*Bucephala islandica*) had high (70+%) inter and intra-annual wintering site fidelity, so it is likely that Common Goldeneye would also return to same wintering areas each year.

With birds wintering further north than in the past, making migration faster and shorter, birds will be better able to track breeding conditions (Hitch and Leberg 2007, Maclean et al. 2008, Ward et al. 2009, Ambrosini et al. 2011, Ambrosini et al. 2019, Knudsen et al. 2011). Tree cavities

are available year-round, so nesting hens are not required to wait on melting snow or ice to open up ground-nesting sites. Thus, goldeneye would be able to start nesting even when there is still snow on ground.

Conditions on the winter grounds will influence phenology

One of the predicted future effects of climate change includes an increasing mean annual temperature and a decreasing winter harshness (IPCC 2012, Guillemain et al. 2013). In many cases, this milder winter temperature creates more ice and snow-free areas that may allow foraging throughout the winter (Knudsen et al. 2011, Ambrosini et al. 2019). Cross seasonal effects have been demonstrated as significant for other species of waterfowl (Sedinger and Alisauskas 2014), but the relationship between wintering conditions and breeding season phenology has not previously been examined in Common Goldeneye in North America. Winter conditions are particularly important to understand for migratory waterfowl, which rely on some storage of nutrients for migration and breeding initiation. Though Common Goldeneye are generally considered to be income breeders that rely on exogenous nutrient reserves for breeding, some endogenous reserves must be gained on the wintering ground to allow for migration to the breeding site, as well as for any activities on the breeding area prior to the breakup of ice on rivers and lakes that opens up foraging access.

Milder winters allow for better body condition, which may allow females to depart for breeding areas and breed earlier in the year and increase reproductive output (Gaston et al. 2005, Knudsen et al. 2011, Guillemain et al. 2010, Fox and Walsh 2012, Stirnemann et al. 2012). Additionally, females' ovaries are reduced during the non-breeding season, and do not start growing until about 60 days before laying, so birds must use winter conditions and cues to prepare

for nest initiation ahead of local/springtime cues. This may result in winter conditions also playing a role in nest initiation dates.

Goldeneyes are bet-hedgers and respond flexibly in reproductive effort among years and conditions

In a life-history analysis of this population, Lawson et al. (2017b) described goldeneye as a species with a ‘bet-hedging’ life history strategy, meaning adult females have relatively high survival, but reproductive success is dependent on climatic conditions. Species that exhibit this life history strategy favor adult survival and may alternate in and out of breeding status when conditions worsen or improve. As such, goldeneye may be highly reactive, not only in reproductive success, but also phenology of nesting.

Summary of predictions

Based on the above framework, I predict that Common Goldeneye will exhibit high variability in nest initiation dates, correlated with the variability observed in spring conditions on the breeding grounds. Specifically, I expect that initiation date for the Common Goldeneye in this population will have a significant and positive relationship with the onset of spring conditions, which I will determine by using the date of ice breakup on a nearby river as an index. Furthermore, I predict that winter conditions will have a significant relationship with body condition of females, where milder, warmer conditions will be related to a higher body condition index. The specific predictions are summarized in Table 1.

Table 1. A summary of biological predictions on the response of Common Goldeneyes to variation in spring and winter conditions. My analyses explore two key response variables (nest initiation date and female body condition) in relation to several predictor variables (see text)

Variable of interest		Biological Predictions
Predictor	Response	
River ice breakup	Nest initiation date	In years of early ice breakup, nest initiation dates will be earlier
Breeding experience	Nest initiation date	Females with more known breeding experience will initiate nests earlier
Body condition	Nest initiation date	Females with a higher body condition index will initiate nests earlier
Winter conditions	Body Condition	In years of more mild winter conditions, females will have higher body condition indices
Winter conditions	Nest initiation date	In years of more mild winter conditions, females will initiate nests earlier

METHODS

Study Area

The study focused on a population of Common Goldeneyes nesting in interior Alaska on the Chena River SRA. The Chena River SRA is located approximately 26 miles northeast of Fairbanks, Alaska and is managed by the Alaska Department of Natural Resources (Figure 1). The Recreation Area extends along the Chena River and covers 254,080 acres of boreal forest, wetlands, rivers, and alpine tundra. This area was established in 1967 to protect a portion of the Chena River Valley from development, logging, and mining activities, while allowing for outdoor recreation opportunities in the Fairbanks area (Alaska Department of Natural Resources, 2006).

Annually, approximately 150,000 visitors utilize the area for fishing, hunting, camping, off-road driving, hiking, and watersports.

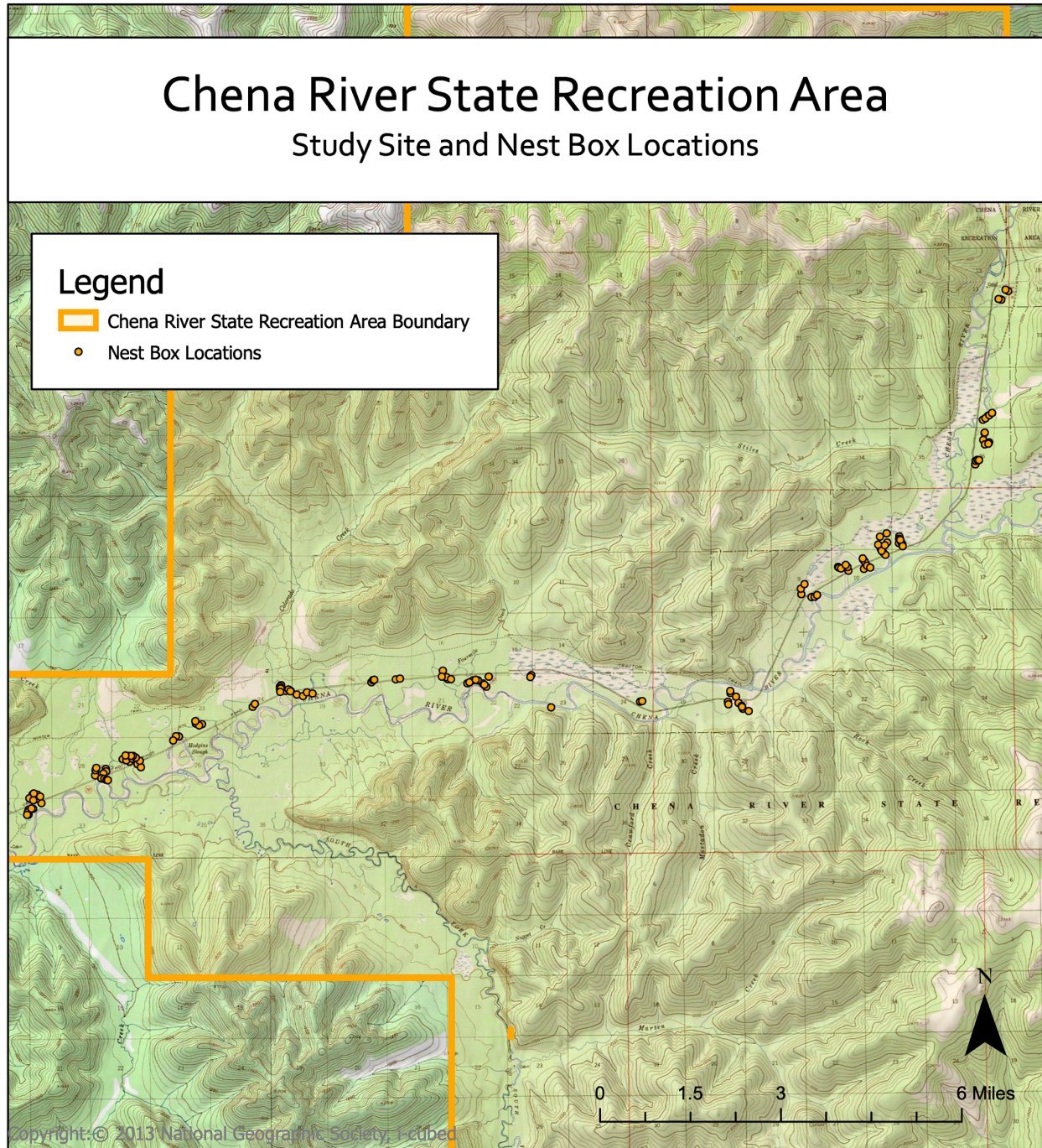


Figure 1. Map of the Chena River State Recreation Area. Nest boxes are distributed <1 mile from the Chena Hot Springs Road, between mileposts 26 and 48, along oxbow lakes, ponds, and the Chena River within the Chena River Floodplain.

Seasonal variation in daylight on the recreation area is extreme, ranging from 22 hours of daylight in June to only 4 hours in December. Winters are cold and dry, reaching extreme temperatures of -40°F, while summers are warm and generally clear, averaging 60°F and only reaching above 90°F for less than two weeks during the summer. Brief afternoon thunderstorms are typical from late-May to mid-July, with more than half of the annual precipitation falling in June through September, accumulating approximately 15-25 inches each year. Wildfires are also a natural element of interior Alaska, with fires periodically occurring within the recreation area.

Nest boxes were erected in the recreation area starting in 1993 by University of Alaska Fairbanks Student Chapter of Wildlife Society. Nest boxes were installed during the winter, by snowmachining to sites and installing boxes directly on trees 10-30 feet above the ground. Boxes were all placed in close proximity to open water without any obstructions to the nest box opening. Goldeneye females take flight by “skittering” on water bodies and fly directly into the box opening and require a clearing around the box entrance.

Data collection

For the first several years of the project, boxes were visited annually at the conclusion of the breeding season to examine occupancy and nesting outcome where possible. Beginning in 1997, the boxes have been monitored throughout the breeding season, collecting data on individual hens, clutch sizes, and reproductive success. Since the start of intensive monitoring, there were five years when boxes were not monitored during the breeding season due to extenuating circumstances (2006, 2007, 2014, 2015, and 2020). For my analyses, I only utilized the period of intensive monitoring, from 1997-2020.

Beginning in April or May each year, all boxes were visited to determine occupancy of each box and to capture females during egg laying. The rate of egg deposition in each box was

used to estimate when females lay eggs and were available for capture and banding, since goldeneyes lay 1 egg approximately every 48 hours and tend to lay in the early morning or evening (Eadie et al. 1995). Each female was banded with a USGS stainless steel butt-end band. (Aluminum bands were used in the early years of the project but experienced severe corrosion and wear in the marine environments that goldeneye occupy during the winter). Females that hatched from the study area may have been banded with a plasticine band, or given a foot web tag as a duckling, so both feet were checked for any sign of marking, including a damaged web that may indicate a lost web tag. (Duckling marking procedures are described in the following paragraph). Known age of females marked as ducklings can then be calculated. Morphometric measurements of the female (culmen length, total head length, and diagonal tarsus length) were obtained for each female at least once per breeding season. Body mass was measured using a Pesola scale for each female at every capture event, unless it was measured less than 7 days previously, to reduce the handling time and stress. Each nest box may have been visited as many as 5 times during a season, so multiple measurements of body mass from the same female were often obtained, though morphometric measurements were only taken once per season. Ideally, hens were captured and weighed during egg-laying to obtain a pre-incubation body mass measurement and measured again during late incubation and hatch. All eggs were measured for largest length and width. Egg mass was measured using a digital scale for eggs that were fresh and unincubated, but not beyond 0 days of incubation, as mass changes rapidly during development of the eggs.

Incubation stage of eggs was determined by candling the egg by holding it towards the sunlight, and looking at the egg through a dark rubber radiator hose, which allows light to illuminate the contents of the egg. When a nest was known to be within early incubation (days 1-14 of a 28-day incubation), we avoided visiting the nest or capturing the hen to reduce the

likelihood of nest abandonment during this sensitive nesting period. Nests were revisited a few times during late incubation to predict hatch date, and until the clutch failed or hatched. Predictions of hatch dates were made by candling, calculating the date of clutch laying completion by using egg laying rates, and any observations of pipped eggs. Pipping first occurs approximately 48 hours before hatch, advanced pipping occurs approximately 24 hours prior to hatch, and the first breakthrough of the duckling through the shell happens within 12 hours of hatch, so we were able to accurately estimate when a clutch will finish hatching by the extent of pipping. When a clutch was estimated to have entirely hatched, the nest was visited for verification. When less than 80 percent of a clutch had hatched, we left the nest site and returned after the appropriate interval determined by the observed progress in hatching. When a nest hatched, ducklings were captured for processing. Despite disturbance during hatch, abandonment by the hen at this stage was very uncommon, so we were able to process ducklings safely and quickly with little adverse effects to survival. Processing ducklings involved measuring mass of each duckling, recording the condition of the duckling (wet, dry, dandruff), and affixing a permanent web tag with a unique identification number to each duckling's right foot webbing. During processing of ducklings, hens were released to the water to reduce handling stress. Hens typically remained on a nearby body of water throughout processing and returned to the box shortly after we replaced the ducklings. Common Goldeneye ducklings jump from the nest within 24-48 hours of hatching and follow the hen to brood territories, so there is a narrow window in which to tag and measure ducklings.

