PHENOLOGY AND MOVEMENT ECOLOGY OF MID-ATLANTIC BREEDING SHOREBIRDS

A Thesis Submitted to the Committee on Graduate Studies in Partial Fulfillment of the
Requirements for the Degree of Master of Science in the Faculty of Arts and Science

Trent University

Peterborough, Ontario, Canada

Environmental and Life Sciences M.Sc. Graduate Program

May 2025

Abstract

Phenology and Movement Ecology of Mid-Atlantic Breeding Shorebirds

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Migration, space use, and phenology play key roles in shaping avian populations and are therefore critical for conservation. My thesis examines the migration strategies and non-breeding spatial requirements of Virginia's beach-nesting American Oystercatchers (*Haematopus palliatus*), as well as the nesting phenology of mid-Atlantic American Oystercatchers and Piping Plovers (*Charadrius melodus*). I assessed migratory decisions using field-readable bands and GPS transmitters, finding that ~90% of Virginia's beach-nesting American Oystercatchers migrate out-of-state during the non-breeding season, though tested hypotheses did not strongly predict migration patterns. I then estimated home range sizes of American Oystercatchers during the non-breeding season, revealing high individual variation (12.1-201.6 km^2) and a potential trend toward larger home ranges in males. Finally, I analyzed clutch initiation timing of American Oystercatchers and Piping Plovers in response to climate change, finding that American Oystercatchers advanced timing of breeding by 10.7 days between 2005-2022, while Piping Plovers showed no significant shift.

Keywords: movement ecology, behavioural ecology, migration, home-range, climate change, phenology, shorebirds, ornithology

Acknowledgements

I would like to first and foremost thank my supervisor, Erica Nol. It is because of you that I have been able to call Chincoteague my home for three extensive field seasons. Chincoteague will forever be in my heart. Thank you for letting me stay at your home, introducing me to the delicacy that is the Chincoteague Oyster, and making my time there so incredibly memorable. From thanksgiving dinners to family gatherings, you always made me feel like family. I would also like to extend these thanks to Chris Risley; I have very much enjoyed our countless bird discussions and everything you have taught me.

Next, I thank Lyn Brown. Thank you for introducing me to the project on American Oystercatchers, and for your endless revisions and insight throughout both my undergraduate thesis and master's degree. Thank you to Kevin Holcomb, my American pseudo-adoptive father, for putting up with me and not immediately shooting down every wild request I made. Your boat was in good hands, and please recall not once did I get a truck stuck on the beach (boats do not count). Thank you, Katie Oliver, for your knowledge and friendly banter, and for considering the needs of Lyn and I even when it made things excessively complicated. My thesis would not exist without the three of you. Speaking of such, thank you to the dozens of research technicians and interns at Chincoteague National Wildlife Refuge for your indirect contributions towards my thesis. If you worked for the refuge between 2005 and 2024, it is inevitable parts of your work can be found in the chapters below.

I am so incredibly thankful for my collaborators in the American Oystercatcher Working Group. Lindsay Addison, Kate Goodenough, Alex Wilke, Shiloh Schulte (to name just a few), thank you for inspiring me. Given the number of my birds which were

resighted in Florida, thank you to Pat and Doris Leary. I am forever thankful for your hard work and dedication towards the conservation and protection of American Oystercatchers. A very big thank you to Kristen Johnson for your time spent uploading all banded American Oystercatcher photos on iNaturalist to the Working Group's database; several of your observations have contributed to my thesis. I would also like to thank my thesis and defence committee members Paul Smith, Nathan Senner, and Gary Burness for their valuable feedback and insightful comments on my thesis.

I would like to thank the rest of the Nol lab, in particular Anne Ausems, Olivia Maillet, Sarah Bonnett, and Andrew Brown for your support and advice. Thank you to my dearest friends Isabelle Decorso, Carolina Koebel, Mitchell Shorgan, Bradley Howell, Mikaella Grant, and Brooklyn Cars. I am sure our supervisors would be thrilled to know how much of our funding went to beer at The Only or games of shuffleboard. Finally, thank you to my parents, Ed and Debbie, for your support and believing in me. I hope I have made you proud.

Finally, I would like to thank coastal Virginia and the surrounding areas for all it has taught me and the many, many great birds it has brought me. Across my three summer seasons, and an additional three weeks in December, I saw 263 bird species. Notable self-finds include an adult male Curlew Sandpiper, Black Rail, Yellow Rail, Great Shearwater, Little Gulls, and of course Leach's Storm-Petrels. I discovered some of my favourite places to explore – including Saxis Wildlife Management Area, Mutton Hunk Fen, and Pocomoke State Park.

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Chapter 1:

General Introduction

1.1 Climate Change and the Environment

Increases in global temperatures and extreme weather events due to climate change are occurring at alarming rates. It is estimated that global temperatures have increased by 0.06°C per decade since 1850 and are predicted to continue increasing at a rate of 0.20°C per decade (NOAA 2023). Under current climate change models, precipitation is expected to increase significantly in coastal environments as greenhouse gas emissions rise (Hennessy *et al.* 1997; Tabari 2020; Konapala *et al*. 2020). The probability of heavy daily precipitation is predicted to increase by half, and global average precipitation is predicted to increase by 10% if atmospheric carbon monoxide concentrations double (Hennessy *et al.* 1997).

Coastal zones have seen significant overall increases in precipitation compared to inland zones (Curtis 2019). Severe storms, adverse weather events, and hurricanes are also becoming more frequent. On the Atlantic coast of the United States, tropical cyclones have intensified by nearly 30% since the late twentieth century (Garner 2023). The rate at which category one or weaker tropical cyclones intensify into category three or greater hurricanes in 36 hours has doubled in the same period (Garner 2023). Tropical cyclone intensity is estimated to increase by 2-11% by the turn of the century (Knutson *et al.* 2010). Hurricanes of this intensity significantly alter coastal environments when they reach land (Houser and Hamilton 2009; Mo *et al.* 2020; Wernette *et al*. 2020) by acting to remove vegetation, renew beach habitat, and reset successional processes in which coastal environments establish themselves (Vinent and Moore 2014; Camelo *et al*. 2020; Vinent *et al*. 2020).

As climate-driven disturbance reshapes coastal landscapes, migratory birds that rely on these ecosystems face growing challenges. Migration patterns of birds are subject to alteration due to shifting climatic conditions, with birds potentially facing changes in the timing of migration, degradation of migratory stopover sites, and the loss of suitable stopover or wintering habitats along traditional migratory routes (Galbraith *et al.* 2002; Foster *et al.* 2010; Canham *et al.* 2021). Additionally, climate change-induced alterations in temperature and precipitation on wintering grounds can affect food availability and habitat quality (Aarif *et al.* 2021). Such changes increase the risks that coastal birds face throughout their annual cycles.

Rising sea levels coupled with increased frequency and intensity of extreme weather events pose direct threats to coastal habitats, including erosion of nesting sites, flooding of breeding areas, and the alteration of estuarine and intertidal ecosystems – all of which are relied upon by coastal breeding birds (Daniels *et al*. 1993; Michener *et al.* 1997). Furthermore, these environmental changes may lead to the loss of key foraging habitats, reducing food availability for both the adults and chicks of birds during critical breeding periods (Burger 2023). Changes in temperature and precipitation patterns may disrupt the timing of reproductive events (Nol *et al.* 1984), such as egg-laying and chick hatching, potentially causing mismatches between the birds' reproductive schedules and the availability of food resources (Grabowski *et al.* 2013; Liebezeit *et al.* 2014; Kwon *et al.* 2017).

My thesis aims to elucidate how coastal shorebirds interact with and use their environment so that we can better understand the current threats they face. Under the context of climate change, I investigate the movement ecology of mid-Atlantic breeding shorebirds to assess migratory behaviours, space use, and phenology and how that might shape risk exposure throughout their annual cycles.

1.2 Focal Species

1.2.1 American Oystercatchers

American Oystercatchers (*Haematopus palliatus*) are obligate coastal nesting shorebirds found along the Atlantic and Gulf coasts of North and South America. The nominate subspecies, *H. p. palliatus*, breeds from the Gulf of Mexico to the Maritime Provinces of Canada (Clay *et al.* 2014; American Oystercatcher Working Group *et al.* 2020). This population is considered a species of special concern (American Oystercatcher Working Group *et al.* 2020). American Oystercatchers are monogamous and breed on barrier islands, sandy beaches, salt marsh islands, and dredge spoil islands, where open, sparsely vegetated substrates provide suitable nesting conditions (Lauro and Burger 1989; Toland 1992; Douglass *et al.* 2001; Wilke *et al.* 2005; Traut *et al.* 2006). In Virginia, the breeding season begins with territory establishment starting in late March or early April and extends through late August (Wilke *et al.* 2005). American Oystercatchers may lay 2-4 egg clutches and may lay second or third nests nearby if failure occurs during incubation (Nol *et al.* 1984). Incubation typically lasts 26 days (American Oystercatcher Working Group *et al.* 2020). Chicks then fledge (reach sustained flight) after 35 days of provisioning from adults (Schulte 2012; American

Oystercatcher Working Group *et al.* 2020). Chicks are semi-precocial and readily disperse from nests soon after hatch (Palmer 1967).

Adult survival is a critical factor affecting the viability of local populations of American Oystercatchers (Murphy *et al.* 2017). American Oystercatchers are long-lived, with lifespans exceeding 15 years (American Oystercatcher Working Group *et al.* 2020). Survivorship is often high, exceeding 85% for males and females (American Oystercatcher Working Group *et al.* 2020). Site fidelity is high for both breeding and overwintering sites (Murphy *et al.* 2017). American Oystercatchers are sexually dimorphic such that males are slightly smaller, with shorter bills, and lacking eye flecks (Carlson-Bremer 2010; Munters *et al.* 2014). Behaviour between sexes is similar during the pre-laying season (Nol 1985). During incubation, females spend more time incubating and less time resting than males (Nol 1985). During chick rearing, both parents feed chicks equally, but males spend more time participating in territorial interactions with conspecifics (Nol 1985).

American Oystercatchers in Virginia feed on mole crabs (*Emerita talpoida*), marine worms (Polychaeta), razor clams (*Tagelus plebeius* and *Ensis directus*), oysters (*Crassotrea virginica*) and mussels (*Modiolus demissus*; Nol 1985; Fedrizzi 2008; Brown and Nol 2024). Specialized bills allow them to sense marine invertebrates buried in intertidal sands or to sever the adductor muscles and consume otherwise inaccessible oysters and mussels. Diet specialization has been observed in American Oystercatchers breeding in Virginia, with some individuals specializing on mole crabs (Brown and Nol 2024). Unlike other species of Oystercatchers, there is considerable dietary overlap between the sexes (Brown and Nol 2024).

In North America populations vary in their willingness to migrate, from fully migratory in the northern part of their coastal Atlantic range to non-migratory in the south, with partial migration occurring in populations at or near the centre of this geographic range (Schulte 1012; Murphy *et al.* 2017). Approximately 48% of Virginia's American Oystercatchers remain in-state year-round, with the rest migrating out-of-state during the non-breeding season (Schulte 2012). Virginia is the only such location with an approximately equal divide between migrants and non-migrants.

The American Oystercatcher Working Group has led a significant banding effort for American Oystercatchers in the United States since 2004 (Schulte 2012; American Oystercatcher Working Group *et al.* 2020). The American Oystercatcher Working Group also maintains a thorough band resighting database with all known records of resighted field-readable alphanumeric bands (American Oystercatcher Working Group *et al.* 2020).

1.2.2 Piping Plovers

The Piping Plover (*Charadrius melodus*) is a small, sand-colored shorebird that breeds along the Atlantic Coast of North America, as well as in the prairie regions of the United States and Canada (Hecht and Melvin 2009). The population of Piping Plovers breeding along the Atlantic coast of the United States is considered threatened (COSEWIC 2013; 89 Fed. Reg. 2024). Piping Plovers prefer open, sandy habitats with sparse vegetation, such as barrier islands or sandbars (Burger 1987; Walker *et al.* 2019; Robinson *et al.* 2021). Piping Plovers can be found on their breeding grounds between April and September (Robinson *et al*. 2021) and, similar to the American Oystercatcher, may renest several times throughout a season if nest failure occurs (Claassen *et al*. 2014). Piping Plovers lay 3-4 egg clutches (Wilcox 1959) and incubate for approximately 28 days (Wilcox 1959). Sustained flight is typically reached 30-35 days after hatching (Wilcox 1959). Piping Plover chicks are precocial and disperse from nests within hours of hatching (Cairns 1977).

Juvenile survival and recruitment are relatively low for Piping Plovers (Wilcox 1959; Calvert *et al.* 2006; Stantial *et al.* 2021). Adults may have lifespans up to 14 years of age (Wilcox 1959; Clapp *et al.* 1982). Breeding site fidelity in Piping Plovers is high, but mate fidelity is less so (Cairns 1982; Haig and Oring 1988). Males are responsible for early territory establishment and nest scraping during the pre-nesting period (Cairns 1982). Piping Plovers are biparental, and both parents participate in incubation and chick brooding (Cairns 1982). Plumage and size are also similar between males and females (Elliot-Smith and Haig 2020).

Piping Plovers primarily forage in mudflats and intertidal areas where they consume a diverse range of invertebrate prey from marine, freshwater, terrestrial, and benthic sources. Their diet includes marine worms, mollusks (Bivalvia*),* crustaceans (Amphipoda), and beetles (Coleoptera; Shaffer and Laporte 1994; Cohen and Fraser 2010). The entirety of Virginia's breeding Piping Plover population is migratory and spends their non-breeding season in Georgia, Florida, Texas, or the Caribbean (Nicholls and Baldassarre 1990; Gratto-Trevor *et al.* 2016).

1.3 An Introduction to Bird Tracking

Bird banding involves affixing small, uniquely marked bands (or rings) to the legs of birds so that they can be identified and tracked over time. Although uniquely marking wild birds likely predates the seventeenth century, it was not until the late nineteenth century that large-scale banding programs were introduced (Wood 1945). Banding birds allows us to track individuals as they migrate (Bairlein 2001), estimate population age structure and demography (Nichols *et al.* 2004), and infer population sizes and individual survivorship (Sandercock 2003; Johnson *et al.* 2010). Bird bands have limitations, however, requiring that marked individuals must either be recaught to be identified, or in the case of field-readable marks, be within visual range of an observer. In an attempt to overcome this limitation, LeMunyan *et al.* (1959) developed the first remote telemetry system for woodchucks (*Marmota monax*), tracking their below-ground movement using radiofrequencies.

Researchers improved upon the work of LeMunyan *et al.* (1959) by creating smaller transmitters that weighed less and could transmit signals further to track a wide variety of terrestrial animals, including ducks and pheasants (Marshall *et al.* 1962; Cochran and Lord 1963; Brander 1968; Nicholls and Warner 1968; Dunstan 1972). The size of transmitters remained restrictive for ornithologists until nearly two decades later, when the first transmitters designed for small (~30 grams) birds were shown to be effective (Raim 1978). In 1971 a tagged elk (*Cervus canadensis*) became the first wild animal to be remotely tracked through satellite technology, no longer requiring researchers to follow animals with handheld receivers (Craighead *et al.* 1971). It was not until two more decades thereafter that the first bird, a Wandering Albatross (*Diomedea exulans*), was remotely tracked with a GPS transmitter, allowing ornithologists to easily study the movement ecology of migrants for the first time (Jouventin and Weimerskirch 1990). Use of GPS transmitters now allow researchers to accurately estimate home range size and space use of a variety of animals. GPS transmitters have the additional advantage of high temporal resolution, taking several thousand GPS fixes throughout a season if desired, allowing for highly accurate home range estimation.

My thesis includes three separate data chapters. In the first data chapter (Chapter 2), I describe the migratory strategies and status of Virginia's (USA) American Oystercatchers and investigate factors that may influence individual migratory decisions. In my second data chapter (Chapter 3), I describe the space use requirements of American Oystercatchers during the non-breeding season and how that may vary between individuals, non-breeding locations, and sexes. In my third data chapter (Chapter 4), I investigate if climate change has shifted nesting phenology in Piping Plovers and American Oystercatchers breeding in Virginia, USA. Finally, in my general discussion (Chapter 5), I discuss the limitations of my thesis and outline directions for future research.

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Chapter 2:

Differential Migration in Virginia's American Oystercatchers

2.1 Abstract

American Oystercatchers (*Haematopus palliatus*) are coastal breeding birds with migration patterns that vary across their North American range, which spans from Florida to Nova Scotia. Northern populations are fully migratory, southern populations are resident, and partial migration occurs in between. Migration can impact survival due to exposure to storms and resource limitations at stopover sites. Climate change has intensified storm events, which may influence migratory decisions. However, the factors driving individual migration remain poorly understood. To address this knowledge gap, I used field-readable bands and GPS transmitters to investigate biological or ecological factors influencing migratory decisions. I tested four hypotheses: (1) the social dominance hypothesis, predicting that males are less likely to migrate than females; (2) the body size hypothesis, predicting that larger-bodied individuals are less likely to migrate than smaller-bodied individuals; (3) the arrival time hypothesis, predicting that successful breeders are less likely to migrate than failed breeders; and (4) the trophic polymorphism hypothesis, predicting that individuals with specialized diets are more likely to migrate than those with generalized diets. Reports of field-readable bands indicate that approximately 90% of Virginia's beach-nesting American Oystercatchers included in our study migrated out-of-state during the non-breeding season, a notable difference from prior studies. However, none of the tested hypotheses strongly explained migration patterns, suggesting other factors, such as genetics, natal philopatry, or broad scale weather patterns may play a larger role than previously expected.

2.2 Introduction

Migratory behaviour is a common adaptive response to changes in seasonal environmental conditions such as weather, resource availability, and predation risk (Åkesson and Hedenström 2007). Migration has been studied in every major group of animals, including birds, fish, insects, and mammals (Hebblewhite and Merrill 2009; Merlin *et al.* 2012; Brodersen *et al.* 2014; Linek *et al.* 2021). Many different strategies are associated with migration, from entirely resident species to entirely migratory species. In entirely migratory species, every individual within the population migrates, whereas non-migratory species remain on their breeding grounds year-round. In the class Aves, partial migration is the predominant migratory strategy (Berthold 1999; Boyle 2008). Partial migration occurs when there is migratory variation within a given population, when some individuals migrate while others remain sedentary. Differential migration is a form of partial migration and occurs when members of the same population migrate different distances.

Despite being the most common migratory strategy (Newton 2008; Sahashi and Morita 2013; Cobben and van Noordwijk 2017; Hegemann *et al.* 2019), and an abundance of literature on partial migration in birds (Partecke and Gwinner 2007; Fudickar *et al.* 2013; Paprocki and Conway 2024), there is still much to be understood about partial migration, especially in shorebirds. Migration can put a significant toll on adult survival through encounters with inclement weather, a lack of resources at stopover sites, or disturbances in non-breeding grounds (Piersma *et al.* 2016; Watts *et al.* 2019; Chan *et al.* 2019; Watts *et al.* 2021). Migration can, therefore, change the risks and benefits affecting an individual throughout its annual cycle. Individuals within a partially or differential migratory population may, in turn, face different degrees of risk between migrants and non-migrants.

Many hypotheses have been proposed to explain partial migration in birds (Table 2.1). The social dominance hypothesis suggests that migratory behaviour may differ between sexes due to sex-specific behavioural dominance, sex-specific selection for individuals of one sex to arrive on breeding grounds earlier (e.g., protandry; Kokko *et al.* 2006), or physiological differences between sexes allowing one to tolerate harsher climates (Ketterson and Nolan 1976; Gauthreaux 1978; Myers 1981). The body size hypothesis (Mayr 1963; Ketterson and Nolan 1976; Chapman *et al.* 2011) suggests that within a population, the body size between migrants and non-migrants differs as larger individuals can better withstand lower temperatures and thus have higher thermal tolerance, making them less likely to migrate. The arrival time hypothesis suggests that birds with higher-quality territories will be less likely to migrate, allowing earlier development of seasonal territorial behaviour, reducing the likelihood of losing their high-quality territories and increasing reproductive success (Ketterson and Nolan 1976; Myers 1981). Finally, the trophic polymorphism hypothesis suggests that individuals with specialized foraging strategies are more likely to migrate than those with generalist strategies, as the abundance of the specialized prey can vary seasonally forcing specialists to follow food availability (Boyle 2008; Boyle *et al.* 2011; Chapman *et al.* 2011; McQueen *et al*. 2022).

American Oystercatchers (*Haematopus palliatus*) are an obligate coastal-nesting species on the east coast of the United States. Adult survival is a critical factor affecting the viability of local populations of American Oystercatchers (Murphy *et al.* 2017). Slight changes in this demographic measure can destabilize a population (Wooler *et al.* 1992; Sandvik *et al.* 2012). Migratory strategies range from entirely migratory at the northern extent of their range to entirely non-migratory at the southern extent (Schulte 2012). Gradients in propensity to migrate are the most common strategy amongst partially

Table 2.1: Summary of hypotheses tested in this chapter with hypothesis name, mechanism tested, and predictions.

Hypothesis	**Mechanism**	**Prediction**	**References**
Social Dominance	Dominant individuals are better able to compete for resources; or dominant individuals participating in territory establishment are more inclined to stay year-round or migrate a shorter distance to return to breeding territories more quickly.	Sex (M) is negatively associated with migration.	Ketterson and Nolan 1976; Gauthreaux 1978; Myers, 1981.
Body Size	Larger individuals can better withstand lower temperatures and thus have higher thermal tolerance.	Body size is negatively associated with migration.	Mayr 1963; Ketterson and Nolan 1976; Chapman *et al.* 2011.
Arrival Time	It is advantageous to maintain higher quality territories year-round, or to remain closer to breeding territories to arrive more quickly to reduce intraspecific competition the following year.	Successful breeding years (fledging at least 1 chick) are negatively associated with migration.	Ketterson and Nolan 1976; Myers 1981.
Trophic Polymorphism	Individuals with specialized foraging strategies are more likely to migrate than those with generalist strategies, as prey abundance varies seasonally	Specialization during the breeding season is positively correlated with migration.	Boyle 2008; Boyle *et al.* 2011; Chapman *et al.* 2011; McQueen *et al.* 2022; Rankin 2023.

migratory species (Newton 2008; Sahashi and Morita 2013; Cobben and van Noordwijk 2017). In Virginia – the central portion of their range – American Oystercatcher populations are believed to be partially migratory. It is currently estimated that approximately 48% of individuals remain within the state year-round (Schulte 2012).