Variables used in analysis

I analyzed climatic trends using two different temporal and spatial frameworks: local climatic conditions and wintering area conditions. To determine local climatic conditions, I used daily weather data from the Fairbanks International Airport Weather Station (64.8039° N, -

147.8761° W) for the years 1997-2020 collected from the National Oceanic and Atmospheric Administration (NOAA) database (<<https://www.ncdc.noaa.gov/cdo-web/datatools/findstation>>). The Fairbanks International Airport weather station is approximately 40 miles west of the Chena River SRA and will have similar climatic trends to the study site. A weather station closer to the study site, at Two Rivers, Alaska, (64.8697° N, -147.0422° W), was only in operation for a single year of the study (2010). To create an index of breeding season conditions, I calculated the mean temperature for spring (March-April), which can be used to examine the impact of inter-annual differences in mean temperatures on nesting phenology. I also obtained dates of ice breakup on rivers, which is another phenological indicator of spring conditions, and is likely related to spring air temperature. Ice breakup from the Chena River in downtown Fairbanks has been recorded nearly annually since 1900. Some data were missing from the historical records of ice breakup of the Chena River (1999-2002, 2011, 2019), and so I obtained ice breakup data from the Tanana River at Nenana, Alaska (64.5652° N, -149.0196° W), which has been recorded annually since 1917 and may have similar phenology.

To determine if ice breakup dates on the Tanana River predicted ice breakup dates on the Chena River, and therefore the Tanana would be a suitable proxy for the Chena River, I conducted a linear regression analysis between the two. I also conducted a linear regression of ice breakup dates on the Tanana River by the mean spring temperature (March-April) to evaluate the validity of using ice breakup as an index of spring condition. Finally, I ran a linear regression on the ice breakup dates by year, for both the entire recorded history (1917-2020) and the years of the study (1997-2020) to examine the trends in ice breakup date over time.

To understand how winter conditions might affect this population, I first had to determine where these birds overwinter, as migration distance and speed can influence a population's ability

to track phenological shifts. Though few band recoveries have been reported for this population of goldeneye, all winter recoveries (November-March, $n = 16$) were from the northern Pacific Ocean. The majority of the recoveries come from Kodiak Island or around Cook Inlet, but 1 recovery was made in January 2001 at Prince of Wales Island (Figure 2). Band recoveries are limited in areas where there are few hunters and parts of remote Alaska may not be accurately assessed. However, based on known recoveries, and the absence of any recoveries outside of Alaska, Chena River goldeneye appear to winter in the Gulf of Alaska, in the Northern Pacific Ocean. Therefore, I used the Pacific Decadal Oscillation (PDO) index to analyze the climatic patterns of the North Pacific Ocean. The PDO is an index of oceanic conditions that follow a recurring pattern of variability, alternating between milder, warmer conditions (positive phase) and colder conditions (negative phase). Evaluating winter conditions using PDO can provide an important indicator of variables that could impact reproductive success but would not be found in local climate data. I used the mean values of the PDO for the winter period (November-March) to create an index of the preceding winter conditions for each breeding year and referred to each winter by its later calendar year. PDO values are available by day, but I used monthly average values over the winter period. Since goldeneyes spend a significant part of each year in coastal habitats, winter conditions play an important role in determining thermoregulatory requirements, foraging conditions, and consequently, spring body condition. These variables have been suggested to impact population size, population dynamics, and reproductive output of sea ducks (Lehikoinen et al. 2006, Guillemain et al. 2010, Flint 2013).

I also examined how the number of occupied nests varied among years fitting a linear, cubic, and quadratic function and assessing fit by using the R^2 values and by visual examination. Nest initiation dates were estimated for each nest based a combination of the date of first hen capture, egg laying rates, number of eggs present, incubation stage of eggs at each visit, and hatch

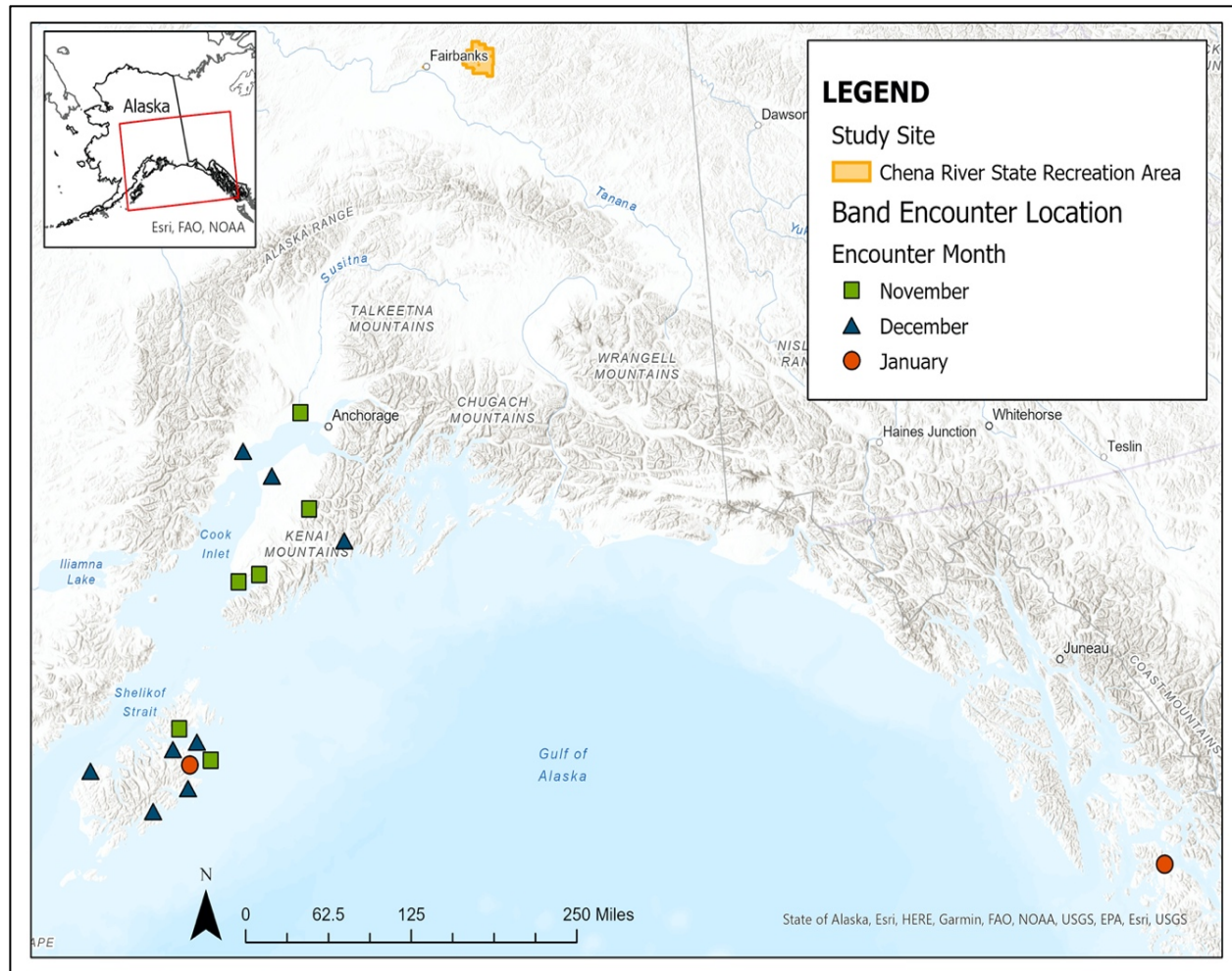


Figure 2. Map of band encounters between November and March of 1997-2020. No encounters occurred during February or March in any year. Map markers were dispersed with a minimum distance of 2 kilometers to allow all overlapping markers to become visible.

date. Egg laying rates were presumed to be 1 for every 1.5 days (Eadie et al. 1995), and so the date of first egg laid in a nest (nest initiation) was back calculated based on female encounters during egg laying and laying rates. If eggs were deposited at rates of >1 every 48 hours, I presumed it to

be the product of conspecific brood parasitism, and the extra eggs were not included in the estimation of initiation date. Each estimate of initiation date was also recorded with an estimate of confidence in accuracy (“known”, “ ± 1 day”, “ ± 2 days”, “ ± 3 days”, or “unknown”). Nests were nearly always visited at hatch, so the majority of hatch dates for the project were known (61.7%) or estimated ± 1 day (15.2%). I used nests with known hatch dates to estimate the start of incubation, in concert with visits to the nest during incubation and the estimated incubation stage obtained by candling. I assumed that incubation began once the final egg was laid and lasted a minimum of 28 days (Eadie et al. 1995). In years where no researchers were present on the study site or a hatch event was missed, hatch date was unknown (19.0%) and incubation start date was difficult or impossible to calculate. In data where a hatch date estimate was unknown, it was excluded from my analyses.

To obtain an index of body condition, I used structural size measurements and body mass measurements of hens to create a scaled mass index. Structural size of hens (diagonal tarsus, culmen length, total head length) was measured at least once per season, and most hens were captured for multiple years and measured by multiple observers. Between years, these measurements theoretically remain the same once a bird reaches adulthood and enters our breeding population, but there was variability in measurements between observers and years. To reduce the effect of interannual and inter-observer differences in structural measurements, I calculated the average measurement of each metric for each female over all years and observers in R Studio to obtain a single measurement of each metric for each female. To obtain a body condition index for each female encounter, I employed a similar method that has previously been used on this study population (Schmidt et al. 2006). I performed a principal components analysis using culmen length, head length, and diagonal tarsus length to create an index of female structural size. I then

conducted a linear regression between body mass and PC 1 scores. I used the resulting residuals from the regression as indices of body condition.

Age and experience of females can also factor into nesting strategies (such as earlier nest initiation; Dow and Fredga 1984, Mallory et al. 1994, Milonoff et al. 2004). I calculated the minimum possible age of each female at each encounter by determining the first year in which an individual was captured as a breeding adult (as an after-second-year bird) and added 2 years to the difference between the current year and the first year of capture. However, this produced a large number of “2-year-old” females in the early years of the study, although many were likely older (Figure 3). This could influence analysis of the impacts of age on breeding phenology. Known age for some individuals could be calculated, as many ducklings on the study site were fitted with plasticine bands or web tags. However, return rates on web tags were low and plasticine band data are not completely digitally available. Due to these factors, I determined that using the number of known breeding attempts would be a better index of hen experience, and so sequentially numbered each breeding attempt of each female. Using this measure will better account for years in which a female does not breed in the study population (Figure 3). With high rates of breeding philopatry, females that are not present in the breeding population one year but are in following years were likely in a non-breeding status rather than emigrating (Savard and Eadie 1989, Lawson et al. 2017b).

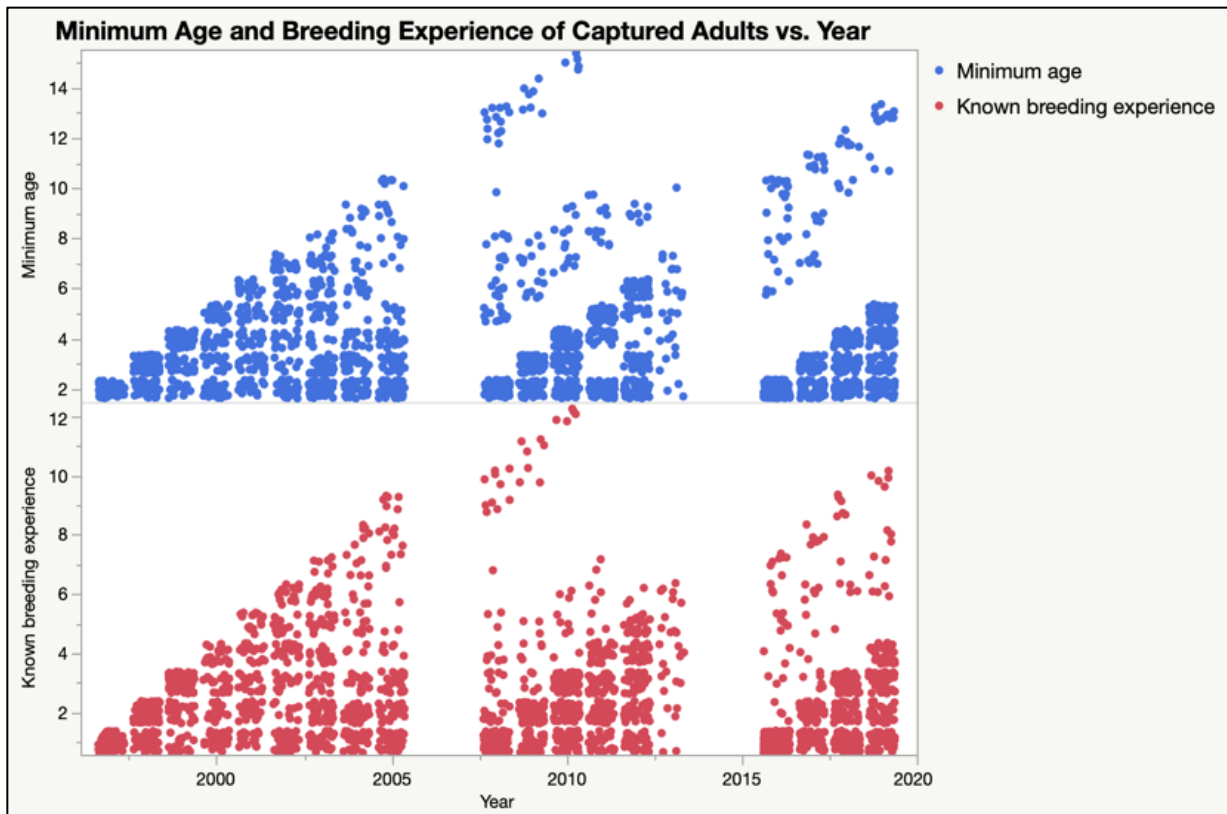


Figure 3. Scatterplot representing the minimum age and known breeding experience of female goldeneyes captured by year. Early years of the study, most birds were presumed to be young, though there were likely females >2 years of age present. Gaps in the study in the years 2006-7 and 2014-15 also influenced the calculated minimum age of females. Using known breeding experience (attempts) of females reduced some of the gaps in the distribution.

Data Analysis

Prior to data analysis, I calculated the standardized values of each variable, to allow for a more direct comparison of the influence of each variable on the same effective scale. The standardized values were calculated with JMP Pro 16 software, by using the observed value, subtracting the mean value, and then dividing the result by the standard deviation. To determine how the PDO influenced body condition of females, I used linear mixed models fitted using restricted maximum likelihood (REML) with the standardized body condition index as the response variable, the standardized mean values of the PDO of the preceding winter as a fixed effect, and

with individual female identity (band numbers) as a random effect. I used female identity as a random effect, since many females were captured multiple times over several years. I ran a second linear mixed model with the standardized body condition index as the response variable and standardized values of the number of known breeding experiences as the fixed effect, as well as a third model using both breeding experience and PDO as predictors of body condition index. I compared Akaike information criterion (AICc) values among the three models to determine the model of best fit.

To examine the trend in nest initiation dates over time, I used linear mixed models using restricted maximum likelihood (REML) with nest initiation date as the response, year as a fixed effect, and female identity as a random effect. Nest initiation dates were normally distributed, so I elected to use observed (Julian) dates, rather than standardized values.

I then ran a series of linear mixed models to examine nest initiation date as a response variable with the ice breakup date, mean spring temperature, breeding experience, body condition, and the preceding winter mean PDO as predictor variables to evaluate the response of nesting goldeneye to phenological shifts. Again, I standardized all variables prior to performing the data analysis and I used female identity as a random effect. I also ran the models with both female identity and box identification numbers as random effects, to examine if particular boxes accounted for variability in initiation date, or if particular boxes tended to be occupied earlier. I compared AICc values across all tested models to determine the model of best fit. Several of the predictor variables were correlated and this multicollinearity may have influenced model outcomes and variance estimates. In future analyses, I will deal with this using methods such as partial least square regression or variable reduction (PCA) analyses. Currently, I could not employ these methods including random effects in mixed models, and I felt that the large number of observations

of the same females and the same nest boxes were essential to control for. Accordingly, I assessed the influence of multicollinearity using the variance inflation factor (VIF) for each predictor variable. Although statisticians caution against using rules of thumb for cutoff values of VIF, a value of greater than 5 is thought to indicate strong multicollinearity and a value less than 2.5 or 2.0 is recommended, although O'Brien (2007) notes that conclusions may still be confidently drawn from regressions with VIF values greater than 4-10.

RESULTS

Study population

Throughout the study, we captured and banded 446 individual Common Goldeneye females. The oldest minimum age, based on the difference between the final and first capture (which is presumed to be captured initially during the first breeding attempt at 2 years old), was 15 years, and the largest number of known years of breeding experiences was 12. Data on the number of breeding attempts indicate that the majority of the Chena River population is comprised of young females that remain in the breeding population for a mean of 2.45 years (Figure 4).

Breeding density and occupancy of nest boxes increased over the course of the study, from 57 goldeneye nests in 1997 to 73 in 2020 (Figure 5), although the number of occupied boxes appeared to asymptote after about 10 years, with the highest occupancy occurring in 2016 (n = 77). The number of nests occupied per year was best fit with a quadratic function ($R^2 = 0.447$, $P = .009$) indicating initial growth and then leveling off after approximately 2010 (Figure 5). During one year of the study, 2013, the study site was only visited over a 3-day period in late May and the number of occupied boxes was likely underestimated since some birds initiate nests into early June. Excluding 2013 resulted in a better quadratic fit ($R^2 = 0.741$, $P < 0.0001$).

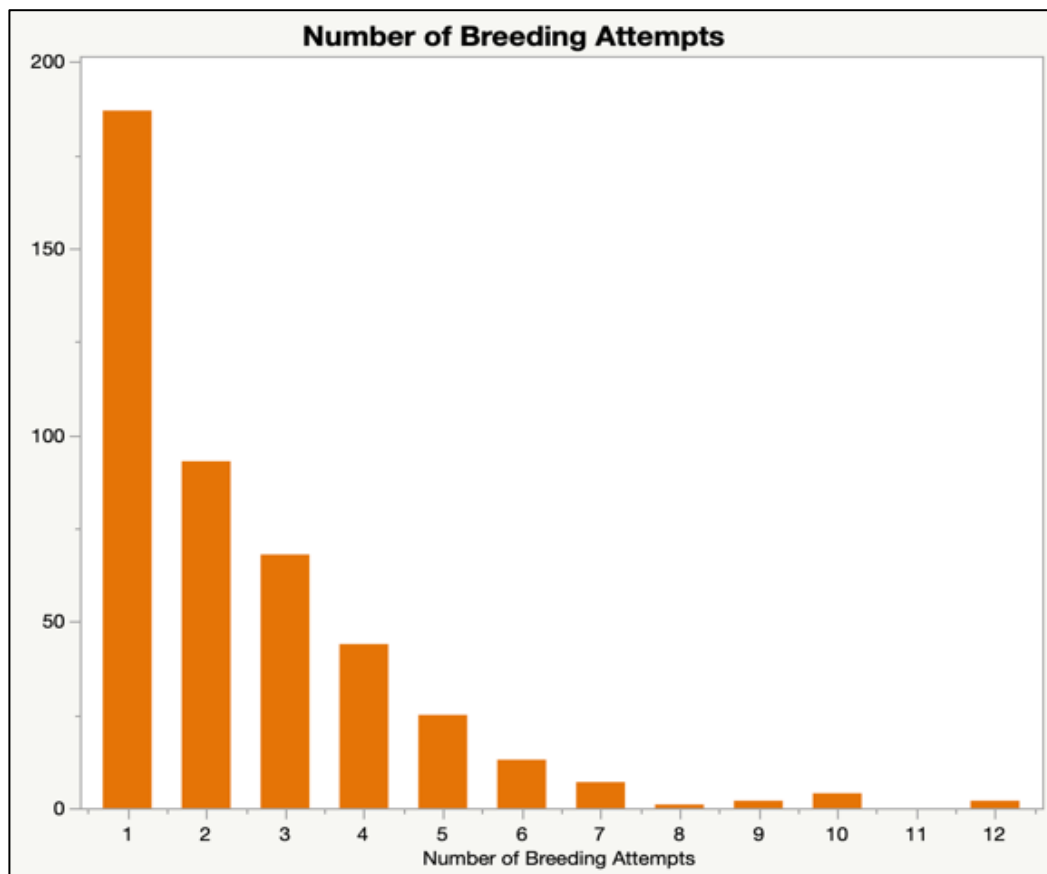


Figure 4. Histogram of the number of capture encounters per female.

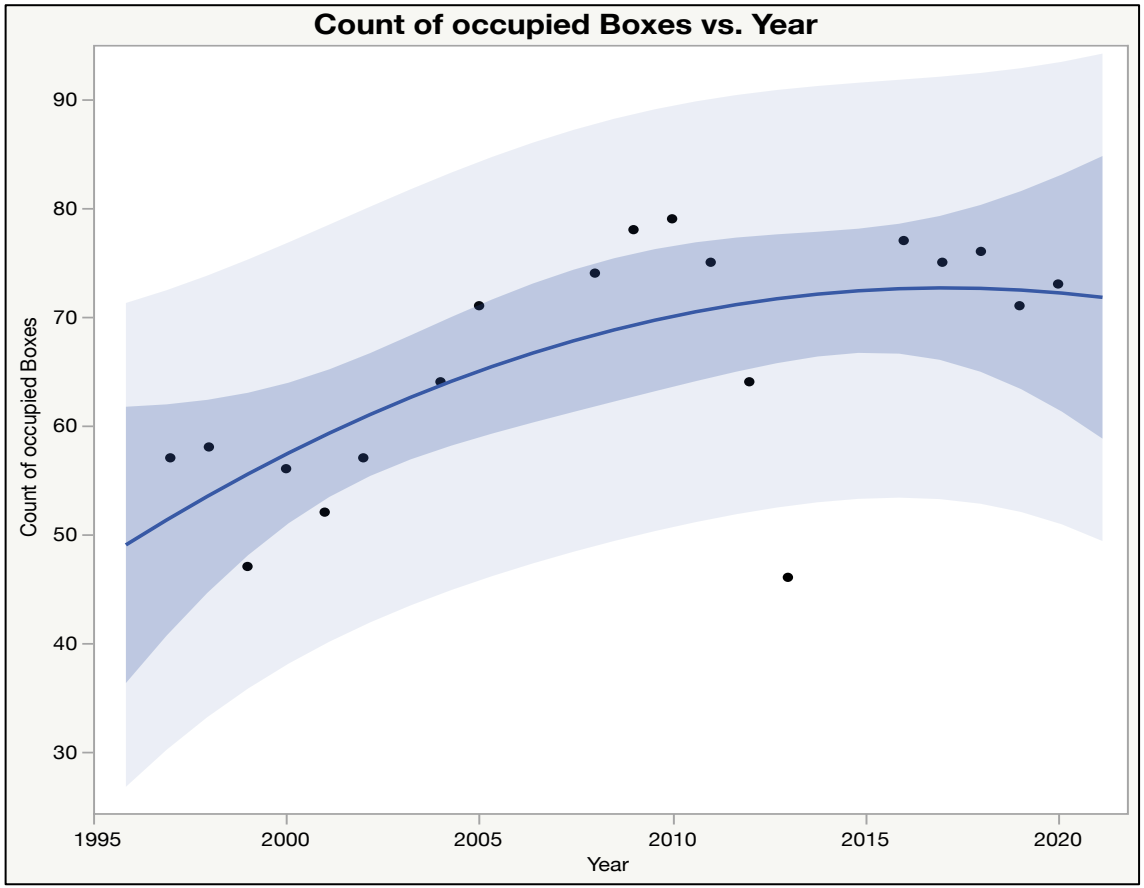


Figure 5. Scatterplot depicting the total number of nest boxes occupied by Common Goldeneye by year. The quadratic line of fit is shown, with 95% confidence interval shown in dark blue and the 95% prediction interval shown in light blue. Nesting density increased in the initial years of the study, maximizing approximately 10 years after initiation of the study.

Metrics of spring conditions

The results of a linear model of ice breakup dates between the Tanana and Chena Rivers indicated there was a significant correlation between breakup dates at the two sites ($R^2 = 0.367$, $P < 0.0001$). When using the entire recorded history of both rivers, it was clear that there was a period between the 1950's and 1970's where ice breakup on the Chena River occurred earlier than the Tanana River (Figure 6). When examining only the years of the study, the correlation of breakup dates between the two rivers was stronger ($R^2 = 0.869$, $P < 0.0001$, Figure 7). These results validate using the Tanana River dates, rather than the sparse Chena River dates, to provide an ice breakup date for each year of the study. Therefore, in all my analyses, I used the Tanana River dates of ice breakup.