Virginia is the only location within the American Oystercatcher breeding range believed to have an equal division between migratory and non-migratory individuals. In addition, the US Fish and Wildlife Service (USFWS) has been continuously monitoring the reproductive success of American Oystercatchers within Virginia's Chincoteague National Wildlife Refuge since 2005, providing a large historical dataset. The propensity to migrate and the factors affecting migratory behaviour is a significant knowledge gap for this species (Simons and Schulte 2009). Here, I examine the environmental and individual characteristics that explain variation in migratory behaviour (e.g., migrate or not), distance, and final locations in a population of American Oystercatchers that have been studied in the center of the geographic range, an Atlantic breeding population in coastal Virginia, USA.

American Oystercatchers are a uniquely suitable species to test factors influencing migratory propensity. Like all oystercatchers, they are sexually dimorphic (the sexes differ in size and plumage) such that females are larger than males with respect to mass, bill length, and wing chord (Nol 1985). Both sexes participate in territory defence during the pre-nesting territory establishment phase, with males exhibiting more aggressive territorial interactions (Nol 1985). Unlike most oystercatcher species, American Oystercatchers have considerable dietary overlap between the sexes showing no sex-specific niche partitioning (Hockey 1996; Nol and Brown 2024).

If the body size hypothesis (Chapman *et al.* 2011) holds true, I would expect larger individuals to be less likely to migrate than smaller individuals. If the dominance hypothesis (Myers 1981) holds true, then more dominant males (Nol 1985) should be less likely to migrate than the less dominant females. If the arrival time hypothesis (Ketterson and Nolan 1976) holds true, then individuals who have succeeded in breeding that season, as a proxy for a better territory, will be more likely to remain on their territory year-round, and be non-migratory. If the trophic polymorphism hypothesis (Chapman *et al.* 2011) holds true, then individuals with a more diverse diet will be less likely to migrate as seasonal prey variation is reduced.

Using the historical and contemporary data on banded and sexed American Oystercatchers, my objective was to understand factors driving migratory strategies of this species in Virginia. While prior research has classified this population as partially migratory based on observations of banded birds during the non-breeding season (Schulte 2012), the extent and patterns of migration remain unclear. To investigate the factors influencing migratory decisions, I apply a Bayesian framework to assess the relative importance of sex, body size, territory quality, and foraging strategies on migratory decisions. Similar studies on Black Oystercatchers (*H. bachmani*), a species that also exhibits partial migration, supported trophic polymorphism as the best predictor of migration, with specialized foragers more likely to migrate than generalized foragers (Rankin 2023). Given the prevalence of dietary specialization on mole crabs (*Emerita talpoida*) in this population of American Oystercatchers (Brown and Nol 2024), I also expect to find support for the trophic polymorphism hypothesis. By examining the ecological drivers of differential migration, this study contributes to a growing body of literature on avian movement strategies and the mechanisms shaping migration patterns.

2.3 Methods

2.3.1 Field Site

Chincoteague National Wildlife Refuge is situated in the Mid-Atlantic seaboard of the United States of America, at the northernmost extent of the Delmarva Peninsula in coastal Virginia. Comprised of a chain of several large barrier islands, Chincoteague National Wildlife Refuge provides over 20 kilometres of undeveloped and otherwise undisturbed coastline (Sittauer and Sloan 2015). The largest section of contiguous beach habitat is found on Assateague Island (37.91° N, 75.36° W), providing over 400 hectares of protected habitat (Sittauer and Sloan 2015). The next largest portion of habitat is directly south of Assateague on Assawoman Island (37.82° N, 75.50° W), which provides an additional 150 hectares of habitat (Sittauer and Sloan 2015). While Chincoteague National Wildlife Refuge protects several more barrier islands in addition to Assateague and Assawoman (most notably Metompkin and Cedar islands) we have limited our study to Assateague and Assawoman due to survey constraints.

2.3.2 Capture and Banding

All work was conducted under Trent University's Animal Care Committee Animal Care Use Approval #27856. Capture and banding of American Oystercatchers occurred during 2022, 2023, and 2024 when individuals had active nests (typically April to July). We used a decoy loop-carpet method to trap breeding adult American Oystercatchers at their nest, following McGowan and Simons (2004). We constructed loop carpets using 2.54 × by 5.08 cm wire fencing with loops tied using fishing line (similar to a bal-chatri; Mehl *et al.* 2003) at alternating corners covering a total area of 1.2 × 0.3 m. We placed three to four traps around the nest cup after removing eggs and placing them in a shaded box away from the nest. We then placed decoy American Oystercatchers and a speaker (FoxPro™ Patriot) playing alarm calls at the nest cup. If the time between flushing a bird from its nest to attempted trapping exceeded 30-45 minutes (temperature-dependent), we halted our attempt and removed our equipment. American Oystercatchers showing signs of stress, with incomplete clutches, or nests with signs of hatch (fracturing or pipping) were not trapped. We limited trapping to temperatures below 30°C, with clear weather and low wind (such that sand was not picked up and blown around). Once an American Oystercatcher was caught, we safely removed it, returned the eggs, and removed all equipment.

After capture, we affixed two unique plastic field-readable alphanumeric leg bands above the tarsal joint and one unique metal band below the tarsal joint as per the American Oystercatcher Working Group protocol (American Oystercatcher Working Group *et al.* 2020). We measured culmen (nearest 0.1 mm), tarsus (nearest 0.1 mm), wing chord (nearest mm), and mass (nearest 0.1 g) using digital calipers and scales. In 2023 we affixed PathTrack™ nanoFix GEO+RF GPS transmitters (~8.5 g) on ten American Oystercatchers using a leg-loop harness. We sexed American Oystercatchers using a combination of culmen length (females have longer culmens), nape shade (males have darker napes), eye fleck (females have pronounced eye flecks), and mass (females are heavier). If uncertain of sex, we compared the individual to its known mate.

2.3.3 Breeding and Field Surveys

To determine territory quality, nesting productivity surveys were conducted following the USFWS and American Oystercatcher Working Group protocols. Surveys were a joint effort between USFWS staff, volunteers, Trent University (Ontario) researchers, and other involved organizations. Between 2022 and 2024, Assateague Island and Assawoman Island were surveyed regularly for American Oystercatcher nest attempts and status. Territories were defined for each pair of nesting American Oystercatchers as the area used during nesting and chick rearing that was actively defended during agonistic interactions. We recorded the location, date, number of eggs, chicks, fledglings, signs of predators, habitat, and substrate. Nest locations were recorded using GPS and cellular telephone units for ease of resighting and future reference. On return visits to previously found nests (2-4 times weekly), we recorded the date, the number of eggs, chicks, or fledglings, and signs of predator activity. Surveys were continued until the fate of all recorded nests was known (e.g., whether the nest failed before hatch, how many eggs hatched, if any, and how many birds likely fledged, if any). Finally, territory was classified into one of two groups: 1, representing territories that fledged a chick in the given year, or 0, representing a territory that did not fledge a chick in the given year.

Survey windows were restricted to relatively good weather conditions to not over-stress or disturb the nesting American Oystercatcher and other beach birds. If rain was predicted to be heavier than a light shower, if winds were too strong, or if the temperatures were deemed too high (indicated by "panting" birds, usually > 30°C), surveys did not occur. If nesting birds exhibited signs of stress, such as panting, or potential predators (Peregrine Falcon *Falco peregrinus*, Great Black-backed Gull *Larus marinus*, etc.) were detected, nests were not checked. Assateague Island and Assawoman Island were surveyed for nesting American Oystercatchers approximately every 2-4 days; due to ease of access, Assateague Island was surveyed more frequently, especially during weekdays.

To assess prey diversity, foraging observations were conducted in ten-minute observation periods. The frequency of consumption, prey species, and location were recorded throughout the period. All observations were taken from a sufficient distance (~50-200 m) so as not to disturb foraging oystercatchers. I categorized individuals as specialists if GPS-tracked birds exclusively foraged along oceanside shorelines, whereas generalists utilized both oceanside shorelines and bayside mudflats (Brown and Nol 2024). For untagged birds, specialists were those that fed solely on mole crabs, with at least three independent foraging records on separate days, though some consumed small amounts (≤ 7%) of coquina (*Donax varibilis*), a transiently available bivalve. Generalists consumed additional prey types and were documented in at least two foraging events. To supplement formal observations, we conducted informal foraging assessments (usually < 2 m in duration) during routine monitoring, checking individuals twice per visit on Assateague Island and once per visit on Assawoman Island.

2.3.4 Movement Tracking and Resighting

I relied on a combination of GPS transmitters deployed by our team and public resights of alphanumeric field-readable bands on American Oystercatchers throughout the non-breeding season to categorize individuals as short-distance or long-distance migrants. GPS transmitters took location fixes on 12-hour intervals between October-March. I retrieved data from all 10 transmitters during the 2024 field season by deploying a remote base station within ~200 m of target individuals to trigger remote downloads. Although data from all tags were recovered, we only received non-breeding season data from 8 tags (one of which only recorded data during a stopover prior to failing before reaching non-breeding territory, so that we tracked only 7 individuals to their non-breeding territory).

For American Oystercatchers with only alphanumeric field-readable bands I referred to the American Oystercatcher Working Group Band Reporting database (https://www.ancperch.org/amoy/public_menu.php). This database consists of reports made by members of the public (e.g., casual birders), state agencies (e.g., Georgia Department of Natural Resources), private organizations (e.g., The Nature Conservancy), and federal agencies (USFWS, US National Park Service). The entire Atlantic coast of the United States is surveyed at least once a year by state, federal, and private organizations with the primary goal of resighting banded American Oystercatchers (although exact timing of individual surveys varies greatly). These locations are reported by site, so locations are approximate. Finally, to increase the probability of resighting banded American Oystercatchers observed by members of the public who may not be aware of reporting procedures to the American Oystercatcher band reporting database, we went through all photos of American Oystercatchers submitted by January 2025 to the community science platforms *'iNaturalist'* and *'eBird'* to document photos of banded American Oystercatchers.

Finally, in December of 2024 we did a thorough month-long survey of the marshes and bays between Assateague, Chincoteague, Assawoman, Gargatha, Fisherman, Skidmore, and Metompkin islands with the primary focus of resighting banded American

Oystercatchers. These surveys were done primarily by boat, midway between low and high tide, when roost sites are most available. This was complimented by daily surveys of the beachfront nesting environment done by vehicle (trucks or ATVs).

2.3.5 Statistical Analysis

All statistical analyses were performed in R (v. 4.3.1; R Core Team 2025), using RStudio (Posit Team 2023) and *'tidyverse'* (Wickham *et al.* 2017) for data manipulation and plotting.

First, I computed the haversine distance between the geographic center of Chincoteague National Wildlife Refuge and the absolute maximum observed distance within a non-breeding season (between October-March) using the package *'geosphere'* (Hijmans 2024). Because some degree of post-breeding dispersal is expected in every individual, I used GPS transmitter data to classify American Oystercatchers as either long-distance migrants (1) or short distance (0). Classifying migration events into dichotomous groups is often difficult and somewhat arbitrary. Many studies simply pick arbitrary distances (Meller *et al.* 2016), while others try to use biologically meaningful criteria. I noted the southernmost point achieved in a single day by a GPS-tracked American Oystercatcher (718 km) and considered any points beyond as a long-distance migration. Thus, I classified individuals as short distance migrants if they were able to reach non-breeding locations within a day's flight, while long distance migrants took several days, often with a stopover event.

To standardize body size metrics and create a single body-size variable I performed principal component analysis with wing chord, culmen, and tarsus measurements to create three principal components (Freeman and Jackson 1990; Rankin 2023). I verified that the first principal component, PC1, was positively associated with body mass using a simple linear regression where: mass ~ PC1. I then used a parametric two sample *t*-test to investigate potential differences in PC1 between male and female American Oystercatchers. Finally, I used a parametric paired two-sample *t*-test to verify that PC1 did not differ significantly between years using data from birds caught both in 2023 and 2024 in the event that there were differences in measurements between observers. Finally, I used a parametric two-sample *t*-test to investigate body mass differences between male and female American Oystercatchers.

Next, I followed a Bayesian mixed-effects logistic regression framework to evaluate whether four ecological parameters influenced migratory decisions in American Oystercatchers breeding in Virginia using the package *'brms'* (Bürkner 2017). This approach is well-suited for small sample sizes, as an *a priori* specification can inform predicted patterns based on literature and lead to better parameter estimates (van de Schoot *et al.* 2015). Because of repeat samples of individuals across years, I included individual as a random effect and ensured its inclusion significantly improved model fit *via* leave-one-out-cross-validation (Gelman *et al.* 1995; Hastie *et al.* 2009). We specified semi-informative priors following a $N(0, 1.2)$ distribution for fixed parameters. I validated specified priors using prior-predictive checks to ensure they produced reasonable distributions of simulated outcomes before incorporating observational data (Supplementary Figure 1).

Finally, I created a candidate model set with no more than two fixed parameters per model (with the added random intercept for individual) to limit overfitting resulting from low sample sizes. I did not include PC1 and sex in the same candidate models. I ran eight chains, each with 15,000 total iterations, of which the first 1,000 were discarded for burn-in for all candidate models. The remaining samples were used for parameter estimation and convergence assessment. A parameterized model would take the form:

$$logit(\pi_i) = \beta_0 + \beta_1 X_1 + \ldots + \beta_i X_i + b_{ID[i]}$$

where β_0 represents the intercept with each parameter and estimate, $\beta_1 \ldots \beta_i$, where $X_1 \ldots X_i$ represents fixed parameters (sex, breeding success, foraging strategy, body size), and where $logit(\pi_i)$ and $b_{\mathrm{ID}[i]}$ are given by the following respectively:

$$migrate_i \sim Bernoulli(\pi_i)$$

$$b_{ID[i]} \sim N\left(0, \sigma_{ID}^2\right)$$

I validated model performance by assessing the convergence of the Markov Chain Monte Carlo algorithm ($\hat{r} < 1.01$), effective sample sizes, and conducting posterior predictive checks by simulating new data based on posterior distributions and comparing them to observed data (Supplementary Figure 2). I then ranked candidate models using leave-one-out-cross-validation (LOO-CV) considering only the most parsimonious models where the difference in standard error of expected log predictive density was less than 2 (Gelman *et al.* 1995; Hastie *et al.* 2009).

2.4 Results

2.4.1 PC1 and Body Size

PC1 of our principal components analysis explained 46.96% of the total variance. PC2 accounted for an additional 34.82%, bringing the cumulative variance explained to 81.78%. PC3 contributes the remaining 18.22%. Therefore, I chose to use PC1 as the body size metric as it explained the most variance. PC1 was primarily defined by a strong positive loading for culmen length (0.69) and a strong negative loading for wing chord (-0.72), while tarsus length contributed weakly (-0.12). There was moderate positive correlation between PC1 and body mass in American Oystercatchers ($P = 0.04$, $R^2 = 0.23$). A *t*-test ($n_{female} = 12$, $n_{male} = 8$) revealed little difference in PC1 values between male and female American Oystercatchers ($t_{16.39} = 1.82$, $P = 0.09$) despite significant differences in mass ($t_{16.12} = -4.0$, $P = 0.001$). A paired *t*-test revealed no significant difference in PC1 values when comparing measurements taken on the same individual across two years ($t_7 = -0.39$, $P = 0.71$, $n = 16$). Finally, male American Oystercatchers weighed significantly less than females ($t_{65.9} = 6.86$; $P < 0.0001$).

2.4.2 Resights and Migration

Of the 61 American Oystercatchers banded in our study area between 2022 and 2024, we received a total 487 band resights (Figure 2.1), of which 68 were non-breeding resights (between November-March) across 32 unique individuals. Of the 32 individuals with band resights, three stayed in Virginia (short-distance migrants), a single individual flew north to New Jersey (short-distance migrant), 3 individuals went to North Carolina (short-distance migrants), 9 individuals went to South Carolina. (4 short-distance migrants; 5 long-distance migrants), and 16 individuals went to Florida (long-distance migrants; Figure 2.2). Therefore, more than 90% of American Oystercatchers (32) we banded at Chincoteague National Wildlife Refuge in Virginia, USA with non-breeding season resights left the state during the non-breeding season, with 50% of all individuals migrating to Florida. Of these, I classified 34% of individuals as short-distance migrants and the remaining 55% as long-distance migrants. The average distance migrated was 729 km, ranging between 3-1,462 km (for distribution see Supplementary Figure 9).

I did not find any of the American Oystercatchers we banded while conducting salt marsh and beachfront resight surveys in December 2024. I counted a total of 104 individual American Oystercatchers, six of which had bands (two from New Jersey, and four from Virginia) and an additional 23 of which were hatch-year birds. I did not locate any American Oystercatchers on beachfront habitats where they would be expected during the breeding season. Detectability was high for banded bird resights during the nonbreeding season. The proportion of banded birds with nonbreeding season resights was 52% (32/61), and the proportion of GPS transmitter birds with nonbreeding season resights (not informed by GPS locations) was 75% (6/8). There was no obvious pattern in nonbreeding season resights by state when comparing band resights to non-breeding locations determined through GPS tracking which would suggest sampling bias.

We collected sufficient information to determine foraging strategy, sex, and PC1 for 20 individuals. Our classifications also included two individuals not banded by our team between 2022 and 2024 (banded in Chincoteague National Wildlife Refuge by the USFWS in 2008 and 2009). In total we had 8 males, 12 females, and an even split of 10 generalists and 10 specialists. Two of ten GPS transmitters failed during the nonbreeding season. An additional GPS transmitter failed in South Carolina, but a report of the same bird later that winter in Florida indicates this was a stopover event. Of the remaining 7 birds with functional transmitters, 4 migrated to Florida, 2 migrated to South Carolina, and only one stayed in Virginia year-round.

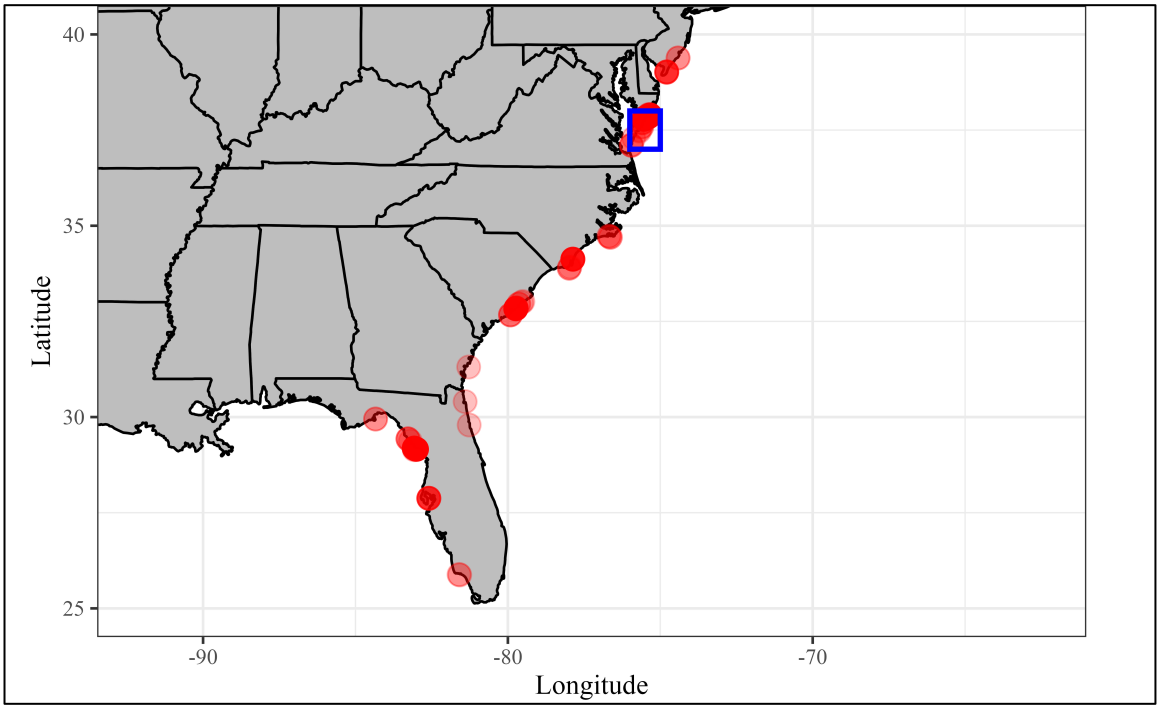

Figure 2.1: Locations of band reports submitted from members of the public, state agencies, federal agencies, and non-governmental organizations for the 31 individual American Oystercatchers (*Haematopus palliatus*) resighted, out of the 61 that we banded between 2022 and 2024 at Chincoteague National Wildlife Refuge, Virginia.

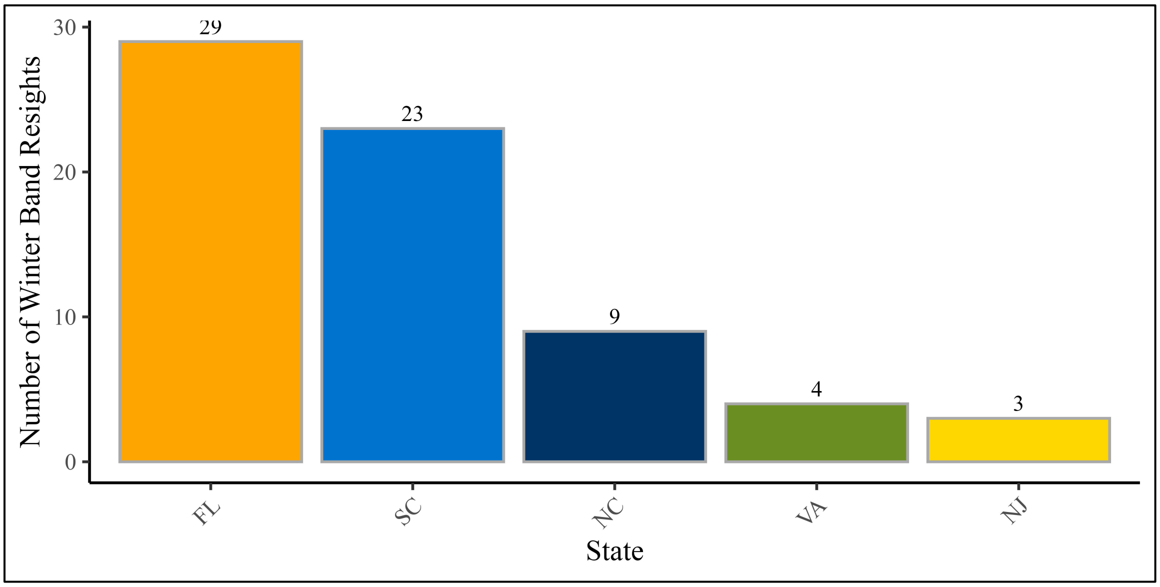

Figure 2.2: Number of non-breeding season (November to March) reports for 32 of the 61 American Oystercatcher (*Haematopus palliatus*) we banded at Chincoteague National Wildlife Refuge (Virginia, USA) between 2022 and 2024 by state. FL = Florida, SC = South Carolina, NC = North Carolina, VA = Virginia, and NJ = New Jersey. Note, this plot does not discriminate between potential multiple reports of the same bird. Organized left to right as south to north.