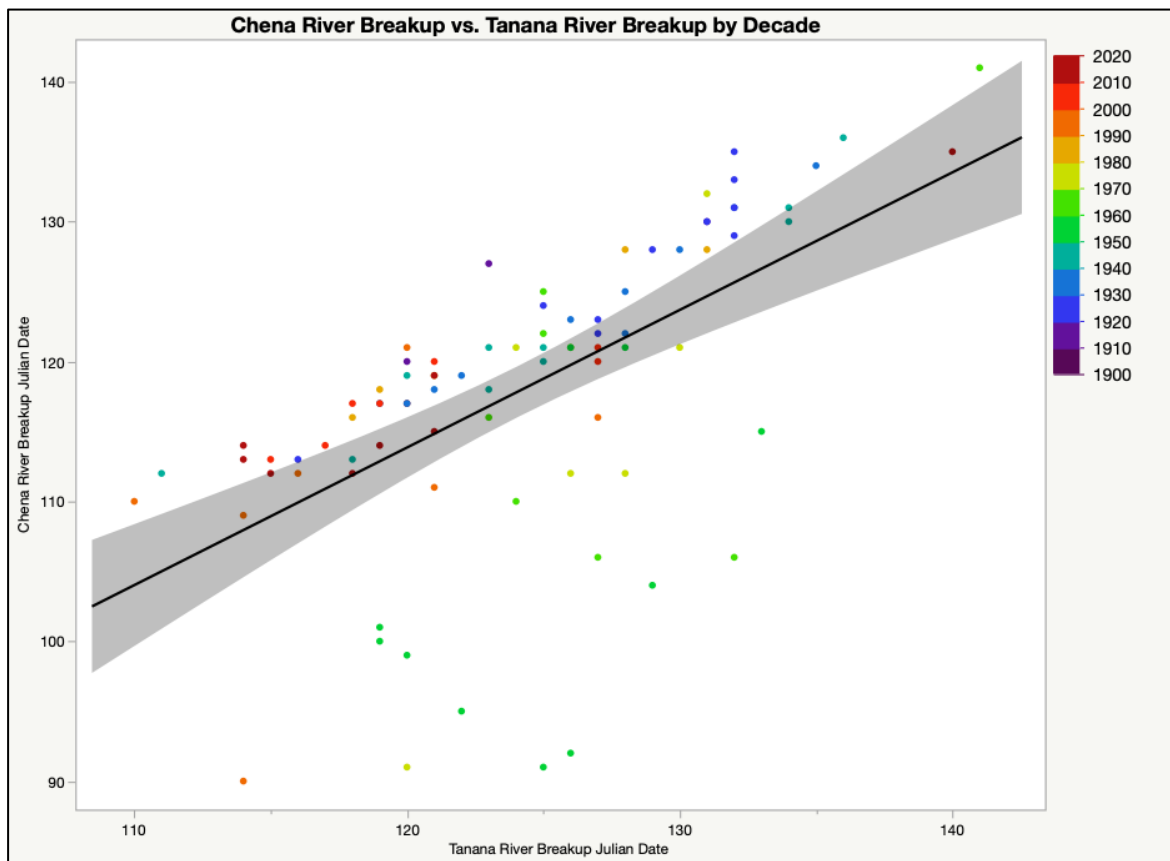


Figure 6. Julian dates of ice breakup on the Tanana River from (1917-2021) plotted against the Julian date of ice breakup on the Chena River (1917-2021). The 95% confidence interval of the line of best fit is shown in gray shading.

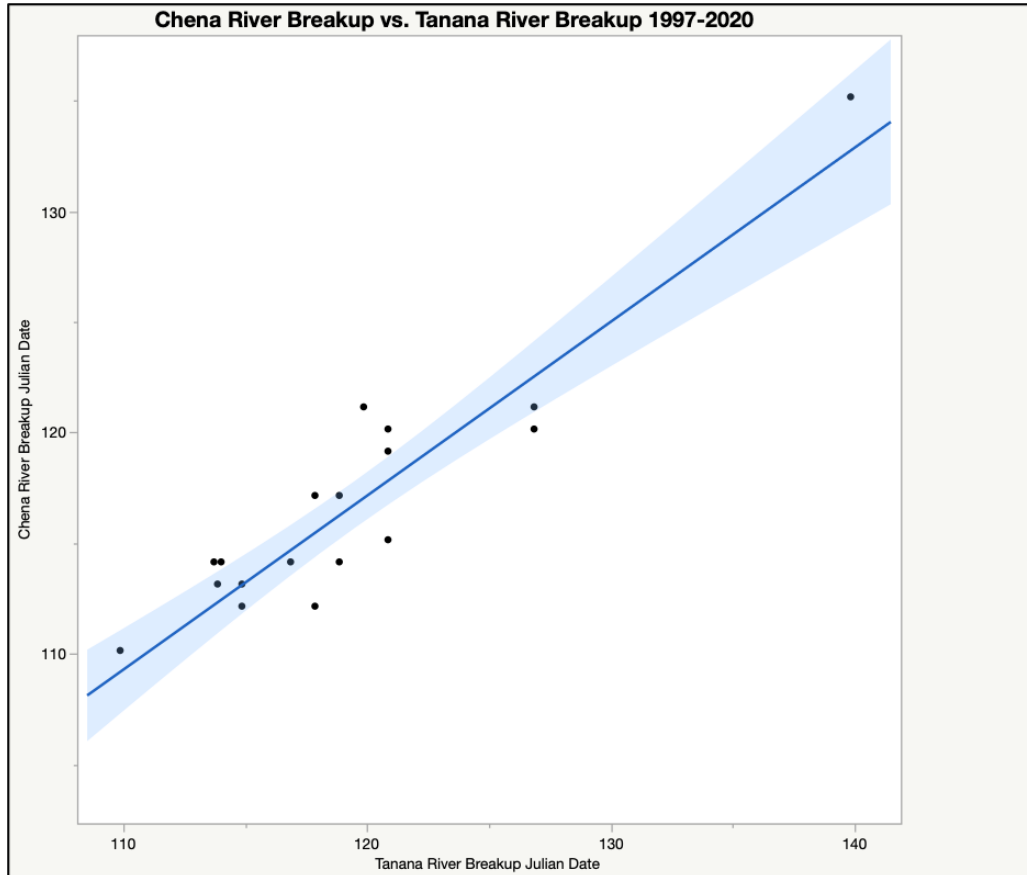


Figure 7. Scatterplot of the bivariate fit between ice breakup dates on the Tanana and Chena rivers during the years of the study, 1997-2020. The 95% confidence Interval of the line of best fit is shown in blue shading.

I examined various linear models of spring temperature and ice breakup dates on the Tanana River, and determined that air temperatures for March and April were better predictors of ice breakup on the Tanana River than March alone, April alone, or March through May. The model of spring temperatures (March-April) on ice breakup dates also indicated a strong correlation between spring temperature (adjusted $R^2 = 0.45$, $P < 0.0001$, Figure 8), suggesting that both spring air temperature and ice breakup are valid phenological indicators for spring conditions in the Fairbanks area. As a result of this correlation, I incorporated tests of collinearity into my models, and determined that either ice breakup dates on the Tanana River or air temperatures may

be used as a phenological indicator of spring, as has been done in similar work on goldeneyes (Clark et al. 2014).

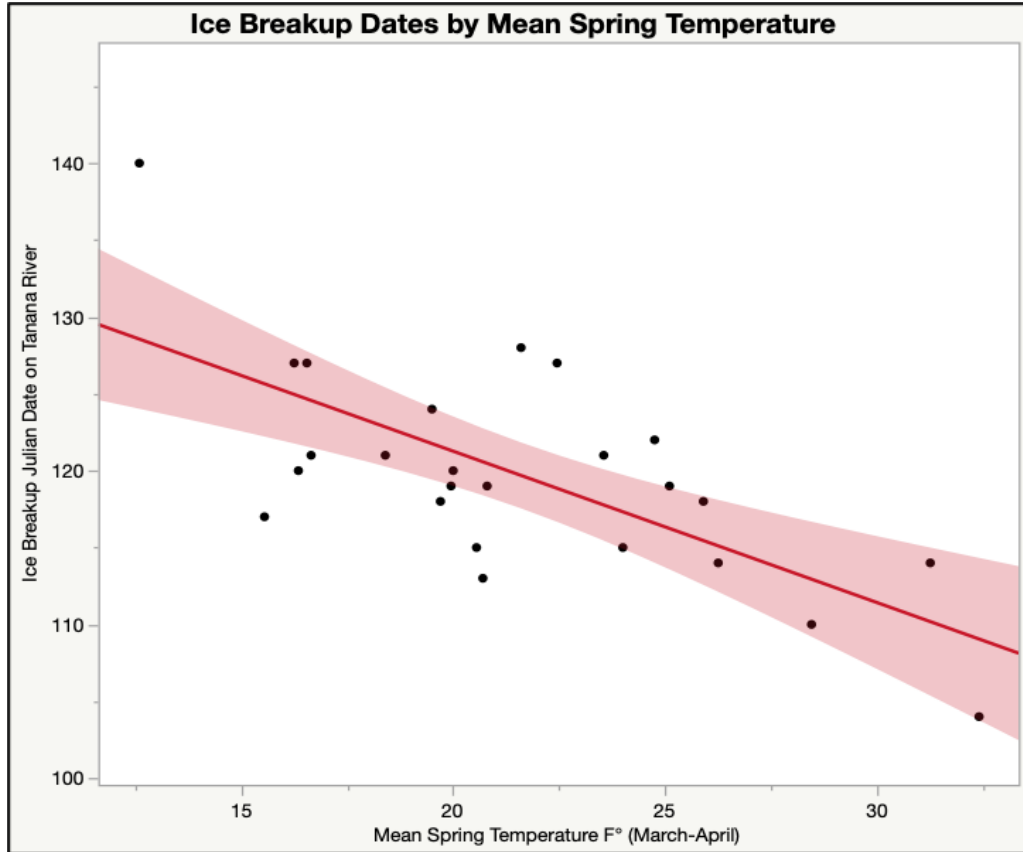


Figure 8. Scatterplot of the bivariate fit of the average spring temperature (F°, March-April) on the Julian Date of ice breakup of the Tanana River at Nenana, Alaska (1997-2021). The 95% confidence interval of the line of best fit is shown in red shading.

Changes in spring conditions over time

Based on linear regressions of ice breakup date by year, the date of spring ice breakup on the Tanana River has trended significantly earlier over time ($p < 0.0001$), advancing 0.09 days per year (1917-2020). The low R-squared value of the analysis ($R^2 = 0.17$) indicates there is high variability among years. Running the same linear regression of ice breakup over only the years of the study, 1997-2020, breakup date still appears to be trending earlier over time, but it is no longer statistically significant ($p = 0.429$, $R^2 = 0.029$, Figure 9). Despite this weaker trend, the project

time period demonstrates high variability in breakup date. Similarly, based on linear regressions of the annual air temperature by year, the average annual air temperature has significantly ($p < 0.05$) increased over the study period, by 0.14 degrees Fahrenheit by year. In this analysis, the lower R-squared value ($R^2 = 0.19$) also indicates that annual air temperature can be highly variable.

Changes in winter conditions over time

Winter conditions in the Gulf of Alaska, as indexed by PDO, also varied considerably over the time period of this study. The PDO typically cycles through warm and cool phases, which is clearly observable from the winter mean PDO values (Figure 10). Within each phase, there is notable interannual variation of the magnitude of the PDO. Over the course of the study, there were multiple shifts between cool and warm phases. Warm phases occurred in the winters of 1997-1998, 2001, 2003-2006, 2010, and 2014-2019. Starting in the winter of 2015, there is a noticeable trend to an extreme warm phase that continued for most of the remaining study years, until a small cool phase in the winter of 2020. Cool phases occurred during the winters of 1999-2000, 2002, 2007-2009, 2011-2013, and 2020. Of particular note are years that would be expected to be within a cool phase but demonstrated a brief shift to a warm phase (2001, 2010). Many of the winters in warm phases were also greater in magnitude than any of the winters in cool phases (Figure 10).

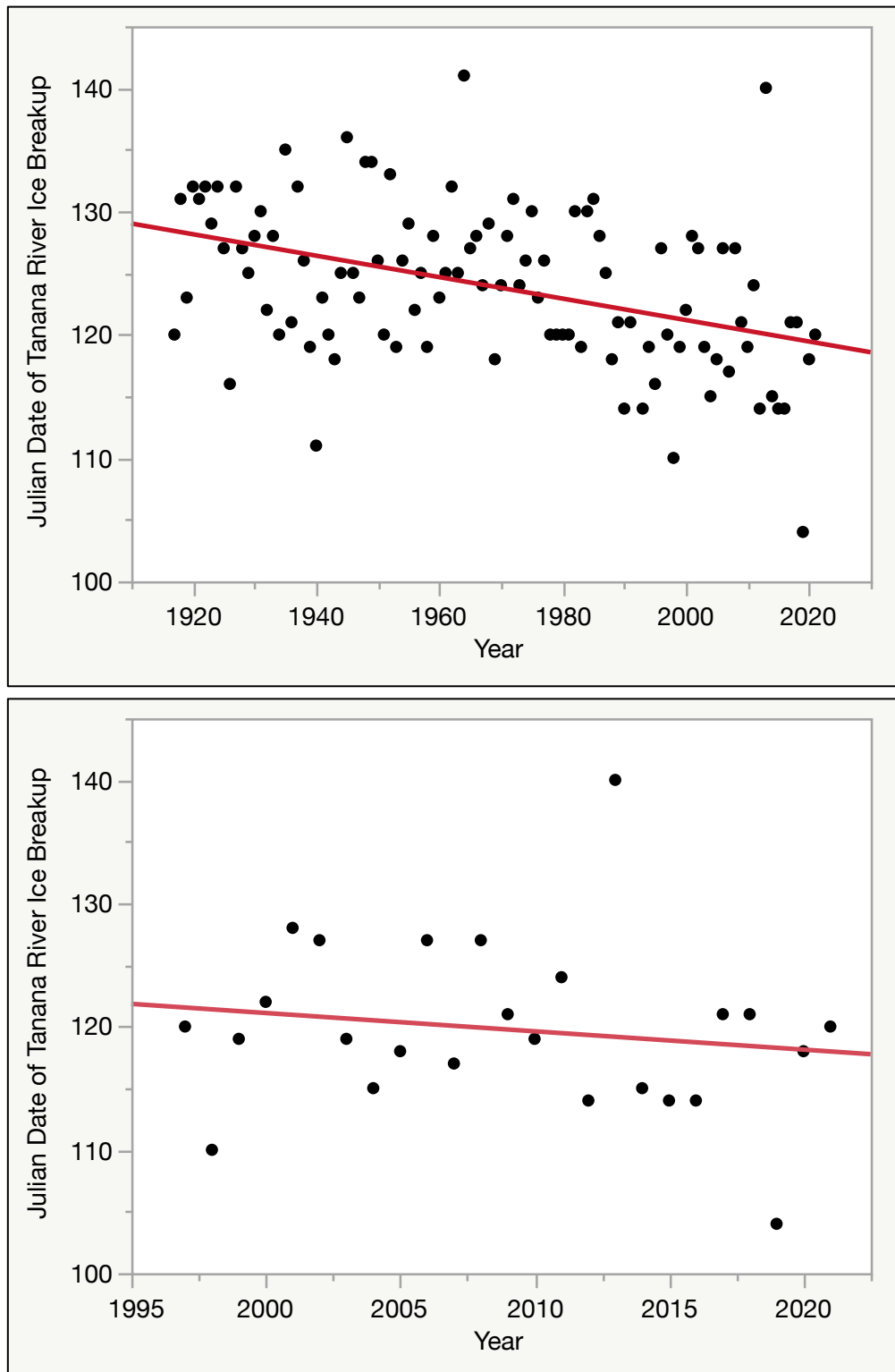


Figure 9. Scatterplots demonstrating ice breakup on the Tanana River. The top figure shows dates over the entire recorded history (1917-2021) with a significant negative relationship ($\beta = -0.09$, p -value < 0.01). The bottom figure shows the trend over the years of the study (1997-2021), which is not significant ($\beta = -0.15$, p -value = 0.45) but exhibits high variability.

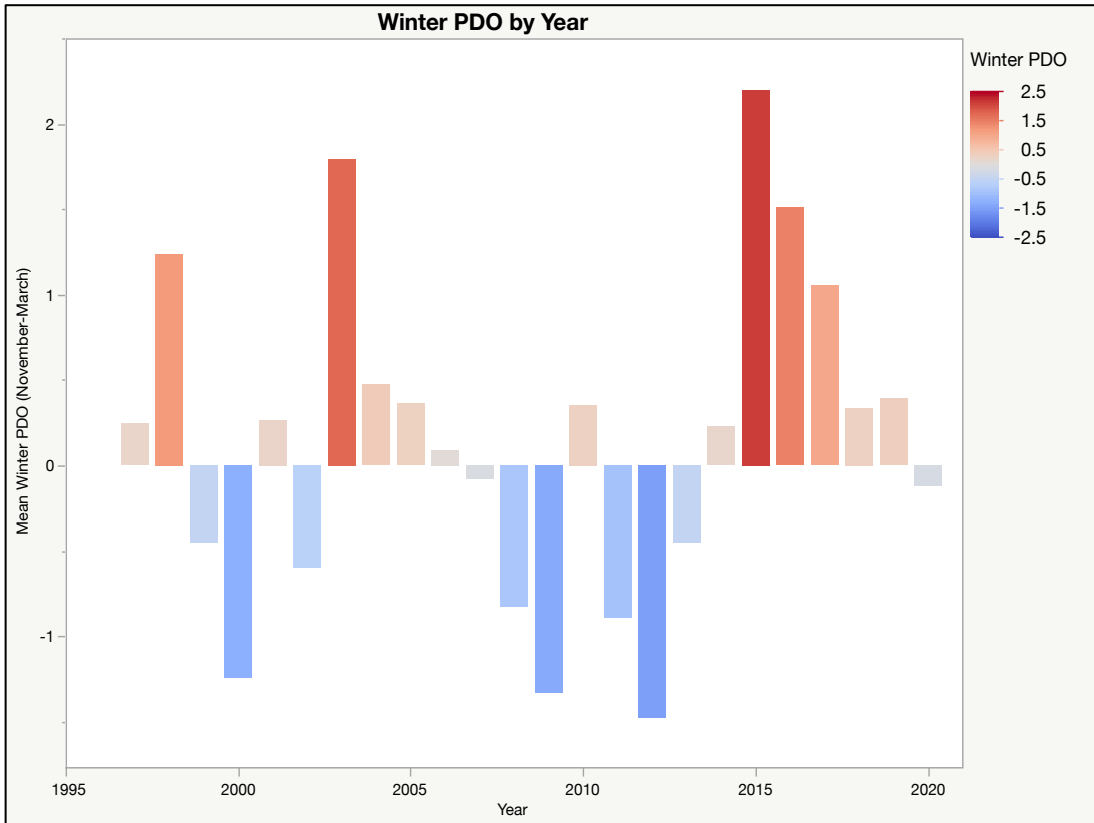


Figure 10. Graph demonstrating the mean winter (November through March) Pacific Decadal Oscillation for the winter preceding each breeding season during the study years. Positive values indicate milder winter conditions, and negative values indicate colder and harsher conditions.

Variation in nest initiation date over time

Nest initiation dates advanced considerably during the course of our study (Figure 11). The mixed model of the effects of year on nest initiation date indicates that nest initiation advanced significantly ($P < 0.01$) over the duration of the study, with a mean β of -0.739 days per year. The regression equation (based on a linear mixed model with female identity and next box as random effects) was $1610.15 - 0.739 * \text{Year}$, $R^2_{\text{adj}} = 0.740$, $df = 791.7$, $N = 2181$, $P < 0.0001$.

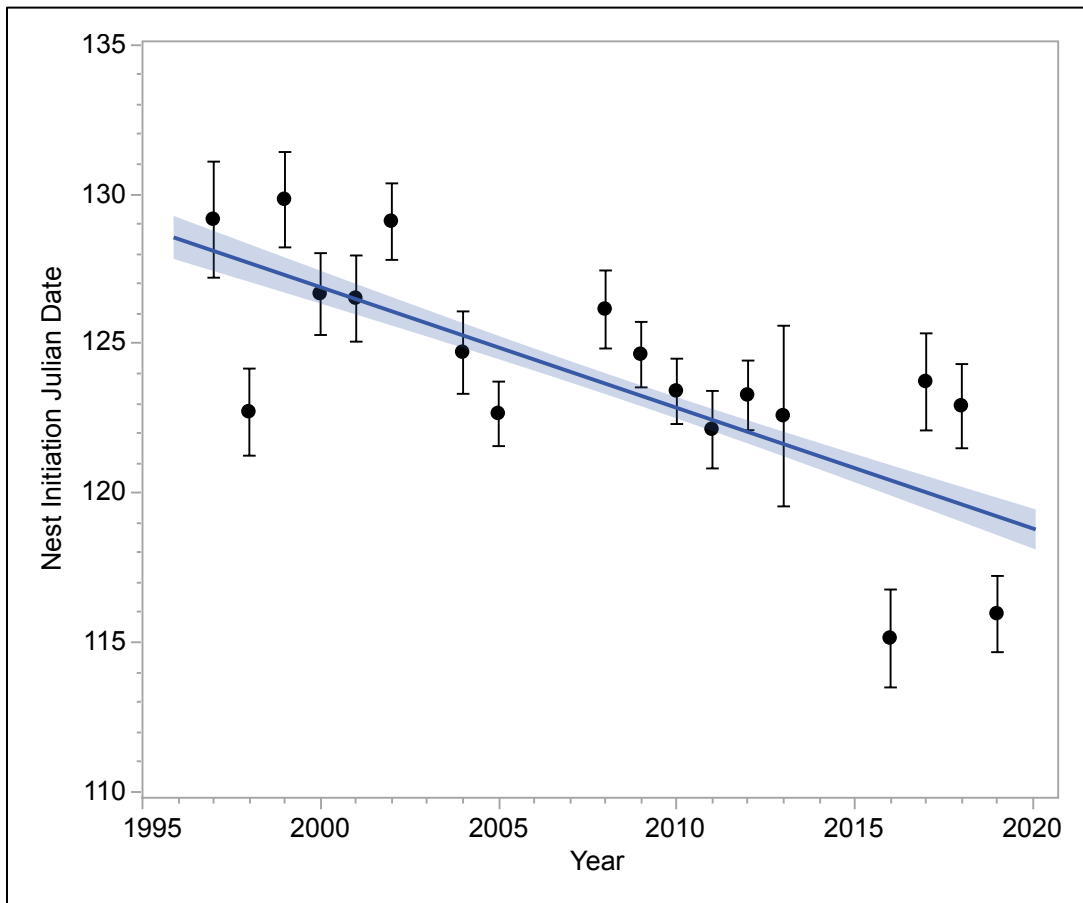


Figure 11. The advance in nest initiation dates among years over the study period (1997-2020). Each point is the mean initiation date \pm 95% confidence interval. The regression line and 95% confidence interval of the fit (blue shaded region) are shown.

Factors affecting nest initiation date

I compared multiple models with nest initiation date as the response variable and found that the model with the best fit, based on the smallest AIC_c value, was one that accounted for fixed effects of ice breakup, body condition, breeding experience, spring temperature, and the PDO, and where female identification and box identity were included as random effects (Table 2). The top model differed by the next best model (which excluded Box Identity as a random effect) by a ΔAIC_c of 158.18 and all weights of evidence were on the top model ($w_i = 1.00$, Table 2). Ice breakup date, breeding experience, and body condition indices all had a significant effect on the

nest initiation date. In all mixed models that included individual boxes as a random effect, box identifiers appeared to have a significant effect on nest initiation. However, the model of best fit included both female and box identity as random effects (Table 2). Variation among females was

Table 2. Comparison of mixed models to examine variation in nest initiation dates (Julian) as a function of standardized values of ice breakup dates on the Tanana River, mean spring temperature, breeding experience, body condition index, and preceding winter mean PDO. Random effects included female identity and box number. Models are sorted by AIC_c values in ascending order. The best fitting model is indicated by the smallest AIC_c value. K = number of parameters, w_i = weights of evidence

Predictors	Random Effects	K	AIC _c	ΔAIC _c	w _i	R ² adj
Ice + spring + experience + condition	Female + Box	6	4112.03	0	0.517	0.791
Ice + spring + experience + condition + PDO	Female + Box	7	4112.26	0.23	0.461	0.791
Spring + experience + condition + PDO	Female + Box	6	4119.33	7.3	0.013	0.789
Spring + experience + condition	Female + Box	5	4120.30	8.27	0.008	0.79
Ice + experience + condition + PDO	Female + Box	6	4183.75	71.72	0.000	0.783
Ice + experience + condition	Female + Box	5	4221.25	109.22	0.000	0.779
Ice + spring + experience + condition + PDO	Female	7	4270.58	158.55	0.000	0.727
Spring + experience + condition + PDO	Female	6	4274.39	162.36	0.000	0.725
Ice + experience + condition + PDO	Female	6	4342.57	230.54	0.000	0.716
Spring + condition	Female + Box	4	4418.69	306.66	0.000	0.745
Ice + condition	Female + Box	4	4474.26	362.23	0.000	0.741
Ice + spring + experience	Female + Box	5	4499.09	387.06	0.000	0.787
Spring + experience	Female + Box	4	4511.53	399.5	0.000	0.785
Ice + experience	Female + Box	4	4614.26	502.23	0.000	0.776
Condition	Female + Box	3	4683.81	571.78	0.000	0.707
Experience	Female + Box	3	4841.26	729.23	0.000	0.748
Ice + spring	Female + Box	4	4846.61	734.58	0.000	0.744
Spring	Female + Box	3	4873.49	761.46	0.000	0.737
Ice	Female + Box	3	4920.22	808.19	0.000	0.734
PDO	Female + Box	3	5103.71	991.68	0.000	0.703
Null (intercept only)	Female + Box	2	5166.33	1054.3	0.000	0.696

high and accounted for a large amount of variation in nest initiation. Additionally, box identity accounted for some variation, and demonstrated that some nest boxes consistently experienced earlier or later initiation dates than others.