Across the 20 unique individuals described above, we had 31 cases where we could determine their non-breeding locations between 2022-2024 (11 individuals had known wintering locations across two years). All prior predictive checks, posterior predictive checks, and Monte Carlo Markov Chain convergence checks indicated good model fit for all candidate models. All four parameters of interest included zero in the 95% credible intervals (Figure 2.3). When comparing candidate models, the null model performed similarly to models that included fixed effects (Table 2.2). Therefore sex, territory quality, body size (PC1), and diet (generalists or specialists) do not consistently predict whether an individual American Oystercatcher migrates. However, sex seems to have the greatest likelihood of all predictors, with the probability of a male being more likely to migrate than females of 94.7% based on posterior distributions.

Table 2.2: Model comparison using leave-one-out cross-validation (LOO-CV) for models predicting drivers of American Oystercatcher (*Haematopus palliatus*) migration. Models are ranked by their difference in Expected Log Predictive Density (ΔELPD), with higher values indicating better predictive performance. ΔELPD represents the difference in ELPD from the best model, with SE ΔELPD as its standard error. Model weights reflect the relative predictive accuracy of each model. Note that the null model is equally competitive as all other models. LOO information criterion (LOO-IC) and associated standard error (SE) are included.

Model	**ΔELPD**	**SE ΔELPD**	**LOOIC**	**SE LOOIC**	**Weight**
Sex + Breeding Success	0.00	0.00	-16.35	1.62	0.07
Sex	-0.05	0.32	-16.40	1.69	0.07
Sex + Feeding Strategy	-0.31	0.70	-16.66	1.86	0.08
Breeding Success	-0.39	1.06	-16.74	1.37	0.08
Null	-0.41	1.08	-16.76	1.37	0.08
Feeding Strategy	-0.84	1.29	-17.18	1.65	0.10
PC1 + Breeding Success	-1.70	1.44	-18.04	2.26	0.16
PC1	-1.84	1.41	-18.19	2.25	0.17
PC1 + FeedingStrategy	-2.15	1.46	-18.50	2.32	0.20

* PC1 represents the first principal component for the combination of wing, tarsus, and culmen measurements. Breeding success is binary and approximates territory quality (1 = high quality territory that fledged at least 1 chick; 0 = low quality territory that did not fledge a chick). Feeding strategy is binary as generalist (0) or specialist (1). Sex is binary as male (1) and female (0).

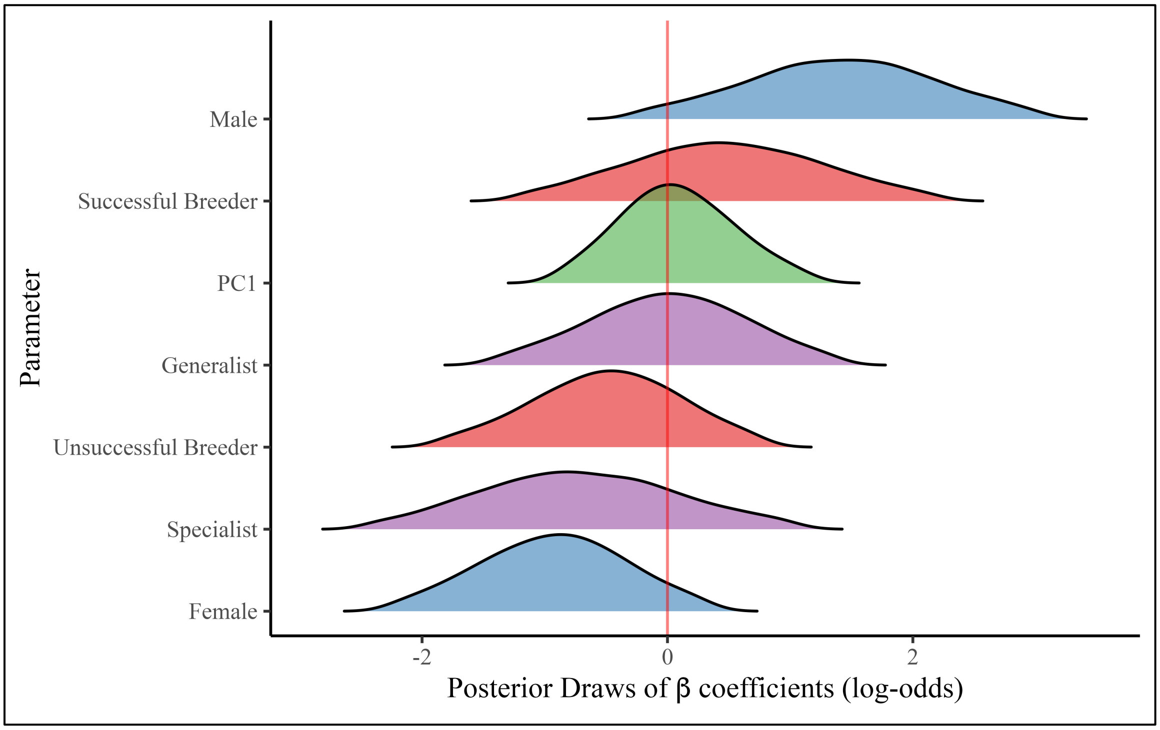

Figure 2.3: Posterior density estimates for four Bayesian logistic mixed-effects models predicting the probability of migration in American Oystercatchers (*Haematopus palliatus*) breeding in Virginia, USA. Each ridge represents the 95% credible posterior distribution of the respective coefficient, with higher densities indicating more probable parameter values. Posterior distributions crossing 0 are not considered strong predictors. Note: Each posterior distribution is derived from single-parameter models with individual included as a random intercept. Colour references pairs of parameters derived from the same model (Sex = blue, Feeding Strategy = purple, Breeding Success = red, and the first principal component [PC1] of wing cord, tarsus, and culmen = green).

2.5 Discussion

2.5.1 Summary

Based on band re-sightings, our study estimates that only 9.4% of American Oystercatchers breeding in Virginia remain in-state year-round, with the majority moving out-of-state during the non-breeding season. I tested four hypotheses to explain differential migration (whether an individual is a short distance [under 718 km] migrant or long-distance migrant) in American Oystercatchers. However, our results did not clearly support any of these factors as drivers of migratory behavior in Virginia's American Oystercatcher breeding population.

2.5.2 The Majority of Virginia's American Oystercatchers are Migrants

Prior studies have shown that nearly half (48%) of Virginia's American Oystercatchers remain in-state year-round (Schulte 2012). However, our methods show that the proportion of individuals remaining in Virginia year-round is substantially lower, with only 9.4% remaining in the state during the non-breeding season. Based on this criteria, prior literature classifies Virginia's American Oystercatchers as partial migrants (Schulte 2012). However, this classification may no longer be accurate, or not accurate for the sub-population in this study. Our findings show that the high proportion of individuals leaving Virginia, and the long distances traveled during the non-breeding season, make differential migration a more appropriate descriptor. Between 2022 and 2024, we banded 61 individuals and obtained wintering locations for 32 through resightings. Geographic spread and consistency of these sightings across years provide strong, if preliminary, evidence that the majority of Virginia's beach-nesting American Oystercatchers migrate. A more comprehensive study, including marsh-nesting individuals, would strengthen our confidence in these results.

Shifts in behaviour or life history strategies over time are often complex processes resulting from a vast array of ecological pressures. For example, migratory and nesting phenology of many shorebirds has shifted earlier in response to climate change (McKinnon *et al.* 2012; Grabowski *et al.* 2013; Liebezeit *et al.* 2014). The proportion of migrants in a partially migratory population of white-tailed deer has declined by 64% in less than 30 years, a change attributed to declining winter severity due to climate change (Morrison *et al.* 2024). Climate change has also resulted in reduced migratory ranges for 9 of 15 passerines studied in Britain between 1964 and 2020 (Pickett *et al.* 2024). One meta-analysis of many taxa across several continents found that non-migrants had increased fitness compared to their migrant counterparts (Buchan *et al.* 2020). Zones supporting partial migration can remain stable across time and space under a wide range of demographic scenarios, provided environmental conditions are stable and genetic diversity is sufficient. Therefore, shifts in the distribution of migratory strategies likely indicate underlying environmental or genetic changes (Cobben and van Noordwijk 2017).

Shifts in the migratory strategies of Virginia's American Oystercatchers are likely driven by (a) shifting environmental conditions due to climate change, (b) reduced fitness, potentially influenced by climate change, or (c) northward range expansion, also driven by climate change (more American Oystercatchers are born in and breed at more northern latitudes, where migration is more likely. Therefore, new breeders in Virginia may be of these populations and may be more likely to migrate as well). These hypotheses are further supported by increasing severity of environmental conditions (e.g., precipitation, temperatures, storm events) during the non-breeding season along the Atlantic coast (Hennessy *et al.* 1997; Knutson *et al.* 2010; Garner 2023), low reproductive success among Virginia's American Oystercatchers (Wilke *et al.* 2005), and the significant northward expansion of breeding American Oystercatchers into Atlantic Canada, an increase from their historical northernmost range limit in New Jersey during the nineteenth century (American Oystercatcher Working Group *et al.* 2020). If migration provides a survival advantage, selection may be favoring migratory individuals over residents. Further studies comparing survival rates between migrant and non-migrant American Oystercatchers would help address this knowledge gap. Finally, a reassessment of the migratory strategies of American Oystercatchers across the remainder of their range will provide updated insights into how climate change might be influencing movement patterns and population dynamics.

It is also possible that subpopulations of American Oystercatchers in Virginia use different migratory strategies. Breeding strategies of American Oystercatchers can generally be summarised into two groups: those that nest on the beach and those that nest in saltmarshes (Shields and Parnell 1990; Nol *et al.* 2012). Inland nesting American Oystercatchers (those nesting in salt marshes) have significantly higher daily nest survival (despite equal fledging success; McGowan *et al*. 2005) and may also nest up to a month earlier than their beach-nesting counterparts (L. Addison, *pers. comm.* 2024). Given systematic differences between subpopulations, there may very well be differences in migratory strategy. Further studies to assess migratory strategies between American Oystercatcher subpopulations would therefore be informative.

2.5.3 What predicts migration?

Despite testing four hypotheses to explain individual variation in migratory behavior, I found no strong support for the social dominance hypothesis (sex), the body size hypothesis, the arrival time hypothesis (territory quality), or the trophic polymorphism hypothesis as predictors of migration in Virginia's American Oystercatchers. This suggests that traditional ecological factors may not fully explain why some individuals migrate while others remain resident, or in this case, migrate shorter distances. Given the near-complete migration of members of this population (~90%), it is possible that external environmental pressures or other differences between individuals are driving migratory decisions.

For instance, endogenous factors aside from sex and size may be driving migratory decisions in American Oystercatchers. Genetic (excluding physiological factors that may have genetic influence; e.g., sex, body size) influence on migration has particularly strong support (Boyle 2008; Cobben and van Noordwijk 2017). Propensity to migrate in a partially migratory population of Eurasian Oystercatchers exhibits strong associations with paternal migratory behaviour, but not maternal, suggesting strong influence from social interactions (Méndez *et al.* 2017). If migration in American Oystercatchers has strong genetic basis, it could explain why none of the tested ecological hypotheses provided strong predictive power. Potential selection favouring migratory individuals may also be increasing genetic predisposition toward migration over time. American Oystercatchers also show a high degree of site fidelity (Murphy *et al.* 2017). Migratory decisions between individuals may therefore also relate to natal site location. Dispersal from natal sites is an advantageous strategy for increasing genetic diversity within a population (Saastamoinen *et al.* 2017). If individuals imprint on migratory or resident behaviors early in life based on their natal environment, then migration patterns may be shaped by early-life experiences rather than immediate ecological conditions. This is further supported by historically low productivity of American Oystercatchers in Virginia (Wilke *et al.* 2005), indicating that the current breeding population may originate from elsewhere (e.g., from more migratory populations or postnatal dispersal).

Although I did not find statistically significant effects of sex on migration, there is some indication that a larger sample size may have revealed more definitive results. The social dominance hypothesis predicts that males, which are often dominant over females, should be more likely to remain resident as they outcompete for limited resources (Ketterson and Nolan 1976; Gauthreaux 1978; Myers 1981). Our findings suggest the opposite: male American Oystercatchers may be more likely to migrate than females. The exact mechanisms driving this behaviour are unknown, but it may be related to larger non-breeding season movements seen in male American Oystercatchers (see Chapter 3). Given more dominant individuals are expected to occupy larger territories (Aliperti *et al.* 2021), male American Oystercatchers may be more willing to face risks associated with migration. Male American Oystercatchers may also be forced to migrate due to within-sex differences in dominance, where dominant males force less-dominant males to migrate, leaving females undisturbed. During the breeding season the energetic costs of conspecific aggression are offset by maintaining higher quality breeding territory. Therefore, during the non-breeding season remaining on-territory may no longer be worth the increased energetic demands (Rödel *et al.* 2016). Female American Oystercatchers are also significantly heavier than males, and they therefore may be less likely to migrate as they are better able to withstand colder winter weather.

I did not find increased migratory propensity in specialist American Oystercatchers. Given that mole crab abundance is substantially lower in December than during the summer months (L. Brown, *unpublished data*), it is highly likely that specialist American Oystercatchers switch feeding strategies and forage on the readily available eastern oysters (*Crassostrea virginica*), razor clams (*Tagelus sp.*) or ribbed mussels (*Geukensia demissa*) in the protected salt marshes. Still, trophic polymorphism best-predicts migration in the Black Oystercatcher (Rankin 2023). This may be a result of an individual’s willingness to switch food sources, as Black Oystercatchers have shown strong preference for limpets across their range (Sorensen and Lindberg 1991) and may therefore be more rigid with respect to their dietary preferences.

2.5.4 Limitations

My study is primarily limited by sample size. Collecting comprehensive data on individual American Oystercatchers encompassing foraging strategy, reproductive success, and non-breeding season resights across multiple years is inherently challenging. A Bayesian framework mitigated these constraints, but my sample size may still be insufficient to generate fully confident parameter estimates. A larger dataset would likely yield tighter posterior estimates and may provide more insight.

Additionally, metrics used to test individual hypotheses may be flawed. Although high-quality territories are more likely to increase reproductive success, differences in stochastic environmental processes causing nest failures (such as storms) between years may result in high-quality territories failing to fledge chicks. Age could also be a confounding factor working against seasonal breeding success as a territory quality metric. Reproductive success increases with age due to a mix of life experience and increased ability to maintain a high-quality territory (American Oystercatcher Working Group *et al.* 2020). Although American Oystercatchers typically wait 4 to 6 years to begin breeding (American Oystercatcher Working Group *et al.* 2020), they are long lived (Nol *et al.* 2012) and thus there is potential for significant age differences among individuals. Although I have classified individuals as either generalist or specialist foragers during the breeding season, I have not been able to follow individuals throughout the non-breeding season to assess if this behaviour persists. If specialists are able to switch to a generalist foraging strategy during the non-breeding season, there would be little pressure to drive migration. Given that specialists did not need to migrate long-distances, my findings suggest that it is unlikely that diet specialization drives migratory decisions in American Oystercatchers. Future research could help address this question by investigating if specialists during the breeding season remain specialists during the non-breeding season.

2.5.5 Summary

This study examined the migratory strategies of Virginia's American Oystercatchers and the factors influencing individual migratory decisions. I found that approximately 90% of the population now migrates, a sharp increase from prior studies suggesting partial migration (Schulte 2012). Despite testing multiple ecological hypotheses including trophic polymorphism, social dominance (sex), body size, and arrival time (territory quality), none strongly predicted migration. While no significant sex effect was detected, a potential trend for greater migratory propensity in males than females may emerge with increased sample sizes. Additionally, high site fidelity in this species suggests that natal origins could influence migration decisions. Future research should focus on the genetic basis of migration, long-term tracking of individuals, and the role of early-life experiences in shaping migratory behavior.

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Chapter 3:

Spatial Requirements of Non-Breeding American Oystercatchers

3.1 Abstract

As climate change threatens ecological communities globally, understanding the habitat requirements of species helps to make informed management and conservation decisions. Understanding spatial requirements through home range estimation allows us to identify key habitats and, hopefully, provide legislators and conservationists with evidence and support to protect them. The American Oystercatcher (*Haematopus palliatus*) is a large coastal shorebird inhabiting, in part, the barrier islands and saltmarshes of the Atlantic Coast of the United States. American Oystercatchers inhabit some of the most at-risk habitats to changing climatic conditions. A better understanding of their spatial requirements provides valuable insight for habitat conservation. I estimated home range size and spatial requirements for American Oystercatchers during their non-breeding season (November-March) using a framework that accounts for potential autocorrelation structures in movement data (autocorrelated kernel density home range estimation). Home ranges for wintering American Oystercatchers varied greatly between individuals (12.1-201.6 km^2), with a population mean of 86.5 km^2 (39.5-166.6 km^2, 95% confidence interval). A post-hoc χ^2-Inverse Gaussian model revealed the possibility of larger home ranges in males (132.0 km^2, 142.1-152.6 km^2) than females (19.4 km^2, 54.0-122.2 km^2; $P = 0.068$). Sample sizes were too low to formally test for differences in home range size between non-breeding locations, but this is worth pursuing in the future.

3.2 Introduction

An individual's home range is the area occupied by an animal going about their regular daily activities such as foraging, mating, raising young, and resting (Burt 1943). Space use requirements differ substantially between species and often along a gradient of size. Polar Bears (*Ursus maritimus*) can have home ranges exceeding 80,000 km^2 (Clubb and Mason 2006), while some dragonfly species may only ever travel under 0.5 km from their natal site (Dolný *et al.* 2014). There may also be significant differences in space use requirements within a species. Within a population of gray wolves (*Canis lupus*), home ranges varied between 259-1,676 km^2 (Mattisson *et al.* 2013). Female wood bison (*Bison bison bison*) have significantly larger home range sizes than their male counterparts (~900 km^2 vs ~450 km^2, respectively; Larter and Gates 1990). Finally, home range sizes may also vary within an individual seasonally. Individuals with active nests or young typically show smaller home ranges than during the non-breeding season or when otherwise not incubating or chick rearing (Tanferna *et al.* 2013; Margalida *et al.* 2016; Zurell *et al.* 2018).

Climate change poses a significant threat to ecological communities globally (Harley 2011; Bellard *et al.* 2012; Weiskopf *et al.* 2020). Habitat loss and alteration are expected to have increasingly severe consequences as climate change progresses, impacting species distributions, community structure, and ecosystem function (Wilfried *et al.* 2008). Rising temperature and more variable precipitation patterns (Hennessy *et al.* 1997, Tabari 2020, Konapala *et al.* 2020; NOAA 2023) may drive range contractions or expansions, disrupt species interactions, and alter resource availability (Parmesan and Yohe 2003; Zhu *et al*. 2011; McCluney *et al*. 2012; Ancillotto *et al.* 2016). These changes are particularly concerning for species with specialized habitat requirements or limited dispersal ability, as they may struggle to adapt to rapidly changing environmental conditions (Thomas *et al.* 2011).

Historically, home range estimation was a method to demonstrate how animals used their environment, at a local scale, and was limited by resightings of uniquely marked individuals as they traverse their territory over time. This technique has several limitations, notably that home range estimation may be skewed if space use differs between night and day, or for cryptic animals inhabiting inaccessible areas where resightings are rare (Broman *et al.* 2014). These issues are exacerbated when considering migratory individuals if their migratory destinations are not known. Remote telemetry has improved our ability to track individuals and is beginning to resolve many of these challenges (Hebblewhite and Haydon 2010).

Variation in home range size and space use requirements may be driven by external environmental pressures or internal variation between individuals. Poor quality habitat with scarce resources, high population densities and thus strong intraspecific competition, or anthropogenic disturbance may all result in larger or smaller home range sizes (Powell and Mitchell 2012; Walton *et al.* 2017; Noonan *et al.* 2019; Tucker *et al.* 2019). Environmental conditions such as tropical cyclones or hurricanes may force individuals to use several different habitats within a season as they become more or less available (Johnson and Winker 2010; Patten *et al.* 2024). Differences between mating systems and reproductive strategies may also result in variation of home range sizes (Gaulin and FitzGerald 1988). Individuals may also differ with respect to their curiosity or boldness, which can influence home range size, as more curious or bold individuals may explore larger areas, while shy or risk-averse individuals may restrict their movements to safer, more familiar locations (Aliperti *et al.* 2021).

The American Oystercatcher (*Haematopus palliatus*) is a partially migratory shorebird breeding, in part, along the Atlantic coast of the United States (Nol and Humphrey 1994). Habitat requirements for American Oystercatchers are well understood, occupying barrier islands, constructed dredge spoils, and coastal saltmarshes for breeding, foraging, and roosting throughout their annual cycle. American Oystercatchers feed on eastern oysters (*Crassostrea virginica*), razor clams (*Tagelus sp*.), false angelwings (*Petricola pholadiformis*), ribbed mussels (*Geukensia demissa*), and mole crabs (*Emerita talpoida*; Tuckwell and Nol 1979; Cadman 1980; Johnsgard 1981; Nol 1989). Both sexes of American Oystercatcher have significant dietary overlaps with no evidence of intraspecific niche partitioning with respect to sex (Brown and Nol 2024).

Male American Oystercatchers are generally more involved in territory establishment and spend more time defending their territories, but slightly less involved during incubation (Nol 1985). Male and female American Oystercatchers are roughly equally involved in chick rearing, and behaviour between the sexes during chick rearing does not differ significantly (Nol 1985).

American Oystercatcher populations in North America are steadily increasing, however habitat loss remains a major threat to their populations (American Oystercatcher Working Group *et al.* 2020). American Oystercatchers can be found year-round in low densities at the northern limit of their range, but most migrate to the coasts of the Carolinas, Georgia, or the Gulf Coast of Florida (American Oystercatcher Working

Group *et al.* 2020; Chapter 2). The coastal ecosystems on which American Oystercatchers rely are at particular risk, as it is where climate change is predicted to have some of the largest impacts (Trégarot *et al.* 2024). Understanding how much space American Oystercatchers need during the non-breeding season will inform conservationists and resource managers to better manage and support this species of special concern. Home range sizes of American Oystercatchers during their non-breeding season have not yet been described in the literature.