Results of the linear mixed model analysis of the best fitting model (Table 3) using standardized values indicated that nest initiation date varied significantly with all predictor variables. Nest initiation date was positively influenced by the date of ice breakup (later breakup, later initiation; $\beta = 0.08$, $p = 0.0001$), and was earlier when spring temperatures were higher ($\beta = -0.21$, $p < 0.0001$). Nest initiation date was also earlier for females with more breeding experience ($\beta = -0.32$, $p < 0.0001$) and those in better body condition ($\beta = -0.07$, $p < 0.0001$). Interestingly, nest initiation date was also influenced by winter conditions, being earlier when PDO was higher/warmer ($\beta = -0.06$, $p = 0.006$, Table 3). Variance Inflation Factors (VIF) were surprisingly

Table 3. Results of a linear mixed model to evaluate the influence of ice breakup date, spring temperature, female breeding experience, female body condition, and winter PDO on nest initiation dates of Common Goldeneyes. The analysis included female identity and box numbers as random effects.

Predictor Parameter Estimates

Term	Estimate	SE	df	t Ratio	95% Lower	95% Upper	P	VIF
Intercept	0.0469	0.055	231	0.85	-0.0613	0.1552	0.394	.
Std Breeding Experience	-0.3227	0.0179	1722	-18.00	-0.3578	-0.2875	<.0001	1.02
Std Spring Temperature	-0.205	0.0228	1712	-8.98	-0.2497	-0.1602	<.0001	2.52
Std Body Condition	-0.0651	0.0152	1601	-4.27	-0.095	-0.0352	<.0001	1.02
Std Ice breakup	0.0807	0.0208	1690	3.88	0.0399	0.1216	0.0001	2.06
Std Winter PDO	-0.0572	0.0206	1798	-2.78	-0.0975	-0.0169	0.0055	1.46

Random Effects Covariance Parameter Estimates

Variance Component	Estimate	SE	95% Lower	95% Upper	Wald p-Value	Percent of Total
Female ID	0.5838	0.0521	0.4817	0.6858	<.0001	56.47
Box ID	0.1797	0.0336	0.1139	0.2455	<.0001	17.38
Residual	0.2703	0.0105	0.2509	0.2921		26.15
Total	1.0338	0.0634	0.92	1.1702		100

small for most predictor variables with most below 2.0 and only one at value of 2.5. This suggests that multicollinearity among variables in these analyses did not strongly influence the results. Additional analyses are planned for the future to further evaluate the potential effects of multicollinearity.

Using standardized values of each of the predictor variables (mean of zero and unit variance), we can directly compare the relative magnitude and direction of effect of each variable on nest initiation date. These relationships are depicted with confidence intervals in Figure 12.

Factors affecting female body condition

Results of the mixed models to examine body condition indicated that the best fit model was with fixed effects of both PDO and breeding experience as predictor variables (Table 4). The top model differed by the next best model (which excluded PDO) by a ΔAIC_c of 8.65 and almost all weights of evidence were on the top model ($w_i = 0.987$, Table 4). The linear mixed model analysis of the best fitting model (using standardized values) indicated that winter PDO had a negative influence on female body condition ($\beta = -0.07$, $p = 0.001$), showing that a higher PDO index, indicative of warmer ocean conditions, was correlated with a lower body condition index during the following breeding season (Table 5). Body condition indices were positively related to previous breeding experience, indicating that more experienced females were in better body condition (Table 5). Variance Inflation Factors (VIF) were very small for both predictor variables (close to 1.0) indicating that multicollinearity among variables did not influence the results.

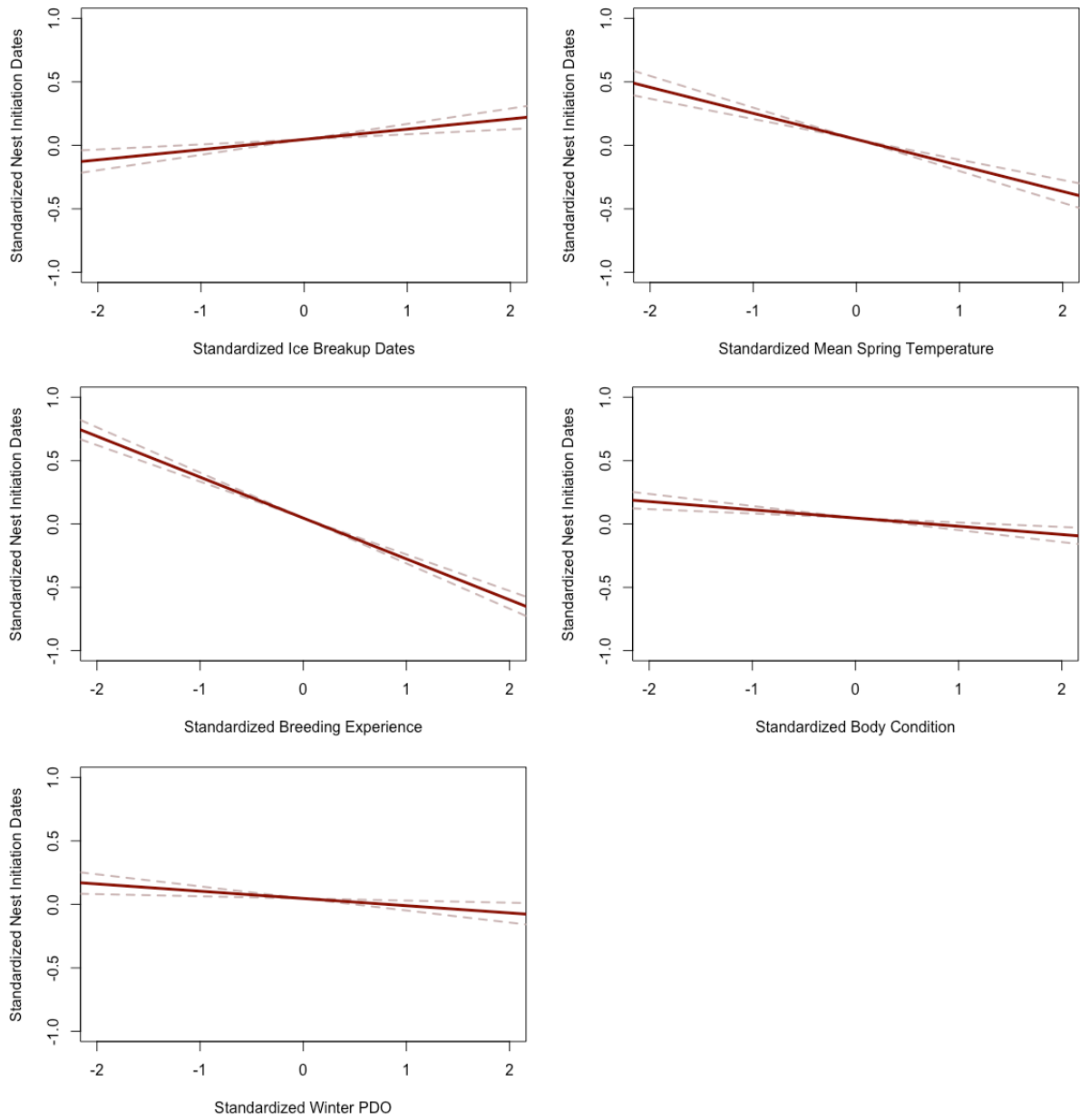


Figure 12. Line graphs demonstrating the modeled linear relationships between the standardized predicted variables and nest initiation dates. The 95% confidence intervals for each variable are shown with dashed lines.

Table 4. Comparison of mixed models to examine variation in body condition of Common Goldeneye females as a function of breeding experience and preceding winter mean PDO. Random effects included female identity. Models are sorted by AICc values in ascending order. The best fitting model is indicated smallest AICc value. K = number of parameters, w_i = weights of evidence.

Predictors	Effects	K	AICc	Δ AICc	w_i	R ² adj
PDO + experience	Female	4	5733.99	0	0.803	0.338
Experience	Female	3	5736.80	2.81	0.197	0.337
PDO	Female	3	5754.10	20.11	0.000	0.326
Null (Intercept only)	Female	2	5757.52	23.53	0.000	0.325

Table 5. Results of a linear mixed model to evaluate the influence of winter PDO and female breeding experiences on body condition of female Common Goldeneyes. The analysis included female identity as a random effect.

Predictor Parameter Estimates

Term	Estimate	SE	df	t Ratio	95% Lower	95% Upper	P	VIF
Intercept	0.0306	0.0335	382.1	0.91	-0.0352	0.0964	0.3611	.
Std breeding experience	0.1255	0.0237	2091	5.29	0.0789	0.172	<.0001	1.01
Std Winter PDO	-0.071	0.0218	2070	-3.26	-0.1137	-0.0283	0.0011	1.01

Random Effects Covariance Parameter Estimates

Variance Component	Estimate	SE	95% Lower	95% Upper	Wald p-Value	Percent of Total
Female ID	0.2446	0.0298	0.1861	0.3031	<.0001	28.8
Residual	0.7414	0.0252	0.6944	0.7934		75.2
Total	0.986	0.0355	0.9199	1.0594		100

Further analysis revealed that body condition exhibited a nonlinear relationship with year (Figure 13). Body condition improved over the initial years of the study, but it then declined during the past decade. The line of best fit was a quadratic relationship (Body Condition Index = -1094.42 + 0.5520*Year - 0.2932*(Year-2007.98)²; R²adj = 0.341, N =2106, F_{yr} = 4.26, df =1,499.7, P = 0.0396, F_{yr}²=56.46, df= 1,924.9, P< .0001)

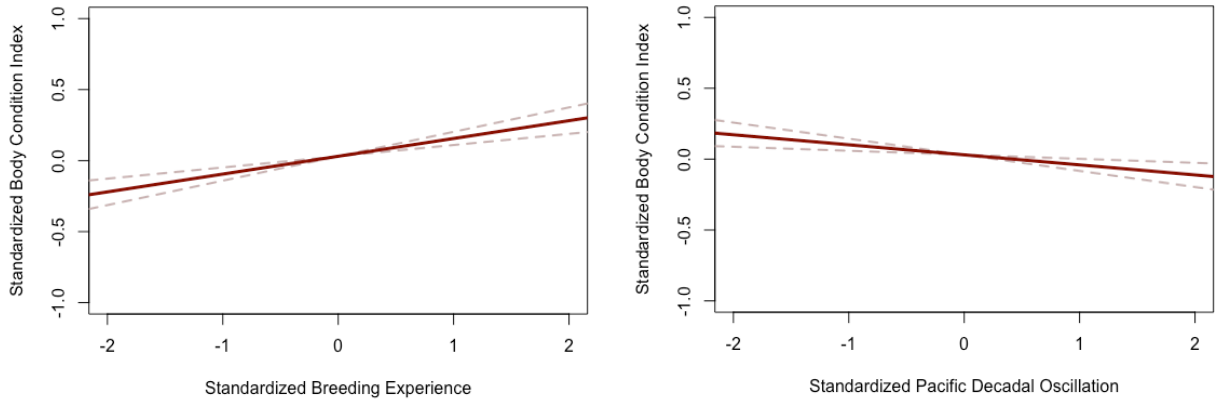


Figure 13. Line graph demonstrating the modeled linear relationships between the standardized predicted variables and body condition indices. The 95% confidence intervals for each variable are shown with dashed lines.

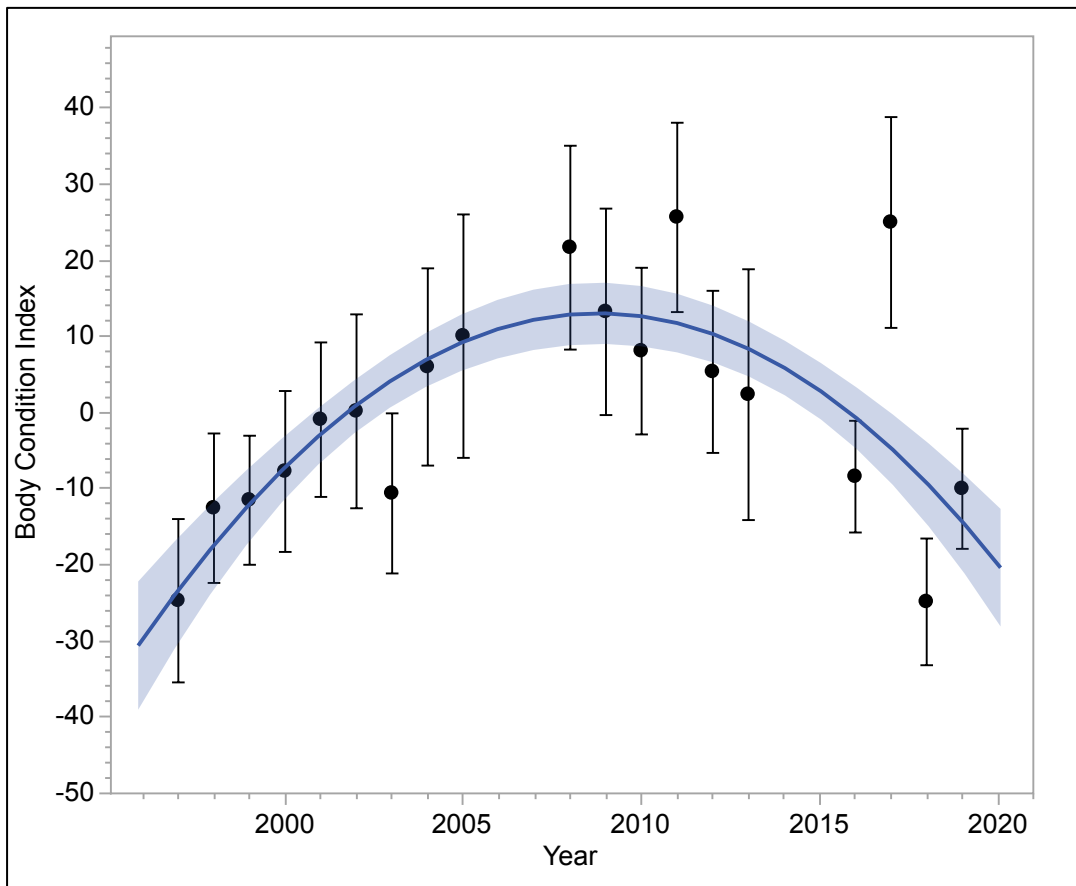


Figure 14. Variation in the body condition index of females among years over the study period (1997-2020). Each point is the mean body condition \pm 95% confidence interval. The line is the quadratic fit with 95% confidence interval of the fit shown in the blue shaded region).

DISCUSSION

Changes in climatic conditions over the study period

My analyses of climate data from an important breeding area of Common Goldeneyes in Alaska revealed considerable climatic variability and changes over the study period. Average annual air temperatures on the study site were variable, but increasing, during the study period with an increase of approximately 3.22 degrees Fahrenheit gained over the 23-year study period.

Examining the trends of ice breakup dates over recorded history (1917-2020) indicated a shift towards earlier onset of spring conditions over time. Over the long term, ice breakup dates advanced by 9.27 days over 103 years (1917-2020, 0.09 days per year). Throughout the study period, there was a slight but not a significant advance in ice breakup date, ($p = 0.4292$). However, ice breakup dates were highly variable between years (range: April 14 – May 20). This large interannual variability in ice breakup dates, reflecting the onset of spring conditions, could also be an indicator of a changing climate, as climatic stochasticity is expected to increase as a result of climate change (IPCC 2012, Guillemain et al. 2013). Additionally, this suggests that longer-term data are needed to observe significant trends in spring ice breakup dates that result from long-term climatic shifts.

Our study population of Common Goldeneyes was also subject to cycling winter conditions in the wintering area, as the PDO shifted between cool and warm phases over the study period. Episodic shifts are typical, much like the El Nino and El Nina phenomenon. However, a most recent warm phase lasted longer (2014-2019) than the prior cool phases, and also was greater in magnitude than any cool phases seen over the study period (Figure 10). In particular, the mean PDO value for the winter of 2015 (November 2014–March 2015) was 2.196, 0.404 higher than the next warmest winter of 2003 (November 2002–March 2003). Beginning in 2020, the winter PDO

shifted into a slight cool phase (-0.122). Spring air temperatures in 2020 were also cooler than in the previous several years. Unfortunately, the 2020 field season was canceled, so it is unclear how the winter conditions may have altered nesting phenology.

Further evidence of climatic shifts in the boreal forest is the increase of fires due to drier, warmer summers that frequently result in large wildfires (Stewart et al. 2013). During our study period, nine wildfires occurred on the Chena SRA, including one in 2019 (Nugget Creek Fire) that burned within 0.5 miles of some nest boxes. Wildfires encroaching on the study area could impact this goldeneye population area by destroying nest sites, as well as the nest sites and habitat of other species. While the boreal forest doesn't boast a high species richness, such disturbance could be detrimental because the boreal forest is one of the most expansive biomes in North America and is a critical breeding habitat for large numbers of birds (Wells and Blancher 2011).

Tests of Hypotheses

Response to spring conditions

The results of my analyses indicate that Common Goldeneyes are responsive to climatic variation, and these responses can be detected in a relatively short time frame. Although some environmental variables, such as ice breakup, did not have a significant trend over the course of the study, breakup dates were highly variable between years, and goldeneyes closely tracked changes in ice breakup phenology between years. As predicted, nest initiation dates were significantly and positively correlated to ice breakup dates. Moreover, the results from multiple mixed models indicated that there are several other factors that also influence nesting initiation dates, and some at a greater magnitude than ice breakup. For example, spring temperature appeared to have stronger relationships with nest initiation dates. The relationship of nesting phenology and spring temperature is well-documented (Cotton 2003, Schaper et al. 2011, Usui et al. 2017), as is

the relationship of ice-out dates and nesting phenology (Clark et al. 2014). My results are consistent with these patterns and I show that both ice-out date and spring temperature are important predictors for goldeneyes.

Life history can contribute to a species' response to shifting phenology, and species that are multi-brooded, have a larger body size, and rely on endogenous energy reserves exhibit greater phenological advancement in response to spring conditions (Bitterlin and Van Buskirk 2014). However, goldeneyes deviate from this pattern, as they are single-brooded, large bodied, and rely more on exogenous reserves than endogenous reserves during egg laying and incubation (Eadie et al. 1995, Zicus and Riggs 1996). Nonetheless, they still showed significant shifts in breeding phenology with climatic variation. Goldeneyes typically rear only a single brood during each breeding season, which allows for a relatively short brooding window. Egg laying typically lasts approximately 14 days, incubation is approximately 28 days, and hens brood ducklings until 35-42 days of age, so the entire hen's breeding cycle occurs in 84 days. Ducklings are abandoned prior to flight stage, which occurs around 56-65 days (Eadie et al. 1995). Since this breeding window is relatively small, there is some potential flexibility of timing of breeding during the season. This may indicate that variables such as body condition and migration distance will be most influential in determining goldeneyes' response to phenological shifts.

Influence of female experience

Goldeneye hens prospect during the summer before a breeding attempt, and so have some knowledge of where suitable nest cavities exist (Eadie and Gauthier 1985). Additionally, goldeneyes exhibit inter-annual nest site fidelity, so older females that return to the same breeding area for several years have information on the location of high-quality habitat and nest cavities that have been successful in past breeding attempts (Dow and Fredga 1985). In goldeneyes, older

females tend to initiate nests earlier, have larger clutches, and generally experience greater hatch success (Dow and Fredga 1984, Milonoff et al. 2004). Goldeneyes typically recruit into breeding populations at age two to three (Eadie et al. 1995) and evidence suggests that a large proportion of Chena River goldeneyes recruit at age two (Lawson et al. 2017b). However, goldeneyes are also conspecific brood parasites, and may spend early years, or years of poorer body condition, in a purely parasitic status (Eadie and Lyon 2008). As a result, many two-year old hens may go undetected due to parasitic egg-laying tendencies (Lawson et al. 2017b). (This may also result in a stronger influence of age and breeding experience, since more old females are detected than young females).

My results for the Chena River population of goldeneyes demonstrate that older, more experienced birds do have earlier nest initiation dates, as breeding experience was a significant predictor in the model of best fit ($\beta = -0.32$, $p < 0.0001$). This pattern was consistent with my predictions, and with existing literature (Dow and Fredga 1984, Mallory et al. 1994, Milonoff et al. 2004). I was unable to calculate true breeding experience, as is explained in the methods section, but known breeding experience acted as a proxy and was a reliable predictor.

Influence of body condition

I found that higher body condition indices were a good predictor for earlier nest initiation dates ($\beta = -0.07$, $p < 0.0001$). This finding is consistent with previous literature that birds in improved body condition depart wintering areas for breeding grounds earlier and are in better body condition at the start of breeding (Guillemain et al. 2010, Fox and Walsh 2012).

Goldeneyes are a bet-hedging species and so may alternate in and out of breeding status if climatic or body condition is inadequate for successful breeding (Lawson et al. 2017b). As a result, there is likely a small group of birds missing from the analysis each year due to poor body

condition. Therefore, true mean body condition of the Chena River goldeneyes may be lower in some years than is represented by my analyses.

Probing the pattern of mean body condition of females over the study period yields another interesting result of my analyses, revealing a quadratic relationship of body condition by year (Figure 13). While mean body condition of females initially increased over the early years of the study, it began decreasing around 2010 in the thirteenth year of the study. As older, more experienced females generally have larger body size, the initial increase of the mean body condition may have been simply due to increasing age and experience of females in the population. Additionally, in the early years of the project, goldeneyes were found in moderate density in the area, and increased in density over time (Figure 5). An increase in mean body condition in the early years of this study could be indicative of females benefitting from the new availability of high-quality nesting cavities and the subsequent expansion of breeding habitat and use of available resources.

Decoding the decrease of mean body condition over the last half of the study period is more perplexing but could be a density-dependent effect. The number of occupied nest boxes increased in the early years of the project and peaked around 2010. The mean body condition likewise peaked around 2011, and so may be related to competition among females for nest sites and resources on the study area. Another possible explanation of this pattern may be environmental and related to winter conditions. During the period of peak of body condition, the winter PDO was in a cool phase. The mean body condition index began to slowly drop after the 2011 peak, but the PDO entered a warm phase in the winter of 2014, after which, mean body condition more noticeably decreased. Since then, the PDO has been predominately in a warm phase, which may also be lowering mean body condition in the latter part of the study.

The year 2017 appears to be an outlier in the pattern, which may be a result of observer bias. Many observers on the study history have remained consistent, but in some years, the project has been maintained by temporary or short-term assistants. This outlier may have been a consequence of a different observer measuring hens than in other years, resulting in inaccuracies in structural size measurements, which in turn would influence calculations of body condition. Future work could examine the feasibility of correction factors between observers in measurements and determine if this outlier in fact was a case of measurement error or some other as yet-unexplored variable.

Influence of winter conditions

Many migratory birds respond to milder winter conditions by overwintering further north than in the past, consequently making migrations shorter distances (Hitch and Leberg 2007, Maclean et al. 2008, Ambrosini et al. 2011, Ambrosini et al. 2019). Chena River goldeneyes are presumed to winter in the Gulf of Alaska (Figure 2) but reports of goldeneyes during the winter and Christmas Bird Counts indicate that goldeneyes may be increasingly overwintering in the Fairbanks area (Sullivan et al. 2009, eBird 2021). Many of these observations of goldeneyes in Fairbanks during the winter come from the Chena River near the outlet of a power plant, from which warm runoff keeps the river from freezing over. Those goldeneyes that winter in the Gulf of Alaska are already short-distance migrants, so those that winter in the Fairbanks area may be even better equipped to track inter-annual variability in onset of spring conditions

My prediction that more mild winter conditions would lead to females having a higher body condition index in the following breeding season, was not supported. The relationship of PDO and body condition indices observed in this study ($\beta = -0.07$, $p = 0.001$) was opposite to the

relationship documented by other work, which showed improvement of body condition in mild and warmer winters (Gaston et al. 2005, Lehikoinen et al. 2006, Knudsen et al. 2011).

This surprising pattern warrants some examination of wintering area, and the effects that these conditions may be having on other waterbirds. In recent years, other bird groups wintering in the Gulf of Alaska have experienced adverse reactions to warming ocean conditions, most notably seabirds. Since 2015, large-scale die-offs of seabirds have occurred throughout the Gulf of Alaska at unprecedented scales. Die-offs in 2015-2016 coincided with a large marine heatwave, which raised the sea surface anomalies 1–2 °C higher than normal throughout the Pacific Ocean and Bering Sea (Walsh et al. 2018). Marine heatwaves can alter the structure of marine invertebrate communities (Ainsworth et al. 2011, Thompson et al. 2019, Kimmel and Duffy-Anderson 2020) or cause upwellings of harmful algal blooms (Van Hemert et al. 2020), which directly affect birds' food supply and health. For instance, algal blooms have caused illness and mortality in waterfowl in the Atlantic (Sasner et al. 1974, Forrester et al. 1997). In the Pacific, die-offs of seabirds have occurred throughout the year, indicating that adverse effects of climate change are felt year-round, which goldeneyes partially avoid by migrating inland during the breeding season. While no large-scale winter die-offs of goldeneyes have been reported, the pattern of lower body condition during years of warmer winters may be early indications of stress on goldeneyes in response to detrimental marine conditions under climate warming. Thus, it is important to continue monitoring and research efforts to understand effects of marine climate on seabirds, while considering other species may also be affected. In many coastal areas, beach surveys (e.g. COASST) are conducted on a regular basis to obtain baseline information on marine bird die-offs, which is a valuable tool in early detection of events and obtaining biological samples for testing.

Changes in goldeneye breeding phenology

Over the course of the study period, mean nest initiation dates of the population demonstrated significant flexibility and correlation with the onset of spring conditions. This indicates that goldeneye breeding phenology has varied over the study period and can change rapidly in response to climatic variability.

The irregularity in ice breakup timing offers an opportunity to examine how goldeneyes might respond to increasing climatic stochasticity. If Common Goldeneyes in Alaska are able to respond to this high-interannual variability in spring phenology, they may be better equipped to respond to future, long-term changes in spring phenology or conditions that may be brought about by climatic change.