In this study, I use high-accuracy GPS transmitters to track American Oystercatchers that breed in Virginia throughout their non-breeding season. By applying autocorrelated kernel density estimation, I account for potential temporal dependencies in movement data to generate robust estimates of winter home range size. This method improves upon traditional home range estimators by incorporating the structure of animal movement, providing a more accurate representation of space use (Calabrese *et al.* 2016). I then use a χ^2-Inverse Gaussian model to test for differences in home range sizes between the sexes and between non-breeding locations. I hypothesize that social and agonistic interactions result in differing home range sizes between sexes. I predict that increased territoriality and aggression in male American Oystercatchers during the breeding season (Nol 1985) will result in males having larger home range sizes than females throughout the non-breeding season as these encounters persist. Understanding spatial requirements is essential for identifying key habitats for conservation and protection.

3.3 Methods

3.3.1 Field Site

I studied American Oystercatchers breeding in Chincoteague National Wildlife Refuge (37.91° N, 75.36° W) in Virginia, USA between 2023-2024. Approximately 90% of beach-nesting American Oystercatchers in Virginia are migratory, while the remainder remain in the state year-round (Chapter 2).

3.3.2 Field Methods

All applicable ethical guidelines for the use of birds in research have been followed, including those presented in the Ornithological Council's "Guidelines to the Use of Wild Birds in Research" (Fair *et al.* 2010). All work was done under Trent University's Animal Care Committee Animal Care Use Approval #27856. We caught ten adult breeding American Oystercatchers using a decoy loop-carpet setup (McGowan and Simons 2004). Loop carpets were constructed using 2.54 × 5.08 cm welded wire fencing, creating 1.2 × 0.3 m panels. Leg loops were tied at alternating welded intersections along the wire mesh using fishing line, in the same fashion as a bal-chatri trap (Mehl *et al.* 2003). Three to four traps were placed around nest cups in triangular or square patterns, with a hand-carved decoy American Oystercatcher sitting on the nest cup. Eggs were removed for this process, placed in a shaded box safely away from banding activities, and returned to the nest when banding was finished. A remote-controlled speaker (FoxPro™ Patriot) playing American Oystercatcher alarm calls was hidden adjacent to the nest cup. Trapping attempts exceeding 30-45 minutes (depending on temperature and behaviour of birds) were ceased for the safety and wellbeing of individuals and nests. American Oystercatchers showing signs of stress, with incomplete clutches, or nests with signs of hatch (fracturing or pipping) were not trapped. Trapping was limited to temperatures below 30°C, with clear weather and low wind (such that sand was not picked up and blown around).

Once an American Oystercatcher was caught in the loop carpet, it was removed along with all equipment and eggs were returned. Two unique field-readable alpha-numeric leg bands were affixed above the tarsal joint, one on each leg, following the American Oystercatcher Working Group banding protocol. A unique metal band provided by the US Geological Survey (USGS) was affixed to one leg below the tarsal joint. Exposed culmen, tarsus, and relaxed wing-chord measurements were taken along with mass using digital callipers and scales. Ten PathTrack^{TM} nanoFix GEO+RF GPS (~8.5 grams) transmitters were fixed to American Oystercatchers using a leg-loop harness. Tag burden varied between 1.3% and 1.7% of total body mass and is well under the recommended maximum tag burden of 3% outlined by the USGS. Tags under 3% total body mass did not affect annual survival in Black Oystercatchers when attached using a leg-loop harness (Rankin *et al.* 2025). Individual American Oystercatchers were sexed in hand and in the field by culmen and mass measurements, as well as prominence of eye fleck, bill colour, and nape colour (Chapter 2; Munters *et al.* 2014).

We programmed transmitters with season-specific fix intervals. Between April-October, GPS fixes were set to take location fixes at 15-minute intervals. Between November-March, fixes were reduced to 12-hour intervals. Each fix was recorded with a spatial resolution of approximately 10 meters. PathTrack^{TM} nanoFix GEO+RF GPS transmitters do not have cellular or satellite data download systems, and therefore data must be downloaded over Bluetooth by placing a base station within 200 meters of the bird. Data on wintering movement was therefore only obtainable once individuals had returned to their breeding grounds the following year.

3.3.3 Statistical Analyses

Statistical analyses were performed using R statistical software v. 4.3.1. (R Core Team 2025). I estimated home range size of American Oystercatchers using the '*ctmm'* framework following Calabrese *et al.* (2016). I ensured that we estimated non-breeding home range sizes of individuals by manually filtering out GPS fixes during the breeding season prior to migration, as well as GPS fixes during migration (any between season southward movement). I confirmed range residency by evaluating movement variograms for each individual. Variograms that plateau over increasing time lags indicate bounded space use, consistent with range residency. In contrast, variograms that continue to rise suggest unbounded movement typical of transient behaviour. To isolate true home range behaviour, I excluded long-distance or spurious excursions such as exploratory forays or brief displacements that did not meet the criteria for home ranges as defined by Burt (1943), which characterizes a home range as the area an animal regularly uses for normal activities like feeding, mating, and shelter over a defined period.

The '*ctmm'* package iterates through independent and identically distributed (IID), Ornstein-Uhlenbeck (OU), and Ornstein-Uhlenbeck with foraging (OUF) movement models and estimates parameters (autocorrelation timescales, Gaussian root-mean-square, velocity, and Gaussian home-range area) using perturbative hybrid restricted maximum likelihood estimation, which is optimized for small effective sample sizes and mitigates associated bias while reducing the overestimation of home range sizes (Calabrese *et al.* 2016; Fleming *et al*. 2016; Noonan *et al.* 2019). Movement models are then ranked by their second-order Akaike information criterion to determine the most competitive model by penalizing overly complex movement models (Calabrese *et al.* 2016). I checked effective sample size, $N_{\text{effective}}$. If $N_{\text{effective}}$ was smaller than 20, I proceeded with a parametric bootstrap approach to further reduce the order of expected bias over 1,000 iterations. Once this process was completed and I had movement models unique to each individual, I calculated 95% utilization distributions and associated confidence intervals using weighted autocorrelated kernel density estimation (wAKDE$_{\text{C}}$).

Estimating home range sizes of animals has largely been done using discrete time movement models due to their relatively low computational demands and simplicity (Calabrese *et al.* 2016; Fleming *et al.* 2016). In recent years, computational power has increased significantly, removing this barrier. Advancements in GPS telemetry devices with respect to their battery size, spatial accuracy, and storage abilities has resulted in exponentially more spatial data for tracked individuals (Gould *et al.* 2024). Therefore, continuous time movement modelling is becoming more common when analyzing movement and spatial ecology of wildlife (Calabrese *et al*. 2016; Fleming *et al.* 2016; Noonan *et al.* 2019). The '*ctmm*' package was created to provide a comprehensive framework for analyzing home ranges of wild animals (Calabrese *et al.* 2016). The simplest home range estimator for movement data assumes that each location fix is independent and identically distributed, meaning that the recorded positions are assumed to be randomly distributed within the individual's home range. The semivariance function (SVF) of this process can be estimated by:

$$\gamma(\tau)=\sigma^2$$

where the SVF is strictly a function of the variance and remains stationary over time (Noonan *et al.* 2021). IID movement can be improved by adding a diffusion process which allows for variance to increase linearly over time proportional to the diffusion coefficient. This process is known as Brownian Motion where the SVF can be estimated by:

$$\gamma(\tau)=D_\alpha|\tau|$$

where D_α represents the diffusion coefficient and τ represents the time lag (Fleming *et al.* 2014). The OU process adds a degree of centrality by assuming individual's trend towards a common center location. The SVF of the OU process can be estimated by:

$$\gamma(\tau)=\sigma_H\left(1-e^{-\frac{|\tau|}{\tau_H}}\right)$$

where τ_H determines the speed in which an individual crosses its home range, σ_H (Fleming *et al.* 2014). The OUF process further improves upon the standard OU process by incorporating a dynamic foraging behavior that allows individuals to shift their movement focus over time in response to resource availability. The SVF for the OUF process can be estimated by:

$$\gamma(\tau)=\sigma_H\left(1-\frac{\tau_H e^{-\frac{|\tau|}{\tau_H}}-\tau_F e^{-\frac{|\tau|}{\tau_F}}}{\tau_H-\tau_F}\right)$$

where σ_H represents variability in movement, τ_H represents the long-term home range crossing timescale, and τ_F the short-term home range crossing timescale (Fleming *et al.* 2014).

Discrete time movement models (such as the IID process) are limited such that they are only comparable if the temporal resolution remains constant within and between individuals (Calabrese *et al.* 2016). Continuous time movement modelling benefits from accounting for irregular sampling schedules and variability in temporal resolution, making it more robust for comparing movement patterns across individuals and time periods. These models use continuous-time stochastic processes to estimate animal movement, interpolating between locations and reducing biases associated with uneven sampling. Autocorrelated kernel density estimation improves upon traditional home-range estimation methods by considering the autocorrelated nature of movement data. That is to say, animal movement is inherently autocorrelated, meaning that an individual's location at one time step is strongly influenced by its previous location (Calabrese *et al.* 2016; Fleming *et al.* 2016; Noonan *et al.* 2019). Failure to account for autocorrelation when estimating home-range sizes of animals can result in significant home range underestimation, being 3-22 times smaller than actual home range sizes (Noonan *et al.* 2019).

Finally, I employ a χ^2-Inverse Gaussian hierarchical model to calculate an unbiased population home range estimate accounting for variability in uncertainty between individuals following Fleming *et al.* (2022). I then applied the same χ^2-Inverse Gaussian hierarchical model to investigate if home ranges differed between males and females, as well as between individuals overwintering in different states (Fleming *et al.* 2022).

3.4 Results

We successfully deployed all ten GPS transmitters on breeding American Oystercatchers; however, two transmitters ceased to function due to unknown circumstances shortly after deployment (16 days and 2 months after deployment). A third

GPS transmitter ceased to function during a stopover event in South Carolina (31.84°N, 81.05°W) on 13 October 2023 before proceeding to where it spent the non-breeding season in Florida, which I learned after receiving a report of a resighting of the individual in Cedar Key Florida (29.16°N, 83.00°W) on 26 February 2023. Finally, a fourth GPS transmitter failed on 23 October due to collision between the bird and a vehicle, after the bird was presumed to reach its non-breeding territory. The remaining 6 transmitters functioned for the duration of the non-breeding season. Out of the eight American Oystercatchers tracked (for at least two weeks) during the nonbreeding season, there was an even split between the sexes (Table 3.1). Four of the tracked American Oystercatchers spent the entire non-breeding season (November to March, roughly) along the Gulf Coast of Florida. An additional two individuals spent the entire non-breeding season in South Carolina. Only a single individual remained in Virginia and did not migrate (Table 3.2). Differences in departure timing between individuals resulted in a single individual, CEJ, arriving on non-breeding territory before the GPS transmitter switched from 15-minute to 12-hour intervals. Therefore, CEJ is the only individual that has variation in temporal resolution within the non-breeding season.

All eight individuals exhibited range residency as assessed by variograms (for example see Supplementary Figures 3 and 4). The top ranked models to describe movement of three American Oystercatchers were IID anisotropic movement, with no autocorrelation structures (Table 3.2). Model selection otherwise favoured OU anisotropic models to account for spatial autocorrelation in the remaining five American Oystercatchers (Table 3.2). Individual home ranges varied between 12.1 km^2 (95%

Table 3.1: Summary of individual American Oystercatchers (*Haematopus palliatus*) fitted with PathTrack nanoFix GEO+RF GPS transmitters at Chincoteague National Wildlife Refuge, Virginia in 2023.

ID	Band no.	Tag ID	Deployment Date	Sex	Mass (g)
CAP	1316-10511	696	2023-05-21	M	576
CKT	1316-10510	627	2023-05-21	F	639
CEM	1316-10505	620	2023-05-17	M	564
CAT	1316-10509	485	2023-05-18	M	523
CAY	1316-10514	160	2023-06-02	F	651
CCK	1316-10515	667	2023-06-02	F	620
CEJ	1316-10501	821	2023-05-16	F	NA
CEK	1316-10502	628	2023-06-17	M	515
CCE*	1316-10516	60	2023-06-02	F	623
CEN*	1316-10504	392	2023-05-17	F	555

ID = Unique identification code on alphanumeric leg band. Band no. = United States Geological Survey metal band number. M = male; F = female. *Tags that failed shortly after deployment and transmitted no useful data.

Table 3.2: Summary of non-breeding GPS transmitter data including days tracked and IID and OU estimates of home range size (Est.) from eight American Oystercatchers (*Haematopus palliatus*) breeding in Chincoteague, Virginia for the winter season of 2023 to 2024.

ID	State	Days Tracked	N	$N_{\text{effective}}$	Est.	95% CI	Top Model
CAP	Fl	195	390	203.3	201.6	175-231	OU anisotropic
CKT	Va	152	304	303.0	12.1	11-14	IID anisotropic
CEM	Fl	158	318	247.6	164.3	144-185	OU anisotropic
CAT*	Sc	11	20	19.0	28.5	17-43	IID anisotropic
CAY	Fl	136	272	264.2	52.4	46-59	OU anisotropic
CCK	Sc	155	310	258.9	62.6	55-70	OU anisotropic
CEJ	Sc	57	135	134.0	88.9	75-105	IID anisotropic
CEK	Fl	168	310	277.1	78.6	70-88	OU anisotropic

Home range estimate (Est.) and 95% confidence interval (CI) in km^2. ID represents individual plastic field-readable alphanumerical band code. Days tracked is the number of non-breeding tracking days included in the analysis along with total (N) and effective ($N_{\text{effective}}$) sample sizes. M = Male, F = Female. Fl = Florida, Va = Virginia, Sc = South Carolina. *Stopover. IID = independent and randomly distributed points, OU = Ornstein-Uhlenbeck process.

Confidence Interval; 10.7-13.5 km^2) and 201.6 km^2 (174.9-230.9 km^2; Table 3.2), with a mean home range size of 86.5 km^2 (39.5-166.6 km^2; Figure 3.1). The χ^2-Inverse Gaussian hierarchical model suggested larger home ranges in males (132.0 km^2, 142.1-152.6 km^2) than females (19.4 km^2, 54.0-122.2 km^2, $P = 0.068$; Figure 3.2a). Unfortunately, sample sizes were too low to investigate if home range size differs between non-breeding locations, but visual inspection suggests that there may be differences (Figure 3.2b). A stopover event in South Carolina revealed a home range size of 28.5 km^2 (17.2-42.7 km^2; Figure 3.1). I could not investigate if home range size varies between stopover events and the remainder of the non-breeding season due to recording only a single stopover event spanning multiple days.

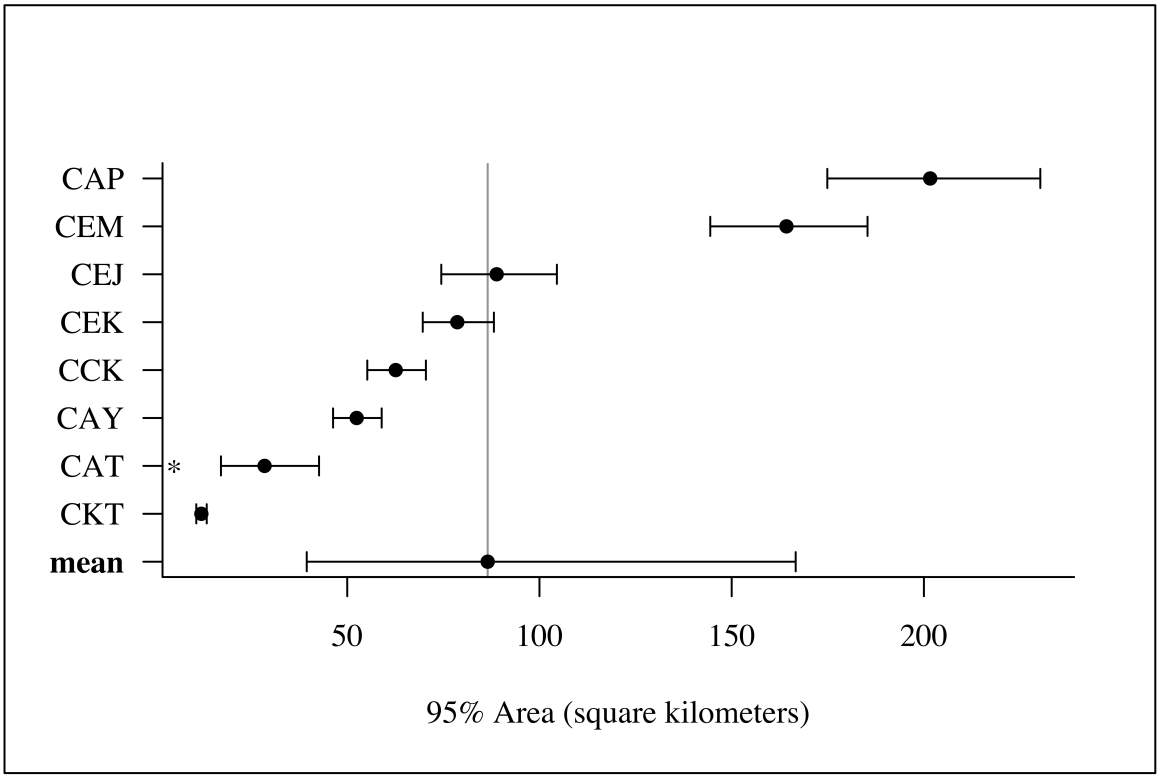

Figure 3.1: Estimated home range size of non-breeding American Oystercatchers (*Haematopus palliatus*) as assessed by weighted autocorrelated kernel density estimation. Individual identification is on the left axis with the population level home range estimate (mean) as determined by a χ^2-Inverse Gaussian hierarchical model accounting for varying uncertainty between individuals. Note, *(CAT) represents a stopover event and is not representative of a non-breeding home range.

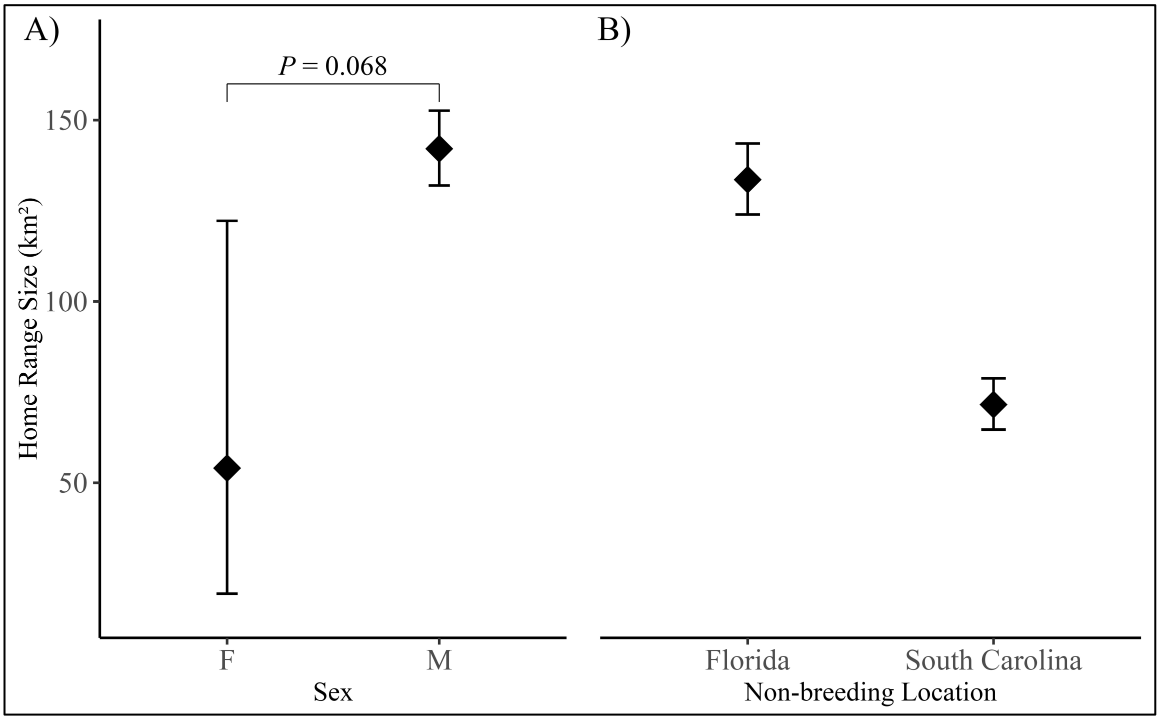

Figure 3.2: A) Home range size (km^2) likely differs between male (*n* = 3) and female (*n* = 4) American Oystercatchers (*Haematopus palliatus*) during the non-breeding season. B) Home range size does not differ between individuals who spend the non-breeding season in Florida (n = 3) compared to South Carolina (*n* = 2). Vertical bars represent standard error.

3.5 Discussion

3.5.1 Summary

Non-breeding home range sizes for American Oystercatchers varied greatly between individuals. Mean non-breeding home range size was ~86 km^2. I found no evidence to support our prediction that home range size varies between non-breeding locations. Our prediction that non-breeding home range size varies between the sexes in American Oystercatchers received modest support, with males tending to have larger home ranges than females.

3.5.2 Space Use, Location, and Sex

American Oystercatchers exhibit considerable variation in their non-breeding space use, with some individuals maintaining relatively small, well-defined home ranges while others range more widely. Variation in home range size within a population is typically a complex function of interactions between energy requirements, habitat quality, sex, and/or social dynamics (Burt 1943; Powell and Mitchell 2012; Walton *et al.* 2017; Noonan *et al.* 2019). Nonetheless, it appears as though American Oystercatchers have relatively large home ranges during the non-breeding season compared to other shorebirds for which this has been documented. In the Gulf of Mexico, four species of shorebird (Willet *Tringa semipalmata*, Black-bellied Plover *Pluvialis squatarola*, Marbled Godwit *Limosa fedoa*, and Long-billed Curlew *Numenius americanus*) all had average home ranges smaller than 15 km^2 (Gabbard *et al.* 2001). In Europe, mean home range of non-breeding Black-tailed Godwits (*L. limosa*) was under 6.5 km^2 (Li *et al.* 2023). Studies on non-breeding Eurasian Curlew (*N. arquata*) indicate home ranges under 24 km^2 and (Donnez *et al.* 2023). However, large home ranges in shorebirds are not unexpected, as mean home range while foraging in non-breeding Whimbrel (*N. phaeopus*) was over 175 km^2 (Handmaker *et al.* 2024).

I expected individuals who spend the non-breeding season in areas with high American Oystercatcher population densities to need larger home range sizes due to intraspecific competition and increased energetic demand resulting from intraspecific interactions. Although I did not directly measure densities of nonbreeding American Oystercatchers, Florida hosts the largest single population of overwintering American Oystercatchers in North America (American Oystercatcher Working Group *et al.* 2020), I expected individuals in Florida to require considerably larger home ranges, especially to avoid other individuals during foraging or due to social interactions. Despite no formal test due to low sample size, it seems like this may be the case. Tucker *et al.* (2019) notes that habitat homogeneity significantly increases home range sizes due to the requirement of habitat variability when a single habitat type does not provide all necessary resources. Additionally, there was no correlation between resource availability or diet on home range size in 36 species of large birds (Tucker *et al.* 2019). This evidence suggests that conspecific social interactions may influence spatial requirements of the American Oystercatcher.

I found that male American Oystercatchers had marginally larger home ranges than females, although this result was not statistically significant. Differences in home range size between the sexes in American suggest that non-breeding home range size is not influenced by density-dependent factors. Diet between sexes in American Oystercatchers overlaps significantly (Brown and Nol 2024) despite morphological differences in body and bill size (Nol 1985). Differences in body mass between the sexes would predict increased home ranges in females to acquire their daily energetic requirements (Carlson-Bremer *et al.* 2010), which is contrary to what I found: females had smaller home ranges. Similar studies on other species of bird have found no influence of body size on home range size (Tucker *et al.* 2019; Mander *et al.* 2022). It is therefore doubtful that the observed difference in home range size between males and females is related to physiological or density dependent interactions.

Behavioural differences between the sexes are probably driving space use differences. Male American Oystercatchers are more involved in territory establishment and aggressive interactions during the breeding season than females (Nol 1985). While in dense non-breeding flocks, often numbering in the hundreds (American Oystercatcher Working Group *et al.* 2020), aggressive interactions between dominant and aggressive individuals are expected to occur more frequently. Aggressive interactions may in turn force less dominant males to move between foraging and roosting locations more frequently (Burton and Evans 2001). Aggressive interactions frequently include long-distance flights and chases which may result in increased home range sizes.

3.5.3 Conservation Implications

Relatively large home range sizes in American Oystercatchers make them particularly susceptible to climate change threats such as habitat loss (American Oystercatcher Working Group *et al.* 2020). Roosting and foraging areas along the Gulf Coast of Florida have been severely degraded by Hurricanes Helene (2024), Debby (2024), and Idalia (2023; J. Brush, *pers. comm.* 2024) resulting in reduced elevation and area for American Oystercatchers to use (P. Leary, *pers. comm.* 2024). Therefore, restoration and development of non-breeding locations for American Oystercatchers is of particular concern and those responsible for habitat management should focus on their protections. Additionally, purchase of habitat less susceptible to tidal flooding, for protection of non-breeding American Oystercatchers, no matter the size, may greatly benefit American Oystercatchers.

Given high nest-site fidelity and wintering site fidelity of American Oystercatchers (Schulte 2012, Murphy *et al.* 2017), continuing to identify important foraging and roost locations will be especially helpful. American Oystercatchers are flexible and readily use artificial dredge spoil islands when available (Parnell *et al.* 1986). Therefore, directing excess dredge spoils for American Oystercatcher conservation (Parnell *et al.* 1986) may be an increasingly effective conservation tool as climate change continues to degrade their natural habitat.

3.5.4 Movement Model Selection

In a comprehensive review of home range analyses in vertebrates, 368 of 369 (99.7%) individuals featured strong autocorrelation structures not well-suited to IID movement models (Noonan *et al.* 2019). Therefore, it was surprising that in our study nearly half of individuals (3/8) exhibited little to no autocorrelation despite relatively large effective sample sizes. The single individual from Noonan *et al.* (2019) which exhibited little to no autocorrelation was a coyote (*C. latrans*), with only 15 location points over 29 days. Coyotes are known to be nomadic (Way and Timm 2008), and thus it is expected that low temporal resolution would result in little autocorrelation. Therefore, individual American Oystercatchers that had no autocorrelation in our study may be a result of a relatively infrequent sampling schedule.

However, if sampling schedule alone informed the extent of autocorrelation observed in our study, I would expect the remaining five individuals to exhibit no autocorrelation as well. Our answer might still lie in sampling schedules. American Oystercatchers are known to show a high degree of site fidelity to nesting locations, roosting locations, foraging locations, and non-breeding locations (Schulte 2012; Murphy *et al.* 2017). GPS fixes were recorded at 12-hour intervals; however, the specific times at which fixes were taken varied randomly among individuals (e.g., one individual may have been sampled at 06:00 and 18:00, while another at 08:00 and 20:00). As a result, I would expect less autocorrelation in individuals whose GPS fixes were recorded cyclically during movements between two successive fixes at two high tides (e.g., 07:00 and 15:00), compared to those whose GPS fixes were recorded at random. This is because GPS points taken opposite (12 hours later) to those at roosting points are highly likely to be directly correlated to non-roosting sites as the bird moves through the daily cycle.

The continuous-time movement modeling framework implemented in '*ctmm'* (Calabrese *et al.* 2016; Fleming *et al.* 2016; Noonan *et al.* 2019) provided a significant advantage for estimating home ranges in our study. Of the eight individuals tracked, five exhibited some degree of autocorrelation in their movement patterns. This temporal dependence violates the assumptions of traditional home range estimation methods such as kernel density estimation and minimum convex polygons, both of which assume independent location fixes (Calabrese *et al.* 2016; Fleming *et al.* 2016; Noonan *et al.* 2019). As a result, applying these conventional methods would likely have led to substantial underestimation of home range sizes by failing to account for the inherent structure in movement data (Noonan *et al.* 2019).

3.5.5 Summary

I present the first study to assess space use requirements of non-breeding American Oystercatchers. Home range size of non-breeding American Oystercatchers varies between individuals and differs between sexes but does not seem to vary between locations. The difference in home range between the sexes is likely due to behavioural differences between males and females (Nol 1985), and not variables such as body mass, habitat quality, or energetics (Burt 1943; Powell and Mitchell 2012; Walton *et al.* 2017; Noonan *et al.* 2019; Tucker *et al.* 2019). Conservation efforts should focus on protecting overwintering habitat for American Oystercatchers as they face increasing threats due to climate change. Dredge spoil islands may prove to be particularly effective.

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Chapter 4:

Nesting Phenology of Two Sympatric Shorebird Species in Virginia, USA

4.1 Abstract

Phenological advancement, or the advancement of biological timing, has been occurring in response to climate change in recent decades. Phenological mismatch occurs when phenological advancement of a species occurs too fast or too slow to match the surrounding environment upon which it relies. Consequently, species may be unable to properly time critical events in their life cycle, such as breeding, with optimal environmental conditions. Birds have adapted to time clutch initiation such that their offspring are fed during peak resource abundance, increasing reproductive success. Many studies have shown that birds have advanced clutch initiation in response to climate change; however, most have focused on Arctic-nesting species or passerines. Piping Plovers (*Charadrius melodus*) and American Oystercatchers (*Haematopus palliatus*) are two shorebirds breeding along the mid-Atlantic coast of the United States. I show that a population of American Oystercatchers has advanced their clutch initiation in response to climate change by 10.7 days between 2005-2022, while sympatric, migratory Piping Plovers showed no advancement between 1986-2022. I show that clutch initiation in American Oystercatchers and Piping Plovers may be influenced by wind speed and temperature, but likely not precipitation. Despite significant warming in the study area, Piping Plovers did not advance their breeding season accordingly. Species unable to advance phenological timing may, therefore, be at increased risk for phenological mismatch and reduced fitness, but this remains to be tested for these species.

4.2 Introduction

Changes in species' phenology in response to climate change are well-documented. Smaller-bodied individuals generally show greater phenological shifts than larger-bodied individuals in response to increasing temperature, precipitation, and other environmental conditions (Cohen *et al.* 2018). In a study spanning 140 years, the peak flowering date in 4 of 7 wildflower species in North America has advanced significantly in response to climate change (Berg *et al.* 2023). There have been significant phenological trends in avian taxa. Climate change has advanced migratory behaviours of 52 migratory species in Central Europe, especially in response to rising spring temperatures (Koleček *et al.* 2020). Timing of arrival from northern breeding grounds was delayed, and subsequent spring departure advanced for three species of waterbirds overwintering on the Texas coast, resulting in shorter wintering seasons (Foster *et al.* 2010). In the Arctic, where climate change is expected to alter biological processes most significantly, birds have advanced their clutch initiation dates in recent years at rates ranging from 1-11 days per decade (Grabowski *et al.* 2013; Liebezeit *et al.* 2014).

Standard operative temperature (SOT) is used to measure the thermal environment an organism is experiencing and is usually a combination of temperature, precipitation, and wind exposure and individual endures (Bakken 1980). When considering that SOTs can significantly alter movement and activity in birds (Bakken 1980; Bakken 1992), it is expected that factors most influencing SOTs (e.g., temperature, wind and precipitation) may also significantly alter an individual's propensity to begin clutch initiation.

Shifts in avian phenology are not without risk. To reduce food uncertainty, birds have adapted to time clutch initiation and subsequent raising of young with peak resource availability (Lepage *et al.* 1998; Visser *et al.* 2006; Carey 2009; McKinnon *et al.* 2012). Phenological mismatch occurs when individuals cannot match phenological advancement at the same rate as their environment (Miller-Rushing *et al.* 2010). Specifically, birds who do not adjust clutch initiation at the same rate as resources in their environment may experience increased food uncertainty and reduced success (Visser and Both 2005; McKinnon *et al.* 2012; Kwon *et al.* 2019). Clutch initiation in females is influenced by endogenous factors and individual plasticity and on a large scale by local factors such as temperature, precipitation, snow cover, and location (Crick and Sparks 1999; Torti and Dunn 2005; Grabowski *et al.* 2013; Liebezeit *et al.* 2014; Kwon *et al.* 2017). These weather factors can work singularly or in combination (e.g., SOTs; Bakken 1980) to affect timing of breeding. Bird species can advance clutch initiation in response to climate change as they often arrive on breeding territories before the optimal nesting period, although arrival time on breeding territory, in some species, does not correlate with the timing of clutch initiation (Visser and Both 2005; Nightingale *et al.* 2024). It is therefore probable that birds use local cues on breeding territories to begin initiating clutches (Thomas *et al.* 2010; Plaschke *et al.* 2019; de Zwaan *et al.* 2022). Phenological mismatch poses a risk to nesting birds if they advance their clutch initiation too fast or not fast enough in response to changing local environmental conditions.

Among the most at-risk avian taxa are shorebirds, more than half of which have declined in abundance by over 50 percent in just three decades, with over 90 percent of species showing declines in overall population trends (Smith *et al.* 2023). The impacts of phenological mismatch on shorebird populations along the Atlantic Coast of North America is exacerbated when considering the cumulative effects of extreme weather events, habitat loss, and anthropogenic disturbances (Pfister *et al.* 1992; Convertino *et al.* 2011). Phenological advancement to match that of their environment by advancing clutch initiation may, therefore, be an important response to preserve the long-term integrity of coastal shorebird populations (McKinnon *et al.* 2012; Mayor *et al.* 2017). Although some shorebird species are advancing clutch initiation dates, it may not be sufficiently fast to keep pace with advancement in their nesting environment with respect to the timing of food emergence or other important events (Visser and Both 2005; Thackeray *et al.* 2016). The inability to keep pace is likely in part due to rapid phenological shifts seen in vegetation and invertebrate communities, which can have fast responses to changing environmental factors such as rising temperatures and increased precipitation (Thackeray *et al.* 2016; Mayor *et al.* 2017). In North America, studies on clutch initiation advancement in shorebirds have primarily focused on those bird species nesting in the Arctic (McKinnon *et al.* 2012; Grabowski *et al.* 2013; Liebezeit *et al.* 2014; Kwon *et al.* 2017), with very few studies done on nesting shorebirds in the mid-Atlantic region.

Piping Plovers (*Charadrius melodus*) and American Oystercatchers (*Haematopus palliatus*) are two sympatric species of shorebird breeding along the Atlantic coast of the United States. Piping Plovers are federally threatened in the United States, and the breeding range in the Atlantic populations extends from North Carolina at the southern limit to Atlantic Canada at the northern limit (Hecht and Melvin 2009). Nesting habitat preference for Piping Plovers consists mainly of sparsely vegetated beaches with sand or shell substrate (Burger 1987; Walker *et al.* 2019; Robinson *et al.* 2021). Incubation lasts, on average, 28 days from laying of the final egg (4 eggs for first attempts), with an additional 30-35 days until sustained flight of the chicks (Wilcox 1959). Piping Plovers are precocial and the young are led to foraging habitat soon after hatch, so proximity to suitable foraging habitat is important when selecting nest sites (Robinson *et al.* 2021). Piping Plovers along the mid-Atlantic typically begin arriving on breeding territories in March after completing their migration from the coasts of Georgia, Florida, Texas, or the Caribbean (Nicholls and Baldassarre 1990; Gratto-Trevor *et al.* 2016).

American Oystercatcher breeding habitat in the US coastal Atlantic extends further south to the Gulf of Texas, but continues along the Pacific Coast as far south as the Galapagos Islands and southern Argentina (Howell and Webb 2007; Clay *et al.* 2014). American Oystercatchers are less stringent in their selection of nesting habitat and have been found nesting in tidal salt marshes, beach habitat, and even rooftops (Lauro and Burger 1989; Toland 1992; Douglass *et al*. 2001; Wilke *et al.* 2005; Traut *et al.* 2006). American Oystercatchers have incubation periods of 26 days (Nol 1985) and longer fledging periods of 36-48 days (Virzi 2008). American Oystercatcher chicks are semi-precocial upon hatch and depend on their parents for food until at least 60 days old (Palmer 1967).

American Oystercatchers feed on a variety of food sources such as eastern oysters (*Crassostrea virginica*), razor clams (*Tagelus sp.*), false angelwings (*Petricola pholadiformis*), ribbed mussels (*Geukensia demissa*), and mole crabs (*Emerita talpoida*; Tuckwell and Nol 1979; Cadman 1980; Johnsgard 1981; Nol 1989). The diet of American Oystercatchers is therefore composed, in part, of food sources available year-round and they are, as a result, able to switch food sources as prey become more or less available (Tuckwell and Nol 1997). The barrier islands of Virginia support approximately 1,134 breeding American Oystercatchers (Wilke 2024). Virginia supports a year-round resident population of American Oystercatchers, in addition to a migratory population only present for the breeding season (Chapter 2). Piping Plovers feed primarily on marine, terrestrial, and benthic invertebrates in mudflats and intertidal areas, such as marine worms (Polychaeta), mollusks (Gastropoda), crustaceans (Amphipoda), and beetles (Coleoptera; Shaffer and Laporte 1994; Cohen and Fraser 2010). Piping Plovers breeding in Virginia are entirely migratory and are not there in winter.

I use long-term beach monitoring data to quantify trends in clutch initiation date in Piping Plovers (between 1986-2022) and American Oystercatchers (between 2005-2022) at Chincoteague National Wildlife Refuge, Virginia. I first investigate if local environmental cues (temperature, wind, and precipitation) that may be used to time clutch initiation are advancing across the study period within the study area. I then test the hypothesis that Piping Plovers and American Oystercatchers have advanced clutch initiation dates in response to climate change. Finally, I investigate minimum temperature, wind speed, and precipitation to determine which climate variables alone, or in combination, have the greatest influence on clutch initiation date.

4.3 Methods

4.3.1 Study Area

We monitored nesting Piping Plovers and American Oystercatchers on Assateague Island (37° 54' N, 75° 21' W) and Assawoman Island (37° 49' N, 75° 29' W) in the Chincoteague National Wildlife Refuge Complex (Sittauer and Sloan 2015) of coastal Virginia (Figure 4.1). Most nesting habitat on Assateague Island is closed to the public but is adjacent to heavily disturbed public beaches; Assawoman Island is entirely closed to the public throughout the breeding season (March 15-September 15). Both islands are ecologically and geographically similar.

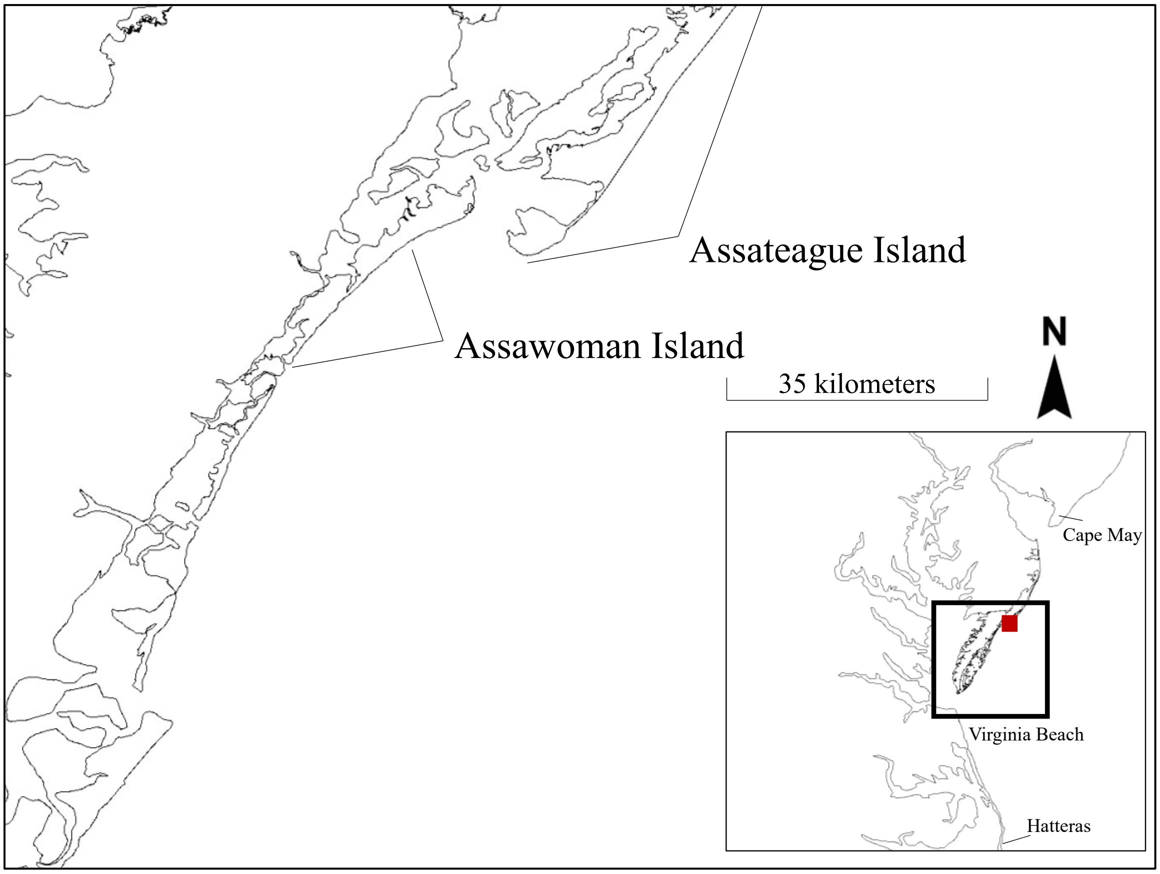

Figure 4.1: Map of Chincoteague National Wildlife Refuge (37° 54' N, 75° 21' W) with two primary survey units, Assateague Island and Assawoman Island.

4.3.2 Data Collection

Suitable shorebird beach habitat in Chincoteague National Wildlife Refuge was surveyed 2-3 times weekly on both Assateague and Assawoman Island. We searched for nests using spotting scopes (minimum 20x magnification) and binoculars (8x magnification) and by observing behavioural cues such as scraping in nest depressions, broken wing displays, or incubation.

Once a nest was found, we recorded the number of eggs in the nest and nest locations with a handheld GPS unit or cellular telephones. We returned to the nest every 1-3 days (although, in certain circumstances, some nests had gaps in visits exceeding seven days) and recorded the number of eggs and looked for signs of hatching (fracturing, pipping, or broken eggshells in or around the nest cup with no signs of depredation). Nests were visited until the fate was known (failed, hatched, or fledged [> 35 days old; Schulte 2012, American Oystercatcher Working Group *et al.* 2020]). If nests failed or broods did not survive, we kept monitoring the territorial pair for second or third nest attempts. Where possible, we determined whether a nest was a primary, secondary, or tertiary attempt. Because a large portion of the birds breeding within Chincoteague National Wildlife Refuge are banded, it was often possible to determine whether nests were renest attempts. However, when individuals in a pair were not banded, we identified nesting attempts by occupancy of stable, consecutive territories. Rates of divorce, extra-pair copulations, or mate-switching within a breeding season in American Oystercatchers are relatively low (Tompkins 1954; Nol 1989; Halimubieke *et al.* 2020), so nests in the same territory were assumed to be renests from the original two adults. I could not determine clutch initiation dates for either species in 2020 due to survey constraints caused by the COVID-19 pandemic.

For Piping Plovers, I estimated clutch initiation dates for nests with fewer than three eggs under the assumption that they were still actively laying (complete clutches contain 3-4 eggs), with an egg-laying rate of one egg every 1.5 days following the first egg (e.g., a nest found at one egg was recorded as initiated the day it was found, a nest found at 2 eggs was recorded to be initiated 1.5 days prior; Wilcox 1959; Haig and Oring

1988). When nests were found with a complete clutch, I estimated the clutch initiation date as 32 days prior to the observed hatch date following (26-day incubation period with a six-day laying period; Wilcox 1959; Haig and Oring 1988). If a nest was found with a complete clutch but I could not determine the hatch date due to nest failure, I could not accurately estimate the clutch initiation date and therefore omitted those nests from analysis. If nests were found at three eggs and hatch dates could not be determined, I estimated the clutch initiation date as 4.5 days prior (Wilcox 1959; Haig and Oring 1988). Broods whose nests were not found were omitted from the analysis. I could not determine which attempt each nest was in Piping Plovers as this was not included in data collection protocols during the initial years of data collection. I could not estimate clutch initiation dates between 2003 and 2015 as nest summary records for those years did not include sufficiently descriptive information.

For American Oystercatchers, I extracted clutch initiation dates from survey data sheets or online databases. If nests had observed or estimated hatch dates, I subtracted 27 days from the hatch date, assuming 26 days of incubation beginning one day after clutch initiation (Nol *et al.* 1984). I estimated clutch initiation dates for nests lacking actual or estimated hatch dates based on the number of eggs laid at the time of discovery. All estimations for clutch initiation date based on the number of eggs laid upon discovery assume that American Oystercatchers lay at a rate of one egg per day (American Oystercatcher Working Group *et al.* 2020). Broods that could not be associated with a known clutch were omitted from the analysis. I only included primary nesting attempts in the analysis for American Oystercatchers, as observers had recorded that information for the entire duration of the study period, except for 2013-2015. I included all nest attempts for 2013-2015 to include any trends in those data, a conservative approach potentially reducing our estimates, lowering our likelihood of detecting advancement in phenology, and underestimating accurate effect sizes.