Understanding why goldeneyes were able to track changes in spring phenology will also be important; understanding the underlying mechanisms that allow goldeneyes to respond could aid in the conservation and management efforts for other species that are less responsive to changing phenology and more at risk of phenological mismatch.

Key importance of multiple factors

The large number of variables that were correlated with shifts in reproductive phenology indicate that goldeneyes experience climatic changes on multiple axes and respond to a variety of different signals. Continuing climatic variation may result in some predictors becoming stronger signals for goldeneyes or, perhaps more worrisome, shifts in some variables could create conflicting signals. Such patterns have already been observed in a population of Common Eiders from Scandinavia which initially exhibited improved reproductive performance under warmer winter and spring conditions (Lehikoinen et al. 2006), but that pattern was later weakened by the

conflicting influence of increasing predators due to warmer conditions (Öst et al. 2021). As a result, non-linear climate effects and weakening or reversing trends should be expected over time.

Of particular note from my analyses of body condition were the conflicting signals already evident in the relationship of body condition and winter conditions to the timing of nest initiation. Body condition was significantly negatively correlated with initiation date, which indicates that females who are in better body condition will generally initiate a nesting attempt sooner than those in poorer condition (Gaston et al. 2005, Lehikoinen et al. 2006, Guillemain et al. 2010, Fox and Walsh 2012, Clark et al. 2014). Additionally, winter PDO values were also significantly negatively correlated with nest initiation date, indicating that warmer winter conditions are important for determining migration and nesting timing (Stirnemann et al. 2012, Fox and Walsh 2012). However, the warmer winter conditions were also significantly correlated with lower body condition indices, which conflicts with the effects on nest initiation dates. This suggests that goldeneyes are currently experiencing opposing signals, and future years may demonstrate one signal strengthening, and the weakening of another. As such, it is important to consider that current benefits to the species under climate change, as seen in several species of waterfowl, may not last long-term and be overtaken by negative effects in the future. Long-term monitoring of this population will be critical to understand the long-term reactions to multiple signals of climatic variation and change that may influence a population to react in divergent ways, and to evaluate how long a population can endure conflicting signals before one overrides another.

My work also emphasizes that wintering areas are critical in considering how a species may respond to climate change and the ability to react to shifts in climate. I found that conditions that birds experience on the wintering ground have a significant influence on breeding phenology, despite the spatial separation between the two areas. It is important to consider the stressors of

both wintering ground and breeding area conditions, even in short-distance migrants where conditions may be similar.

Implications for common goldeneye nesting in Alaska

This population of Common Goldeneyes are near the far leading edge of their northern range in Alaska, and so may be a population at risk under continually changing climate regimes. Much of the area to the north of the study site is alpine tundra (Brooks Mountain Range and the northern Arctic Coastal Plain) which would limit the expansion of breeding range into new habitats, and northward, as a result of climate warming, as has been observed in other species (Sedinger et al. 2006, Ward et al. 2009). The boreal forest that goldeneyes breed in is typically old-growth, as only older trees hold cavities large enough for goldeneyes to nest in. While ‘shrubification’ and northward spread of trees have been documented in Alaska (Zhang et al 2013, Mekonnen et al. 2021), it would likely be many years before a new forest is large enough to support Common Goldeneyes nesting. Therefore, Common Goldeneyes may be restricted to their current breeding range for the time being. Goldeneyes may instead respond with changes in phenology, as is observed in my analyses.

A likely reason goldeneyes have thus far been able to respond rapidly to climate shifts is the short breeding migration this population undertakes between wintering areas in the Gulf of Alaska and the Chena River, as has been found in other populations of short-distance migrants that may be able to track conditions on breeding grounds, since close-by wintering grounds exhibit similar climatic patterns (Lehikoinen et al. 2006, Oja and Pöysä 2007, Miller-Rushing et al. 2008, Clausen and Clausen 2013, Bitterlin and Van Buskirk 2014, Clark et al. 2014, Usui et al. 2017). This pattern may be expected to continue, and managers may be able to estimate when goldeneyes on the Chena River study site may begin breeding, based on the winter and spring conditions.

Similarly, other waterfowl species that both winter and breed in Alaska may also similarly show rapid responses to variation in phenology.

Though my analyses indicate that nesting initiation occurs earlier in years of earlier spring conditions, I was unable to determine if Chena River goldeneyes are arriving on the breeding grounds earlier. The presence of goldeneyes in nearby Fairbanks during the winter suggests that earlier migration to breeding areas may be possible, as well as the earlier nest initiation dates in years of warmer winters or earlier spring conditions, as has been seen in other species (Knudsen et al. 2011, Ambrosini et al. 2019).

It should be acknowledged that this project takes place in an artificial nest box system that has increased the number of consistently available nesting sites and results indicate this has also increased the local population of Goldeneyes relative to historic population size. Despite the increase in nesting adults, the system appears to have reached a maximum nest density within the first few years of the study and is unlikely to increase further. This nesting density may be maintained by the amount of suitable habitat available, or because goldeneyes are highly territorial on breeding and brooding grounds and would likely not allow for higher nesting densities. This increase in numbers of nesting adults is likely a result of high productivity, as some studies have shown that reproductive output is typically increased in nest boxes compared to artificial cavities (Brazill-Boast et al. 2013, Norris et al. 2018). However, this nest box system closely mimics elements of natural cavities through the placement of nest boxes in diverse habitats where large trees are present and natural cavities might normally be found. Furthermore, the lack of predator guards on the nest boxes allows for natural levels of predation and nest failure. Maintenance and periodic replacement of nest boxes may increase productivity by improving nest site quality, but all nest boxes on the study site are constructed of untreated wood attached to trees that will closely

mimic the characteristics of a natural cavity. Due to these factors, I believe that this system replicates many behaviors and patterns that would be seen in a natural cavity-nesting population as closely as possible.

Implications for other boreal-nesting waterbird species

Since this population of Common Goldeneyes are short-distance migrants, they are evidently able to readily track changes in spring phenology. Similar responses may be found in the other cavity-nesting waterfowl species that utilize the nest-box system, such as the Bufflehead (*Bucephala albeola*) and Common Merganser (*Mergus merganser*). Other species that nest on the study site, such as the Canvasback or Redhead, are longer-distance migrants and may not track these changes as closely because wintering grounds may be experiencing different climatic conditions (Jones and Cresswell 2010, Reynolds et al. 2017, Ambrosini et al. 2019). These species are also ground-nesting species, so rely on no snow cover to initiate nesting, unlike goldeneyes, which has cavities available year-round. While research has not been done specifically on ground-nesting waterfowl of the area, they may be more at risk of phenological mismatch, and as a result, reduced survival, lower breeding success, and reduced forage availability (Miller-Rushing et al. 2010, Doiron et al. 2015).

Management Implications

Given the threat that changes in climate have to the future, it is vital to be proactive in understanding how it may affect wildlife species. Little work has previously been done to understand how climatic and phenological shifts are impacting cavity-nesting waterfowl, and these results indicate that Common Goldeneyes are flexible in exhibiting responses to climatic changes. These results also emphasize the importance of long-term monitoring projects that track individual

species' responses to climate change. Many research projects are conducted over a short time period, and so may miss critical responses to climatic variation. Within the window of this study, clear climate signals were detected, which may not have been detected without a minimum of twenty years of monitoring. Continued monitoring of goldeneyes on this study site will allow for further understanding of climate effects, be important in determining how goldeneyes respond to multiple and contrasting climate signals and detect if goldeneyes begin to experience adverse effects from climate change. Goldeneyes in particular may serve as an indicator species for the health of wetlands and health of mussel and invertebrate communities, which support many other taxa.

It is possible that other changes in goldeneyes breeding ecology have occurred over the study period, such as clutch size, clutch volume, or hatching success. While these are also important variables to consider, they were not included in this analysis because the data were not available digitally. Future work may further examine the impacts of climate stochasticity on breeding ecology and individual hens by examining these variables over the course of the study.

Future work is also planned to consider the effects of inter-individual variation in responses to climate variability in the population-level response. Examination of nest initiation date by female identity indicates that this population exhibits high inter-individual variability in nesting phenology (Figure 14). Analyses of variation in nest initiation date (Table 2) and body condition (Table 4), in which female identity was included as a random effect, revealed that significant and substantial source of variation resulted from consistent variation among females over years. This variability may be indicative of individual hen personalities, or consistent between-individual behaviors or within-individual consistency in behavior that might influence a population's ability to respond to climatic variability and long-term change. If a population exhibits a shift in response

to climatic variability, it will be useful to know if climatic changes are selecting for females that consistently nest earlier or if the entire population is shifting to nest earlier. Understanding this, a manager would be able to assess whether selection for certain individuals and/pr personality types could influence the genetics and reproductive output of a population. For example, in a population of goldeneyes in central Finland, females were observed to have variable flexibility in responding to the variation in spring conditions, similar to the pattern observed in the Chena River. In the Finnish population, this variability also appeared to contribute to recruitment of young, as earlier-nesting females generally produced more ducklings (Clark et al. 2014). Further examination of the source of population-level shifts will enable researchers to understand what makes certain species, or individuals, more resistant to climate change impacts, and how to protect species under climate change.

In conclusion, Common Goldeneyes appear to be adapted to track short-term climatic variability, as short-distance migrants that winter in close proximity to breeding areas. Goldeneyes, however, seem to be susceptible to climate on their wintering grounds, which appears to have negative effects on body condition in warmer years, and this, in turn, may be an early signal of an uncertain future under continuing climate change. While Common Goldeneyes have been a focus of a moderate amount of reproductive research on waterfowl, it appears that much remains to be discovered about how individual female personalities may affect their response to climatic changes.

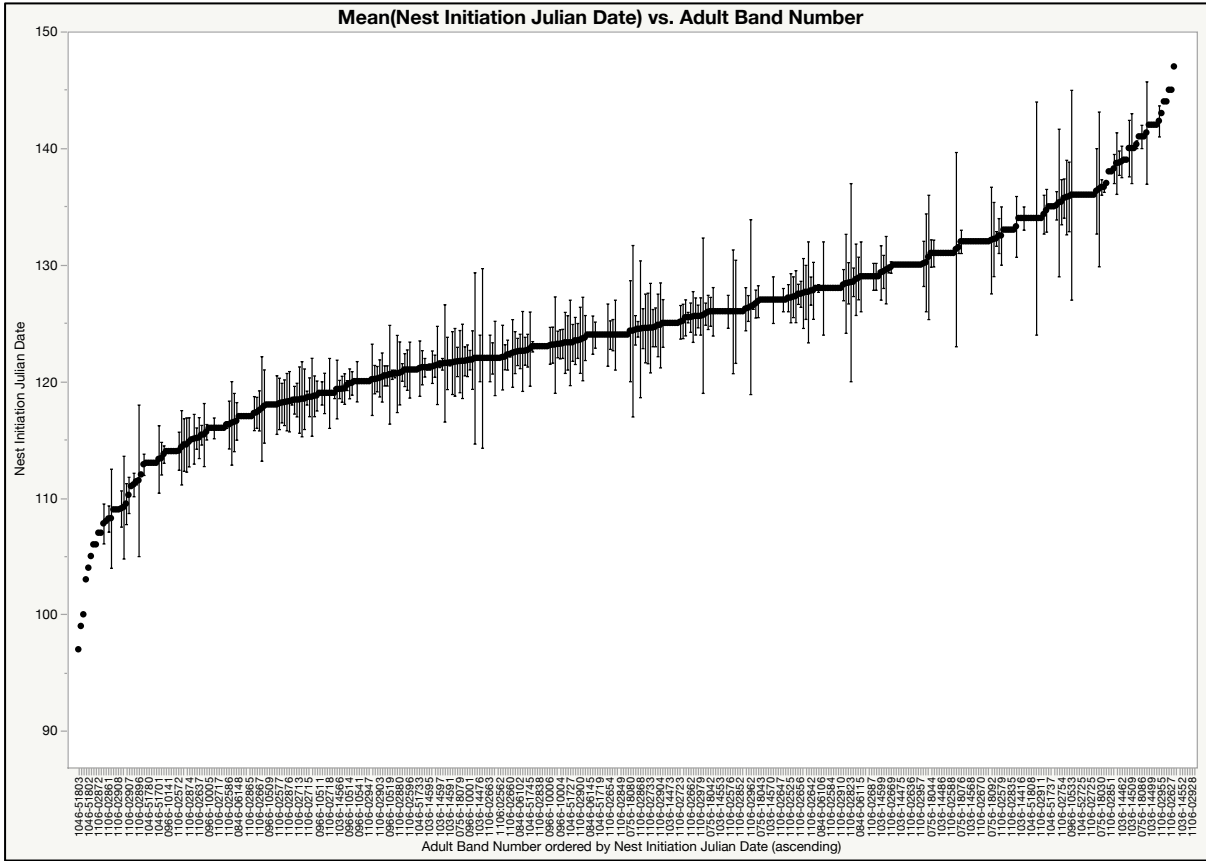


Figure 15. Graph demonstrating mean initiation dates by individual female identification numbers (adult band numbers used here). Bars show the range of initiation dates over the female’s known breeding history.

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