I obtained data on nearby weather conditions from the National Oceanic and Atmospheric Administration Wallops Island monitoring station situated midway between Assateague Island and Assawoman Island through the Climate Data Online portal (https://www.ncei.noaa.gov/cdo-web/). This weather station provided daily minimum temperatures (degrees Celsius), precipitation (millimetres), and wind speeds (meters per second) for the study period. Wallops Island weather station is approximately 12 kilometres West of Assateague Island and 13 kilometres North-West of Assawoman Island.

4.3.3 Statistical Analyses

All statistical analyses were performed in R (v. 4.3.1; R Core Team 2025), RStudio (Posit Team 2023), '*tidyverse*' package (Wickham *et al.* 2017), '*MuMIn*' (Barton 2023), and '*car'* (Fox and Weisberg 2019). Statistical analysis followed a three-part approach: I first determined if potential weather covariates are changing over time at our study site, I second determined if the clutch initiation date is advancing, and third, I determined if there were associations between weather covariates and trends in timing of clutch initiation.

To determine if the mean minimum temperature, total precipitation, and mean wind speed between March and May (for the entire three-month period) increased in our study area across years, I used three linear models with mean minimum temperature, mean daily precipitation, and mean daily wind speed predicted by year.

To determine if Piping Plovers and American Oystercatchers are advancing their clutch initiation dates, I used two linear models (Clutch Initiation Date ~ Year) for each species separately. Clutch initiation dates were first converted to ordinal days (number of days since December 31). For Piping Plovers, where it was not possible to restrict the analysis to primary nest attempts, I performed two additional post-hoc exploratory analyses (in addition to one retaining all data) with a set cutoff period. The first period was defined as the point at which 95% of primary Piping Plover nest attempts had occurred in an additional study year (2023), and only data within this timeframe were included in the analysis to mimic the restriction used for American Oystercatchers. Because this method also retained 75% of secondary nest attempts, I included a second restriction which only included the first 5% of secondary nest attempts based on the same years' (2023) distribution (removing 95% of secondary attempts). I assessed the assumption of normality and homogeneity of variances using the residuals versus fitted and quantile-quantile residuals plots, which were met for both species.

To assess the influence of temperature, wind speed, and precipitation on American Oystercatcher and Piping Plover nest initiation, I examined the effects of minimum daily temperature, average daily wind speed, and total daily precipitation on the timing of clutch initiation. I defined species and year-specific environmental windows based on the physiological processes leading up to egg-laying. Specifically, for each year, I calculated the median lay date for American Oystercatchers and Piping Plovers and extracted weather data from a window beginning 19 days prior to this date, corresponding to an estimated hormonal spike ~5 days before laying (Crosta *et al.* 2003), plus a two-week period of environmental influence, and a 1-day egg formation period for American Oystercatchers (American Oystercatcher Working Group *et al.* 2020) and a 2-day egg formation period for Piping Plovers (Wilcox 1959; Haig and Oring 1988). Given that Piping Plovers and American Oystercatchers begin arriving on breeding territories in Virginia by early March (Patterson *et al.* 1991; Wilke *et al.* 2005), it is highly likely that all individuals were present on breeding grounds during the specified time window.

I then constructed a candidate set of generalized mixed-effect models using *'glmmPQL'* from the *'MASS'* package (Venables and Ripley 2002) for Piping Plovers and American Oystercatchers with permutations of the above variables. I controlled for temporal autocorrelation using a first-order autoregressive correlation structure from the package *'nlme'* (Pinheiro *et al.* 2025) and included year as a random intercept. I ranked models according to their second-order Aikake Information Criterion (AICc) values, considering only the most parsimonious models with ΔAICc < 2 (Burnham and Anderson 2002). I tested for multicollinearity between covariates using the variance inflation factor with a maximum cut-off of < 5 (Kim 2019). Finally, I complimented this approach using detrended regressions for each environmental variable and species separately following a similar approach as Iler *et al.* (2017). First, I regressed the nest date against year. I then regressed each environmental variable against year in separate models. Finally, I regressed the residuals of the nest date model against the residuals of each environmental model.

4.4 Results

4.4.1 Clutch Initiation Dates

I estimated clutch initiation dates for 828 Piping Plover nests and 1,066 American Oystercatcher nests. The median clutch initiation date for Piping Plovers was 24 May, with the earliest nest occurring on 14 April 2019 and the latest occurring on 23 July 1993. The median clutch initiation date for initial nesting attempts in American Oystercatchers was 9 May but varied greatly year-to-year, with an earliest median date of 29 April 2022 and a latest of 31 May 2007. The earliest American Oystercatcher nest observed with one egg was initiated on 30 March 2012, while the latest was initiated on 8 August 2005 (after two prior failed attempts). For American Oystercatchers, initial clutch initiation attempts peaked in the last week of April, secondary attempts peaked in the third week of May, and tertiary and quaternary attempts peaked by late June (Figure 4.2).

Piping Plovers did not significantly advance their clutch initiation dates between 1985 and 2022 when considering all nests ($P = 0.47$; Figure 4.3), nor when excluding 95% of secondary nests ($P = 0.49$; Figure 4.3). For Piping Plovers with the post-hoc cutoff window including 95% of primary Piping Plover nest attempts in the 2023 study year, clutch initiation dates were delayed at an average rate of 1.1 days per decade (0.2-1.9 days per decade, 95% confidence interval; $P = 0.02$, $R^2 = 0.006$, $F_{1,733} = 5.494$; Figure 4.3). Removing 95% of secondary nest attempts resulted in only 53% of primary nest attempts being included in the analysis as assessed by nesting distributions from 2023. American Oystercatchers advanced clutch initiation dates of their first nesting attempt at an average rate of 6.3 days per decade (3.3-9.3 days per decade, 95% confidence interval; $P < 0.0001$, $R^2 = 0.02$, $F_{1,740} = 16.72$; Figure 4.4).

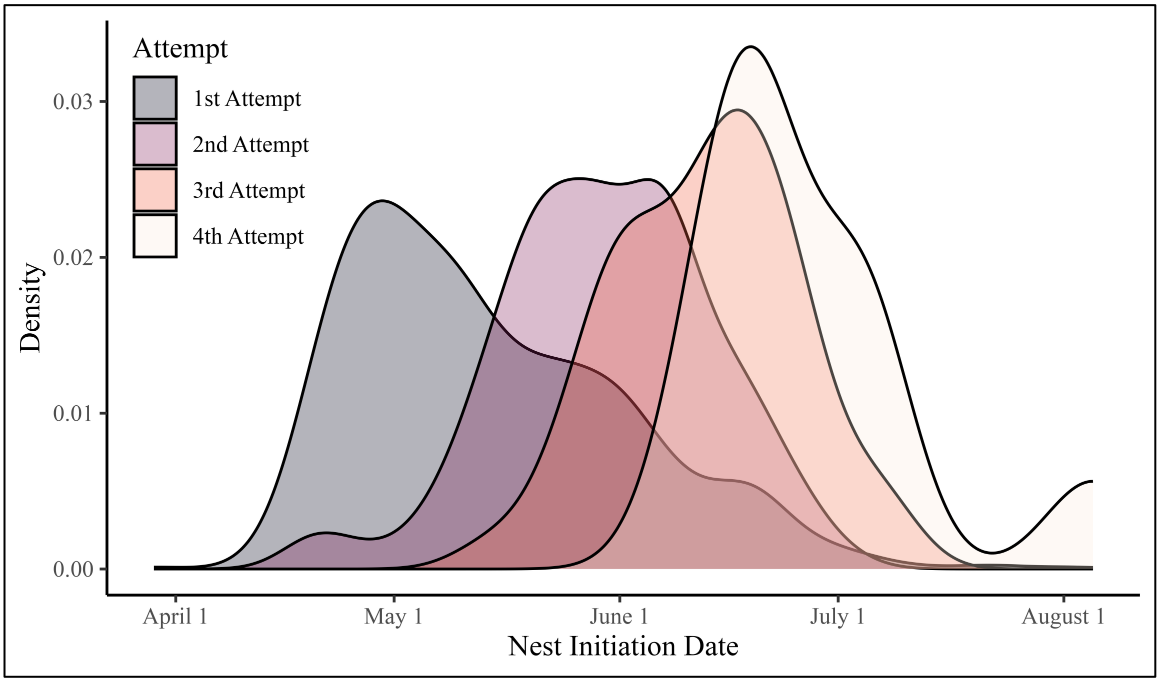

Figure 4.2: Frequency distributions of American Oystercatcher (*Haematopus palliatus*) nesting attempts in Chincoteague National Wildlife Refuge between 2005 and 2022 for first, second, third, and quaternary clutches.

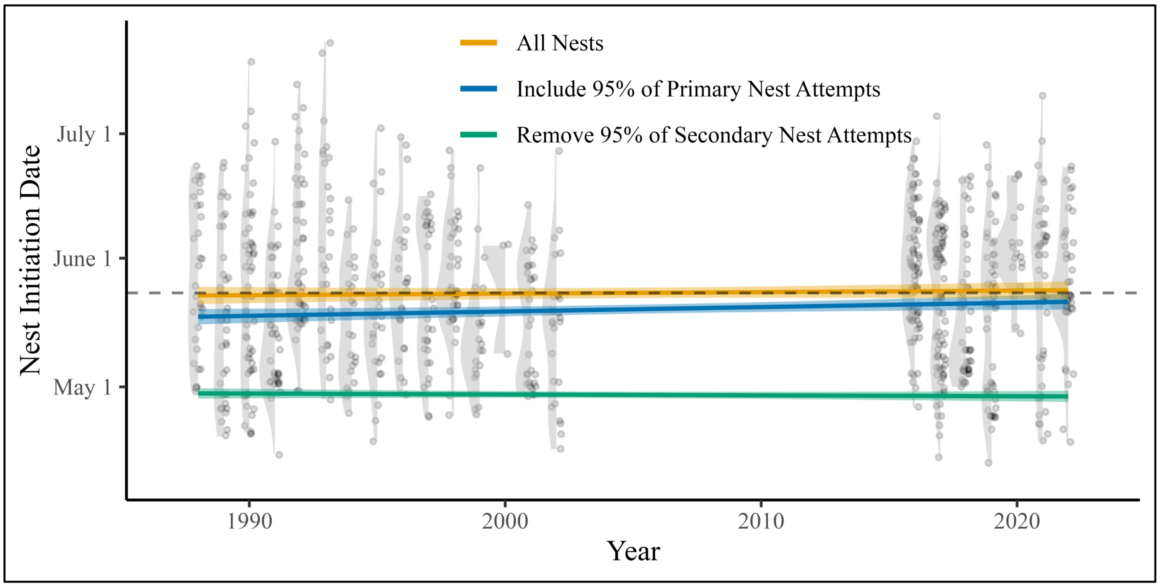

Figure 4.3: Clutch initiation dates and distributions for nesting attempts of Piping Plovers (*Charadrius melodus*) at Chincoteague National Wildlife Refuge between 1986 and 2022. The orange area represents the 95% confidence interval (95% CI) for clutch initiation trends for all nests, the blue area represents 95% CI when applying the cutoff to include 95% of primary Piping Plover nest attempts (determined from surveys done in 2023), and the green area represents a similar restriction, this time removing 95% of secondary nest attempts from the same distribution. Dashed horizontal line represents mean clutch initiation date throughout the study period with no advancement occurring.

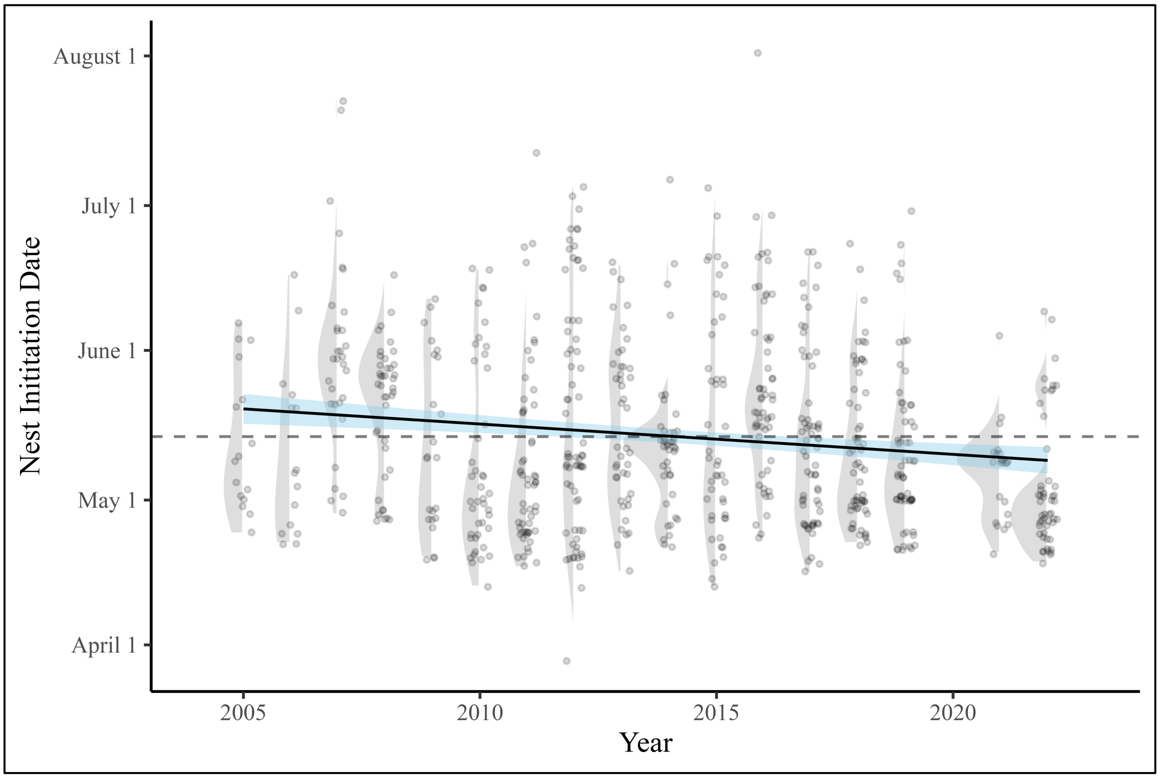

Figure 4.4: Clutch initiation dates and distributions for primary nesting attempts in American Oystercatchers (*Haematopus palliatus*) at Chincoteague National Wildlife Refuge between 2005 and 2022. Blue shaded area represents the 95% confidence interval for clutch initiation advancement; dashed horizontal line represents mean clutch initiation date throughout the study period with no advancement occurring.

4.4.2 Environmental factors

Mean minimum monthly temperature between March-May increased at an average rate of 0.46°C per decade at our study site (0.45-0.48°C per decade, 95% confidence interval; $P < 0.001$, $R^2 = 0.007$, $F_{1, 3586} = 27.57$; Figure 4.5). This corresponds to an increase in the average minimum daily temperature between March-May of 1.72°C between 1985-2022. I found no significant change in mean daily precipitation or mean daily average wind speed at our study site throughout the duration of the study period ($P = 0.51$, $R^2 = 0.01$; and $P = 0.47$, $R^2 = 0.01$ respectively; Figure 4.5). The top ranked model for predicting clutch initiation date in Piping Plovers only included mean wind speed and temperature (Table 4.1). Piping Plovers nested earlier when temperatures were warmer and when wind speeds were slower (Table 4.1). American Oystercatchers showed an inverse trend, nesting earlier in colder temperatures and with more wind (Table 4.1).

Detrended analyses showed that American Oystercatchers nested earlier in the season when temperatures were colder ($\beta_{TMIN} = 1.1 \pm 0.45$ [standard error], $P = 0.015$, $R^2 = 0.0066$), when there was less precipitation ($\beta_{PRCP} = 0.06 \pm 0.015$, $P < 0.0001$, $R^2 = 0.02$), and when there was more wind ($\beta_{WIND} = -4.8 \pm 1.5$, $P < 0.0001$, $R^2 = 0.002$). Piping Plovers only nested earlier in the season when there was less precipitation ($\beta_{PRCP} = 0.05 \pm 0.015$, $P < 0.0028$, $R^2 = 0.01$). There was no trend in temperature or wind speed and nest timing in Piping Plovers ($P = 0.93$; $P = 0.18$).

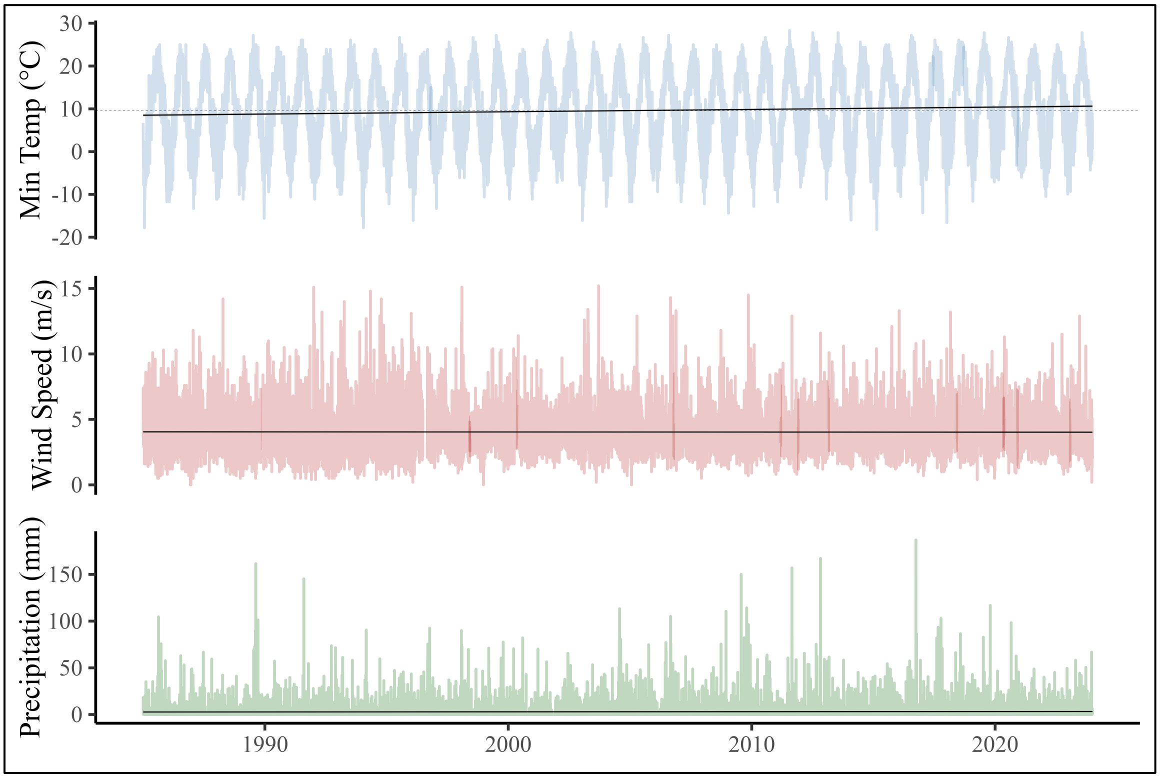

Figure 4.5: Summary of daily climate trends for precipitation, wind speed, and minimum temperature on Wallops Island (37° 56' N, 75° 28' W) between 1985 and 2023. Data accessed from National Oceanic and Atmospheric Administration Climate Data Online portal. Data was restricted between 1986 and 2022 for analyses.

Table 4.1: Rank of linear models best predicting clutch initiation in American Oystercatchers (*Haematopus palliatus*) and Piping Plovers (*Charadrius melodus*) nesting in Chincoteague National Wildlife Refuge. An estimate represents the inclusion of a given model parameter as a fixed effect. TMIN represents average minimum temperature, WIND represents average wind speed, and PRCP represents total precipitation during the specified window.

	Parameters			*Model Information*			
Species	**TMIN**	**WIND**	**PRCP**	***df***	**LogLik**	**AICc**	**ΔAICc**
Piping Plovers (*n* = 735)	**-0.270**	**1.175**		**6**	**-1222.421**	**2457.0**	**0.00**
		1.113		5	-1224.631	2459.4	2.37
	-0.206			5	-1225.376	2460.9	3.86
	-0.178	1.136	-0.024	7	-1223.320	2460.9	3.86
				4	-1227.551	2463.2	6.16
		1.094	-0.025	6	-1225.572	2483.3	6.30
	-0.113		-0.025	6	-1226.303	2464.8	7.76
			-0.025	5	-1228.519	2467.2	10.14
American Oystercatchers (*n* = 742)	**2.950**	**-8.182**		**6**	**-1256.930**	**2526.1**	**0.00**
	3.084	-8.522	-0.018	7	-1257.518	2529.3	3.24
		-6.319		5	-1259.701	2529.5	3.48
	2.536			5	-1260.907	2532.0	5.90
		-6.164	0.012	6	-1260.356	2532.9	6.85
				4	-1263.603	2535.3	9.24
	2.543		-0.000	6	-1261.551	2535.3	9.24
			0.022	5	-1264.299	2538.7	12.68

4.5 Discussion

I found that Piping Plovers are delaying clutch initiation at a rate of 1.1 days per decade when a cutoff is applied to only include 95% of primary nests (based on 2023 data). I found no significant trends when no cutoff window was applied, or when excluding 95% of secondary nest attempts (based on 2023 data). American Oystercatchers in our study area have advanced their clutch initiation dates at a rate of 6.3 days per decade throughout the study period. This corresponds to an advancement in clutch initiation of 10.7 days across the 17-year study period.

Generally, estimates for clutch initiation advancement of shorebirds in North America range between no advancement to ~10 days per decade (Table 4.2). Pectoral Sandpiper (*Calidris melanotus*), phalaropes (*Phalaropus spp*.) and Semipalmated Sandpipers (*C. pusilla*) nesting along the North slope of Alaska advanced clutch initiation by 4-8 days per decade (Liebezeit *et al.* 2014). White-rumped Sandpipers (*C. fuscicollis*) on Bylot Island, Nunavut (Canada) advanced clutch initiation by 1.5 days per decade (McKinnon *et al.* 2012). Dunlin (*C. alpina*), Sanderling (*C. alba*), and Ruddy Turnstone (*Arenaria interpres*) in northern Greenland advanced clutch initiation by 4-11 days per decade (Høye *et al*. 2007). Willet (*Tringa semipalmata*), Black-necked Stilt (*Himantopus mexicanus*), and Wilson's Plover (*Anarhynchus wilsonia*) advanced clutch initiation by, on average, 1 day per decade across southern United States (Abernathy *et al.* 2013). Our finding of a decadal advancement of clutch initiation in American Oystercatchers of 6.3 days represents a larger phenological shift than most studies done in the Arctic (Høye *et al.* 2007; McKinnon *et al.* 2012; Liebezeit *et al*. 2014; Kwon *et al.* 2017). Although climate change is expected to impact Arctic ecosystems the most (Liebezeit *et al*. 2014; Rantanen *et al.* 2022), our findings highlight that phenological advancement at the mid- and southern latitudes of the United States are not to be underestimated.

Phenological shifts in shorebirds also show inverse trends, with some populations delaying clutch initiation. In Alaska, Western Sandpipers (*C. mauri*), Semipalmated Sandpipers, and Red-necked Phalaropes (*P. lobatus*) delayed clutch initiation by 4.3-4.8 days per decade (Kwon *et al*. 2017). Populations of Hudsonian Godwits (*Limosa haemastica*) delayed clutch initiation in Alaska (8 ± 1 days prior) and advanced clutch initiation in Churchill, Manitoba (5 ± 7 days after) relative to peak resource abundance

(Senner *et al.* 2017). Therefore, variation in nesting phenology of shorebirds likely results from differences in the cues used to begin clutch initiation, how individuals are affected by these cues, how these cues are responding differently to climate change, and the degree of advancement in temperature in the local environment.

Table 4.2: Summary table highlighting current rate of phenological shifts for 16 species of shorebird. Positive values mean birds are delaying clutch initiation (getting later in the season), and negative values mean birds are advancing clutch initiation (getting earlier in the season).

Species	**Location**	**Trend (days/decade)**	**Study**
American Oystercatcher	Virginia, USA	-6.3	Current study
Piping Plover		0 to +1.1	
Dunlin	Zackenberg, Greenland	-3.9	Høye *et al.* 2007
Sanderling		-5.8	
Ruddy Turnstone		-10.1	
Black-necked Stilt	Southeast USA	-0.9	Abernathy *et al.* 2023
Wilson's Plover	Southeast USA	-0.9	
Willet	California, USA	-0.9	
White-rumped Sandpiper	Nunavut, Canada	-1.5	McKinnon *et. al.* 2012
American Golden-Plover		0	
Baird's Sandpiper		0	
Semipalmated Sandpiper	Alaska, USA	-4 to -8	Liebeziet *et al.* 2014
Pectoral Sandpiper		-4 to -8	
Red-necked Phalarope		-4 to -8	
Red Phalarope		-4 to -8	
Baird's Sandpiper	Yukon, Canada	-5.2	Grabowski *et al.* 2013
Semipalmated Sandpiper		0	
Western Sandpiper	Alaska, USA	+4.3	Kwon *et al.* 2018
Semipalmated Sandpiper		+4.8	
Red-necked Phalarope		+4.8	

*American Oystercatcher (*Haematopus palliatus*); Piping Plover (*Charadrius melodus*); Dunlin (*Calidris alpina*); Sanderling (*C. alba*); Ruddy Turnstone (*Arenaria interpres*); Black-necked Stilt (*Himantopus mexicanus*); Wilson's Plover (*C. wilsonia*); Willet (*Tringa semipalmata*); White-rumped Sandpiper (*C. fuscicollis*); American Golden-Plover (*Pluvialis dominica*); Baird's Sandpiper (*C. bairdii*); Semipalmated Sandpiper (*C. pusilla*); Pectoral Sandpiper (*C. melanotos*); Red-necked Phalarope (*Phalaropus lobatus*); Red Phalarope (*P. fulicarius*); Western Sandpiper (*C. mauri*).

I question why advancement in the timing of laying has not occurred in Piping Plovers while it has in American Oystercatchers? Differences in life history between American Oystercatchers and Piping Plovers could be one explanation. The diet of the Piping Plover is restricted in Virginia – and is not available year-round. Macroinvertebrates, which comprise the majority of a Piping Plovers diet (Shaffer and Laporte 1994; Cohen and Fraser 2010), are strongly governed by environmental conditions such as water temperature or salinity (both of which are increasing; Stott *et al.* 2008; Bonacina *et al.* 2023). Therefore, the restricted window of peak food abundance (corresponding with macroinvertebrate emergence with warming summer temperatures) more strongly selects for Piping Plovers to time hatching of young to maximize reproductive success (McKinnon *et al.* 2012). American Oystercatchers, feeding on both ephemeral macroinvertebrates and perpetually available bivalves (Nol 1985; Brown and Nol 2024), have not faced the same degree of environmental pressure from food availability to time hatching of young. If there is little pressure for American Oystercatchers to time clutch initiation with resource abundance, they would be better-able to advance clutch initiation in response to other cues, especially if they might incur a reproductive advantage in doing so (Møller *et al.* 2006).

Piping Plovers and American Oystercatchers also have different breeding strategies. Like many shorebirds, American Oystercatchers do not typically breed until their second or third year (Tomkins 1954; Palmer 1967; Cadman 1980; Nol and Humphrey 1994; Clay *et al.* 2014). Piping Plovers often breed immediately after hatch year, and as a potential method to reduce conspecific competition with more experienced breeders, second-year individuals arrive later and begin breeding later than after second-year birds (Gratto-Trevor *et al.* 2010; Catlin *et al.* 2015). Although this allows Piping Plovers to rapidly respond and recolonize habitats, this strategy likely curtails our ability to detect if phenological advancement occurs and favours inverse trends, especially if the ratio of 2nd year to older breeders increased across the study period or otherwise was not stable.

There may also be a strong genetic role governing phenology in these species. Przybylo *et al.* (2000) claims that phenological advancement in the Collared Flycatcher (*Ficedula albicollis*) can be entirely attributed to population-wide phenotypic plasticity. One difference between the Piping Plover and the American Oystercatcher is the apparent greater ability of the American Oystercatcher to adapt to and use its environment (i.e., phenotypic flexibility; Piersma and Drent 2003). American Oystercatchers are flexible with respect to their nest-site selection, using sandy beaches, salt marshes, and rooftops (Lauro and Burger 1989; Toland 1992; Douglass *et al.* 2001; Wilke *et al*. 2005; Traut *et al*. 2006). American Oystercatchers have longer breeding seasons, which in our study ranged from late March into the first week of August. The breeding range of the American Oystercatcher in North America is also extensive, ranging from Atlantic Canada to the Gulf Coast of Texas, with isolated populations on the west coast of Mexico and southern South America, and the isolated islands of the Galapagos (Howell and Webb 2007; Clay *et al.* 2014).

By contrast, Piping Plovers are more selective with more specific nest-site selection, narrower windows for their breeding seasons, and a more restrictive breeding range. Piping Plovers almost exclusively nest on sandy and shelled beaches or embankments with sparse vegetation (Burger 1987; Walker *et al.* 2019; Robinson *et al.*

2021). Piping Plovers begin clutch initiation later than American Oystercatchers, with the earliest nest laid almost two weeks after that of the oystercatcher and the latest almost two weeks before, with a resulting breeding season that is one month shorter than that of American Oystercatchers. Differential phenological shifts may therefore be a result of differences in interspecific adaptive capacity. Piping Plovers exhibit less flexibility than American Oystercatchers and, thus, may not be able to advance clutch initiation to the same degree.

I also aimed to provide a general exploratory investigation into which cues are being used by both American Oystercatchers and Piping Plovers to time clutch initiation by exploring the effects of temperature, wind speed, and precipitation. However, these mechanistic pathways are complex. Temperature not only alters behaviour during incubation (Conway and Martin 2000; Sharpe *et al.* 2021) but can directly influence hormones involves in egg formation or an individuals' propensity to nest as well (Rozenboim *et al.* 2004). Temperature may also alter salt marsh and barrier island vegetation growth and greenness (Charles and Dukes 2009), or invertebrate communities on which birds feed (Czaja *et al.* 2023). If American Oystercatchers and Piping Plovers use prey abundance or vegetation as cues to begin nesting, then temperature, in part, governs these processes. Finally, environmental cues that influence clutch initiation may not operate similarly in closely related species and can vary substantially between species even under identical conditions (Blank *et al.* 2023).

It is also likely that American Oystercatchers and Piping Plovers experience these environmental pressures differently. American Oystercatchers are larger than Piping Plovers (~10 times the size). Given that larger-bodied individuals are better able to withstand harsher environmental conditions (Mayr 1963; Ketterson and Nolan 1976; Chapman *et al.* 2011), I would expect that American Oystercatchers are more robust than Piping Plovers to increases in precipitation, wind speeds, or colder temperatures during the early nesting period. If Piping Plovers are delaying clutch initiation to wait out storms and harsher weather that occurs early in the breeding season (which is extending later into the spring season with climate change; Feng *et al.* 2016), then this would explain opposing phenological trends in sympatric populations.

Nonetheless, during our study mean minimum temperature between March-May increased at a rate of 0.46°C per decade. We did not see significant trends in wind speed or precipitation across the study period. The mixed-effect analyses suggested that Piping Plovers nest earlier in warmer temperatures and with less wind, while American Oystercatchers nested earlier when temperatures were colder and with more wind. By contrast, the detrended analysis approach suggests that Piping Plovers only nested earlier when there was less precipitation, while American Oystercatchers nest earlier when temperatures are colder, when it is windier, and with less precipitation. It is clear from both methods that the rate of advancement in clutch initiation of American Oystercatchers far outpaces the rate of warming, and thus American Oystercatchers are nesting earlier, when it is colder. This is not the case with Piping Plovers, and as expected, they tended to nest earlier when temperatures were warmer, and conditions were calmer. It is peculiar that both approaches did not yield similar results for all three climate variables. This suggests that temperature, wind, and precipitation may not play significant roles in the timing of clutch initiation for American Oystercatchers and Piping

Plovers. It also reduces our confidence in these results, and a more comprehensive study would be beneficial.

Our use of long-term environmental averaging may have masked the effects of short-term extreme events, which have been linked to shifts in clutch initiation in other species (Heckscher 2018). While gradual climatic trends shape broad scale phenological patterns, short, intense storms or unseasonal cold spells could have localized impacts that our approach did not capture. Future work incorporating event-based analyses may clarify how extreme weather influences shorebird nesting phenology. Given that American Oystercatchers may time clutch initiation with high-tide events in an effort to reduce the probability of the nest flooding during subsequent high tides (and increase hatching success as a result; Nol *et al.* 1984), this may be particularly useful.

Interestingly, a study on American Oystercatcher clutch initiation in the same area as ours in the 1980s noted that the earliest clutch initiation date for first nesting attempts, was 6 April and the latest was 13 May (Nol *et al.* 1984). Median clutch initiation date during our study was just 4 days earlier (9 May) than the latest nest discovered by Nol *et al.* (1984), for primary nesting attempts. This clearly suggests that clutch initiation dates between 1981-1984 were much earlier than in our study. If American Oystercatchers are advancing clutch initiation, how can nests now be later? Two possible explanations for this come to mind, one more probable than the other. (1) Clutch initiation in American Oystercatchers nesting in and around Chincoteague Virginia was notably earlier in the late twentieth century than it is today, has shifted significantly later, and has since started advancing; or (2) since the majority of birds studied by Nol *et al.* (1984) were those nesting in saltmarsh, and ours were strictly those nesting on the beach, it is possible that there are differences in nesting phenology between these two populations. Evidence from a nearby population of American Oystercatchers in North Carolina suggests that marsh nesting American Oystercatchers may nest as much as a month prior to their beach nesting counterparts (L. Addison, *pers. comm.* 2024).

Nesting conditions within the microclimate of a saltmarsh differ from those on the beach. Microclimates created by retained humidity and vegetation likely increase temperatures in salt marshes compared to nearby beaches (Şimşek and Ödül 2018). Furthermore, the protected nature of salt marshes would reduce the cooling effects of cold winds coming off the ocean. American Oystercatchers breeding in saltmarsh habitat later in the season face higher temperatures than their beachfront counterparts and would in turn be expected to nest earlier in an effort to reduce thermal stress (Rodríguez and Barba 2016). Saltmarsh nesting American Oystercatchers also nest much closer to food. Reduced time required to travel to and from foraging areas may provide more time for piping displays, higher caloric intake, or other interactions associated with stimulating egg formation in females (Nol *et al.* 1984) due to unconstrained time budgets. To explore these possibilities, a study should be done to compare phenology and reproductive success between these two populations in Virginia.

My study highlights the need for additional research assessing phenological shifts in shorebird species along the mid-Atlantic and Pacific coasts of the United States, where the impact of climate change is often overlooked. Finally, more research on phenological advancement in coastal communities should be done to assess if American Oystercatchers can match the advancement in their environment, as studies of other shorebirds in other locations suggest this is not the case (Visser and Both 2005).

My findings suggest that Piping Plovers may face future struggles as phenological mismatch becomes a larger threat. Piping Plovers rely on invertebrate communities in mudflats and intertidal areas for sustenance, and these communities are advancing their phenology the greatest in response to climate change (Cohen *et al.* 2018; Robinson *et al.* 2021). As Piping Plovers do not appear to advance their clutch initiation, leading to phenological mismatch, they could likely face an increased risk of reduced reproductive success and fitness (McKinnon *et al.* 2012; Mayor *et al.* 2017). There is ongoing discussion about a potential northward range shift in Piping Plovers (K. Oliver, *pers. comm.* 2024). Those currently nesting in Virginia may benefit from moving further north. As phenology of the environment occurs earlier in southern regions, phenological shifts in the northern range of Piping Plovers could begin to align with the historical timing seen in the southern part of their range.

Clutch initiation date advancement at a rate of 6.3 days per decade in American Oystercatchers is notable in comparison to other studies (McKinnon *et al.* 2012; Grabowski *et al*. 2013; Abernathy *et al*. 2023) but may still not be enough to match phenological advancement in their environment. Studies that have compared phenological advancement in landbirds have found that they do not keep pace with the phenological advancement of their environment (Youngflesh *et al.* 2023). Therefore, although clutch initiation advancement at a rate of 6.3 days per decade seems significant, further studies on the United States East Coast are needed to quantify the rate of change in timing of key environmental cues such as prey availability. Fortunately, American Oystercatchers appear flexible to changing environments and most breeding individuals have a broad diet. American Oystercatchers may, therefore, be able to be resilient to the impacts of climate change. A follow-up study linking temperature advancement to individual reproductive success could help to determine any potential costs to earlier nesting in American Oystercatchers.

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Chapter 5:

General Discussion

5.1 Summary

My thesis furthers our understanding of the movement ecology and phenology of mid-Atlantic shorebirds, with particular focus on the American Oystercatcher. In Chapter 2, I found that individual migratory decisions of Virginia's American Oystercatchers are likely not linked to territory quality, body size, or foraging strategies. My results suggest that sex may play a role, with a trend of male American Oystercatchers being more likely to migrate; however additional data will be needed to increase our confidence in these data. I also show that of beach-nesting American Oystercatchers in Virginia, over 90% migrate out-of-state during the non-breeding season. This finding differs from estimates in other studies (Schulte 2012) and emphasizes the need for further research on the subject.

In Chapter 3, I found great variation in the non-breeding space-use requirements between individual American Oystercatchers (12.1-201.6 km^2). Mean home-range size for all American Oystercatchers tagged was 86.5 km^2 (39.5-166.6 km^2; 95% confidence interval). This mean value is lower than that recorded during the breeding season, when American Oystercatchers can forage up to 15 km away (which, if described as the radius of a circle centered at the nest, would be ~700 km^2) from their nest (L. Brown, *unpublished data*; K. Goodenough, *pers. comm.* 2024). I found evidence that there may be sex-based differences in non-breeding home range size, but a larger sample size is needed to solidify this relationship. Sample sizes were too small to formally test for differences in non-breeding home range size between locations, but visual assessment indicates American Oystercatchers in Florida have larger home ranges than those in South Carolina.

Finally, in Chapter 4 I show that American Oystercatchers nesting in Virginia are advancing clutch initiation at a rate of 6.3 days per decade (3.3-9.3 days per decade; 95% confidence interval). By contrast, the sympatric Piping Plover (which often nests within a few dozen meters of American Oystercatchers) showed no significant trend in dates of clutch initiation over time, with a suggestion that, if anything, they may be slightly delaying clutch initiation. Given that these two species are experiencing the same climatic conditions at breeding sites, my findings suggest that differences in environmental cues, behavioural plasticity, or breeding ecology may explain these differences.

5.2 Management Implications

Individuals managing habitat for non-breeding American Oystercatchers should recognize the critical role of small barrier islands. Despite their limited size, these habitats can offer essential roosting and foraging opportunities. Given that some American Oystercatchers maintain home ranges of less than 12 km^2 (Chapter 3), even a single small island may support a significant portion of their daily or seasonal habitat needs. Protecting and maintaining these areas could be particularly important for sustaining local populations, especially in regions where larger, undisturbed habitats are scarce. Linhart (2025) discusses increased shorebird diversity across patches of smaller stopover habitats than larger habitats and emphasizes how these should not be discounted.

Given that the majority of American Oystercatchers breed in Virginia and migrate during the non-breeding season (Chapter 1), protecting key roosting sites across their migratory range is critical for maintaining population health. Roost sites play a pivotal role in ensuring birds can recover from the energy demands of migration and survive harsh conditions during the winter months (Walsberg 1986; Schmaljohann *et al*. 2022). Carry-over effects, where conditions in one season directly impact the following, may be relevant (Norris and Marra 2007). If birds are forced to use suboptimal roosting habitats due to habitat loss or disturbance, their physical condition may deteriorate, which can reduce survival rates and affect their ability to return to breeding sites in optimal condition (McGowan *et al*. 2011). Therefore, protecting undisturbed roost sites, especially at key stopover locations and non-breeding areas, is vital for the species' long-term survival and reproductive success.

To better manage American Oystercatcher populations, it may be necessary to monitor these birds earlier in the breeding season. Monitoring earlier could allow managers to predict and mitigate the potential negative effects of storms, which can disrupt American Oystercatcher foraging and roosting behavior. By closely tracking the timing of storms, we can better understand how weather patterns influence habitat use and survival, ensuring that management strategies are adapted to these environmental changes. Management actions may include beach revitalization, antipredator exclusionary fences or control, or creation of protected habitat behind barrier island systems (such as dredge spoil islands; Parnell *et al.* 1986).

5.3 Future Directions

A reassessment of American Oystercatcher migratory strategies employed across the entirety of their range would be informative. Given the northward range expansion of American Oystercatchers (American Oystercatcher Working Group *et al.* 2020), a revision of the leapfrog migratory strategy previously described (Schulte 2012; American Oystercatcher Working Group *et al.* 2020) might also be worthwhile, especially with recent advances in GPS tracking technology. Differing results between my thesis and the works of Schulte (2012) raise interesting questions about potential shifts in migratory strategies. An assessment of migratory strategies between marsh-nesting and beach-nesting American Oystercatchers would be particularly useful, as there is merit to the suggestion that beach and marsh nesting individuals have different migratory strategies. This is especially important given the significant physiological costs, and the elevated risk of mortality associated with migration (Wikelski *et al*. 2003; Klassen *et al*. 2014; Lok *et al*. 2015).

The stark difference in clutch initiation timing between marsh-nesting American Oystercatchers, as described by Nol *et al.* (1984), and beach-nesting birds in this thesis highlights a significant research gap in understanding the differences in phenology and annual cycle between these two subpopulations. Although difficult, investigating if there are differences in reproductive success between marsh-nesting and beach-nesting American Oystercatchers may provide insight into the recent collapse of breeding productivity in Virginia's population (US Fish and Wildlife Service 2023) despite increases in overall population (American Oystercatcher Working Group *et al*. 2020). Considering high site-fidelity of American Oystercatchers (Schulte 2012; Murphy *et al.* 2017), investigating if natal philopatry informs an adult's decision to breed in the marsh or on a barrier island could be done if there is enough information to construct pedigrees in this well-studied shorebird species. Such a pedigree would be comprised of many years of monitoring efforts to track natal sites of offspring and in relation to their predecessors, such as in the Song Sparrow (*Melospiza melodia*), where researchers were able construct familial pedigrees for a population on Mandarte Island (British Columbia, Canada) over many decades (Arcese 1989; Reid *et al.* 2019).

Finally, the contrasting results in Chapter 4 between my two study species, raises questions about phenological responses to climate change and highlights the need for further research at lower latitudes. Most studies on clutch initiation advancement in shorebirds (Høye *et al*. 2007; McKinnon *et al.* 2012; Liebezeit *et al.* 2014; Kwon *et al.* 2017) occur in the Arctic where climate change is having very pronounced impacts (Rantanen *et al.* 2022). However, our estimated rate of clutch initiation date advancement in American Oystercatchers exceeds many similar studies done in the Arctic. Therefore, more focus should be given to better understand latitudinal trends in phenology in response to climate change. The underlying mechanism for this advancement (e.g., earlier arrival, faster development of prey necessary for egg development, improvements in nutrition of prey as a result of change in freshwater runoff) could be addressed through dedicated study of the food base for both species.

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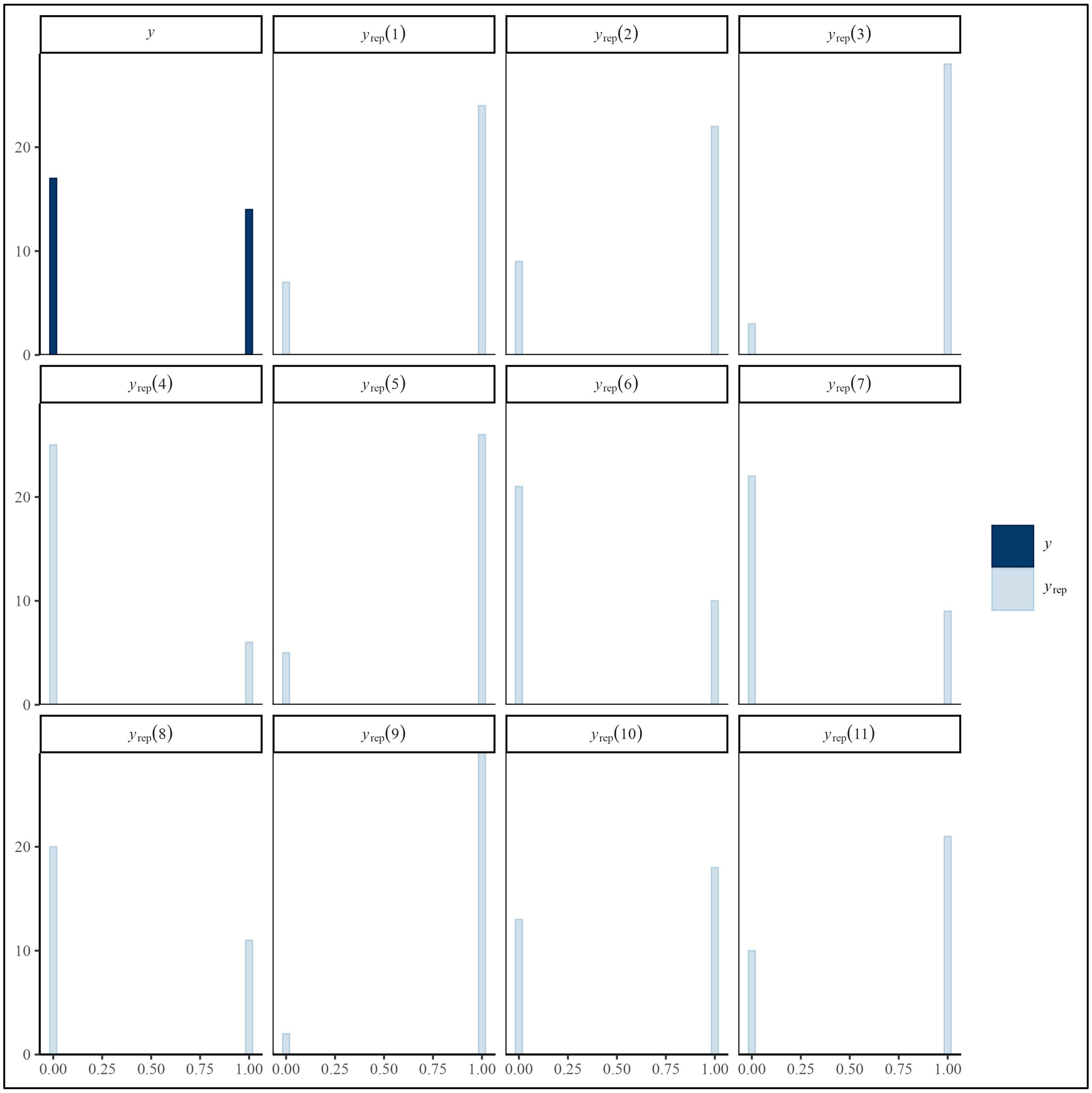
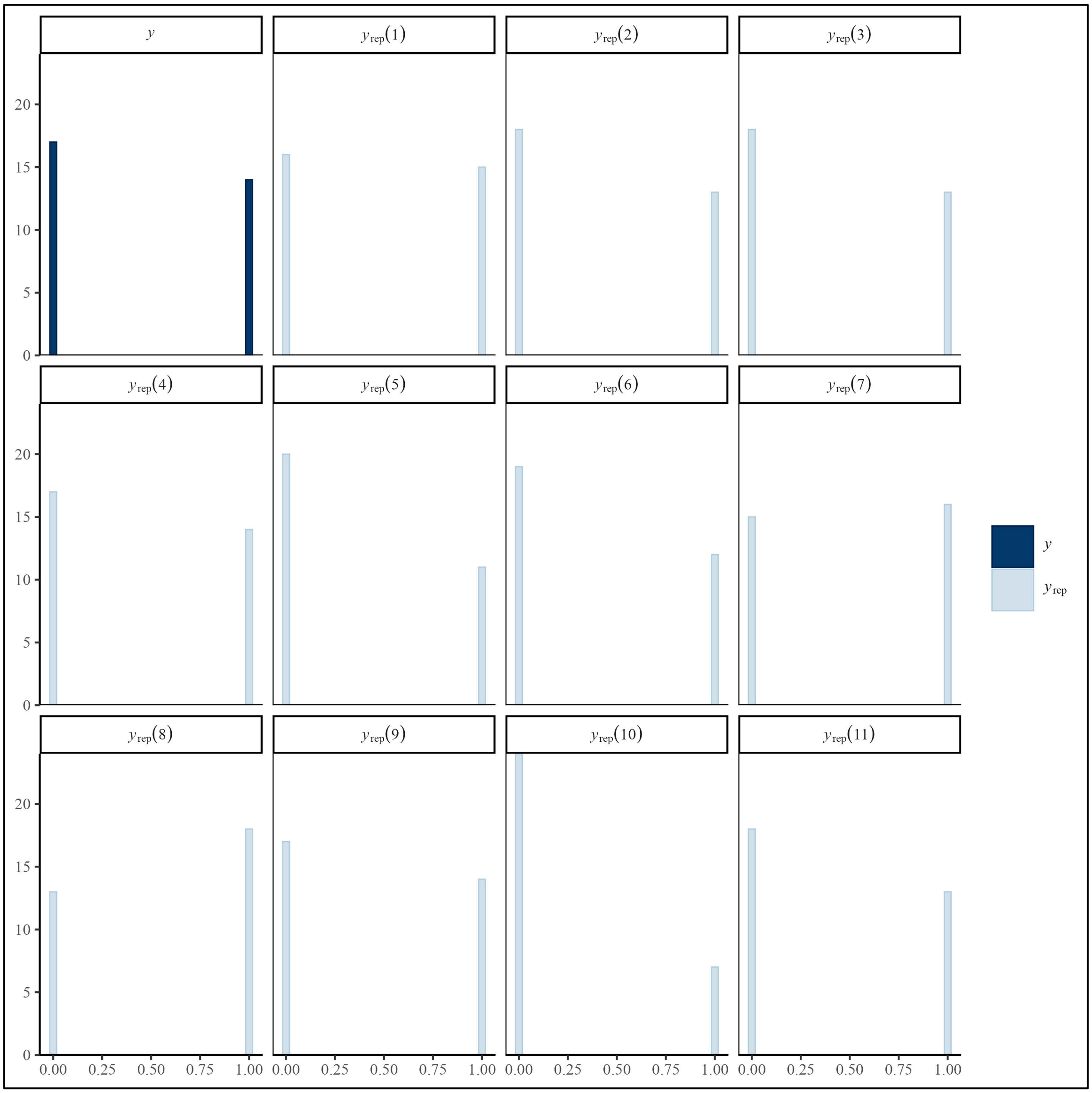
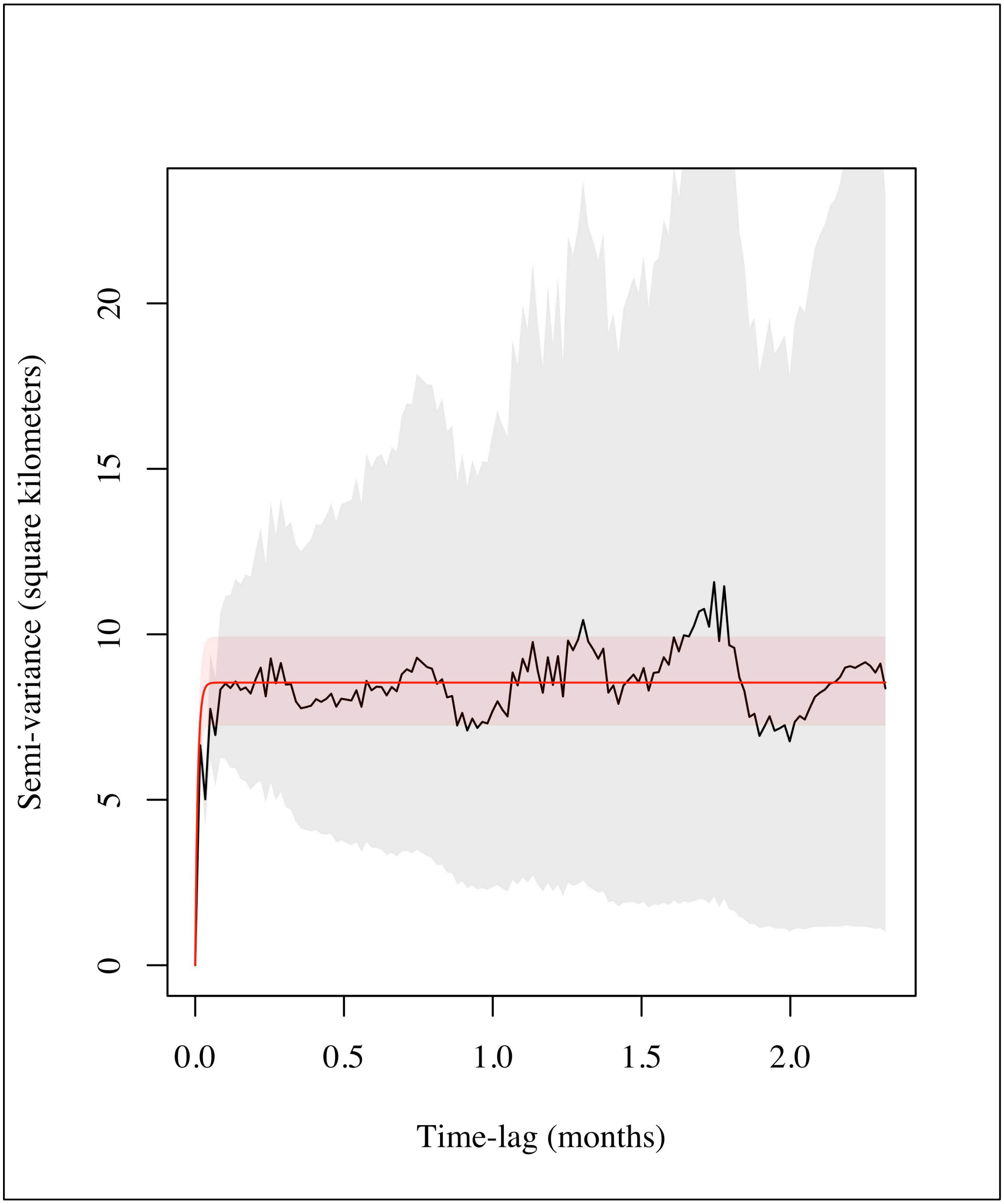
APPENDIX



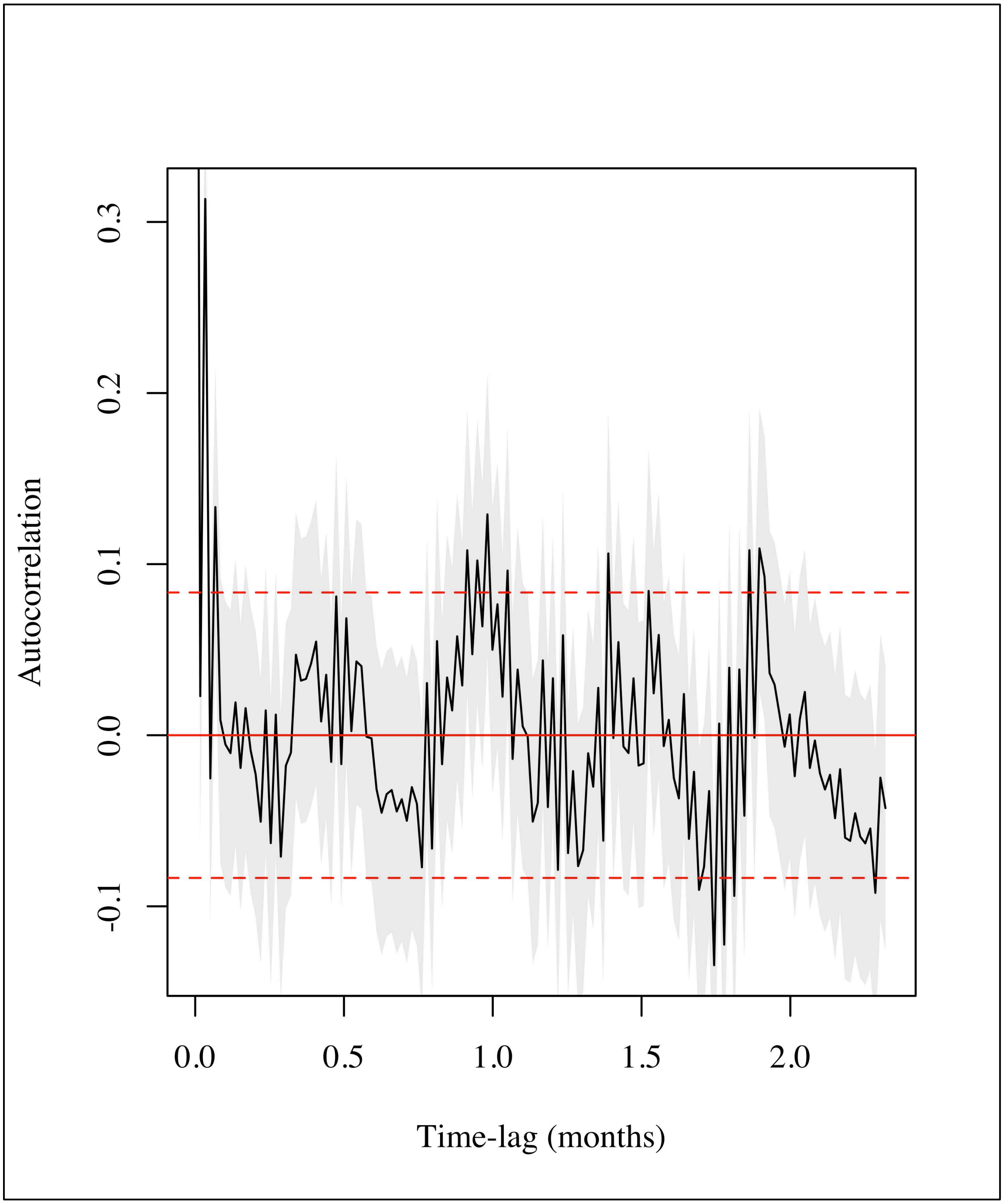
Supplementary Figure 1: Prior predictive checks for the null Bayesian logistic regression model predicting migration in American Oystercatchers (*Haematopus palliatus*). The plots compare simulated data from the prior predictive distribution (*y_rep*) with the observed data (*y*). These checks evaluate whether the priors generate plausible outcomes in the absence of predictor effects. Prior predictive distributions that approximate observed data indicate better-fitting priors.



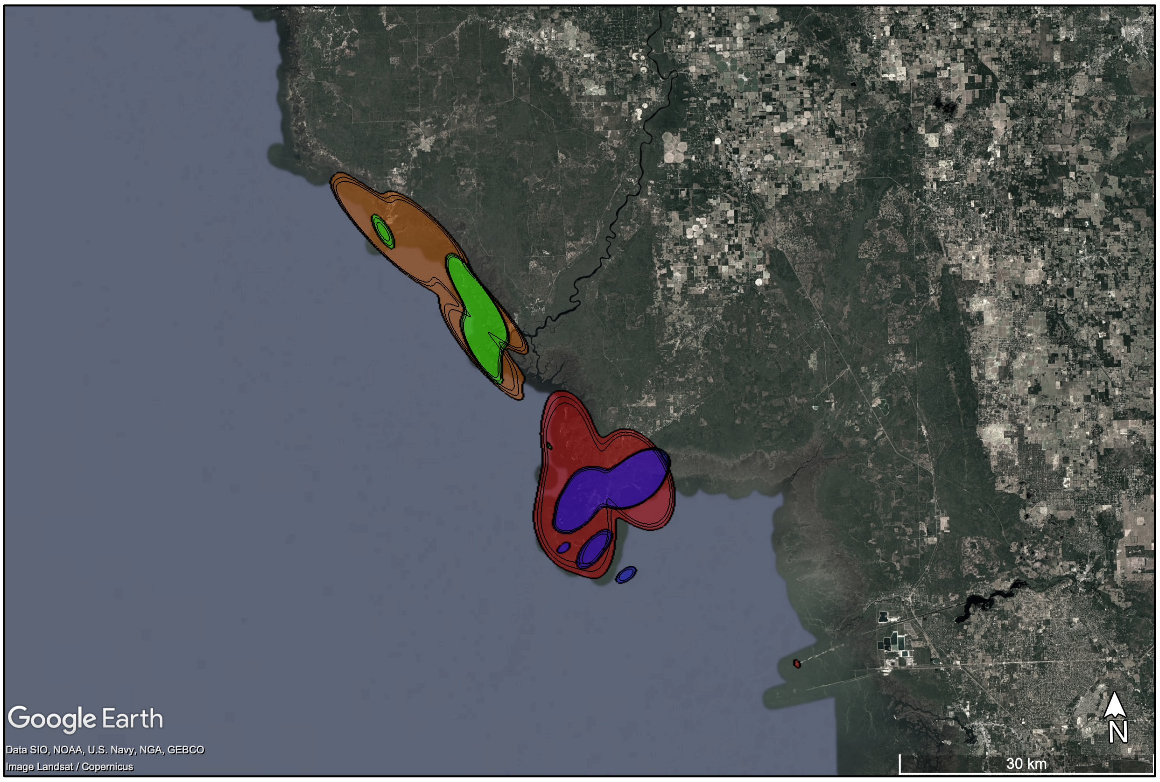
Supplementary Figure 2: Posterior predictive checks for the null Bayesian logistic regression model predicting migration in American Oystercatchers (*Haematopus palliatus*). The plots compare simulated data from the posterior predictive distribution (*y_rep*) with the observed data (*y*). These checks assess how well the fitted model reproduces the observed outcomes, indicating model fit and adequacy.



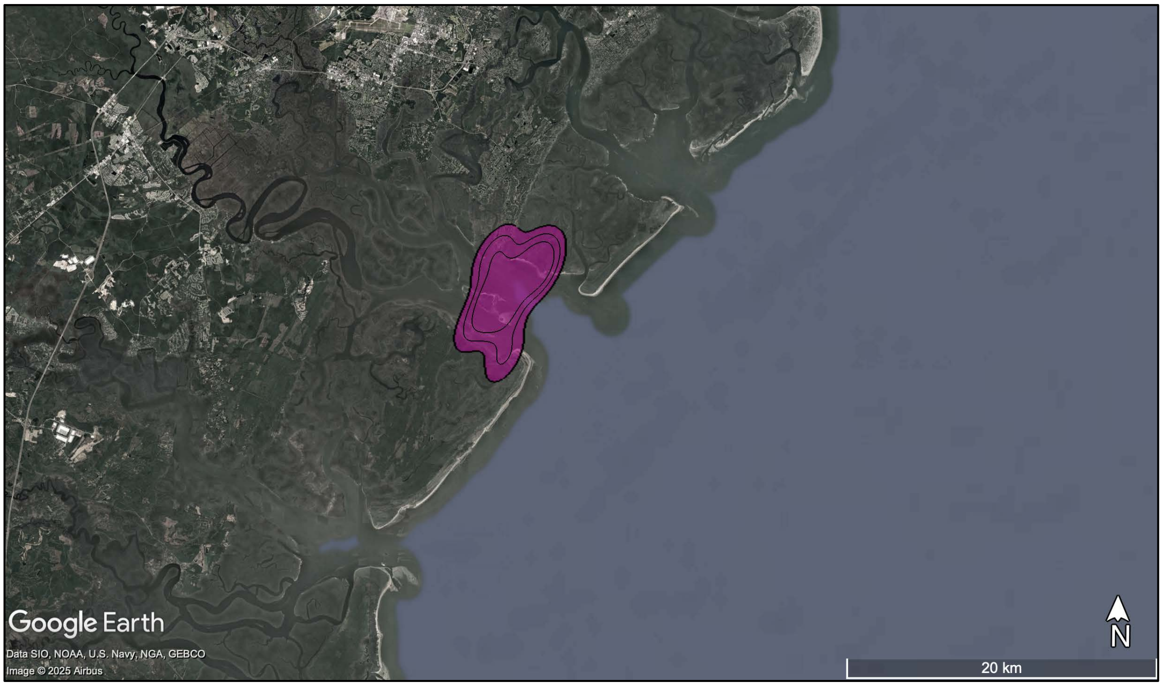
Supplementary Figure 3: Semi-variance of spatial displacement as a function of time-lag (months) for a non-breeding American Oystercatcher (*Haematopus palliatus*). The black line represents observed semi-variance, while the red line indicates the fitted model. The shaded regions denote uncertainty, with the gray band representing broader variability and the red band showing the confidence interval around the fitted model.



Supplementary Figure 4: Correlogram of residuals from the Continuous-Time Movement Model (CTMM), displaying the spatial autocorrelation across multiple lag distances for the non-breeding movements of an American Oystercatcher (*Haematopus palliatus*). The plot examines the extent to which residuals at different locations are correlated. A significant correlation at specific lags suggests potential model misspecification or the need for additional explanatory variables.

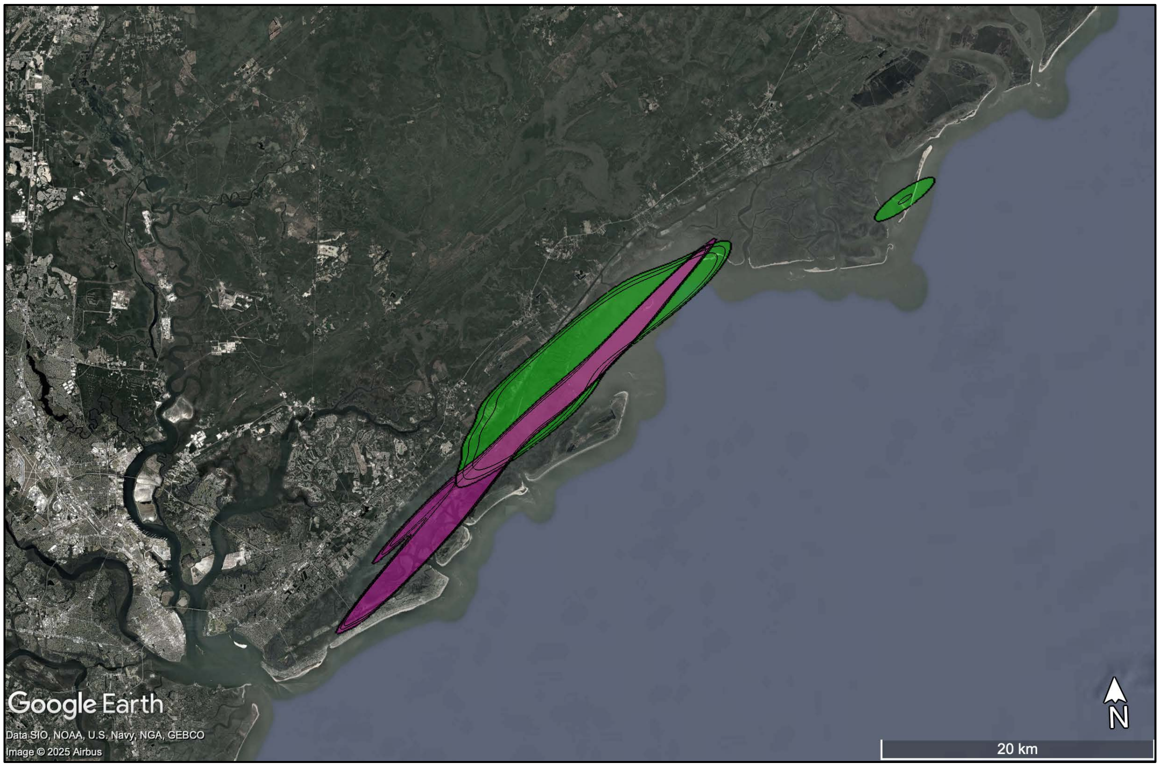


Supplementary Figure 5: Home ranges of non-breeding American Oystercatchers (*Haematopus palliatus*) in Florida, USA. Red represents CAP, blue represents CEK, orange represents CEM, and green represents CAY.

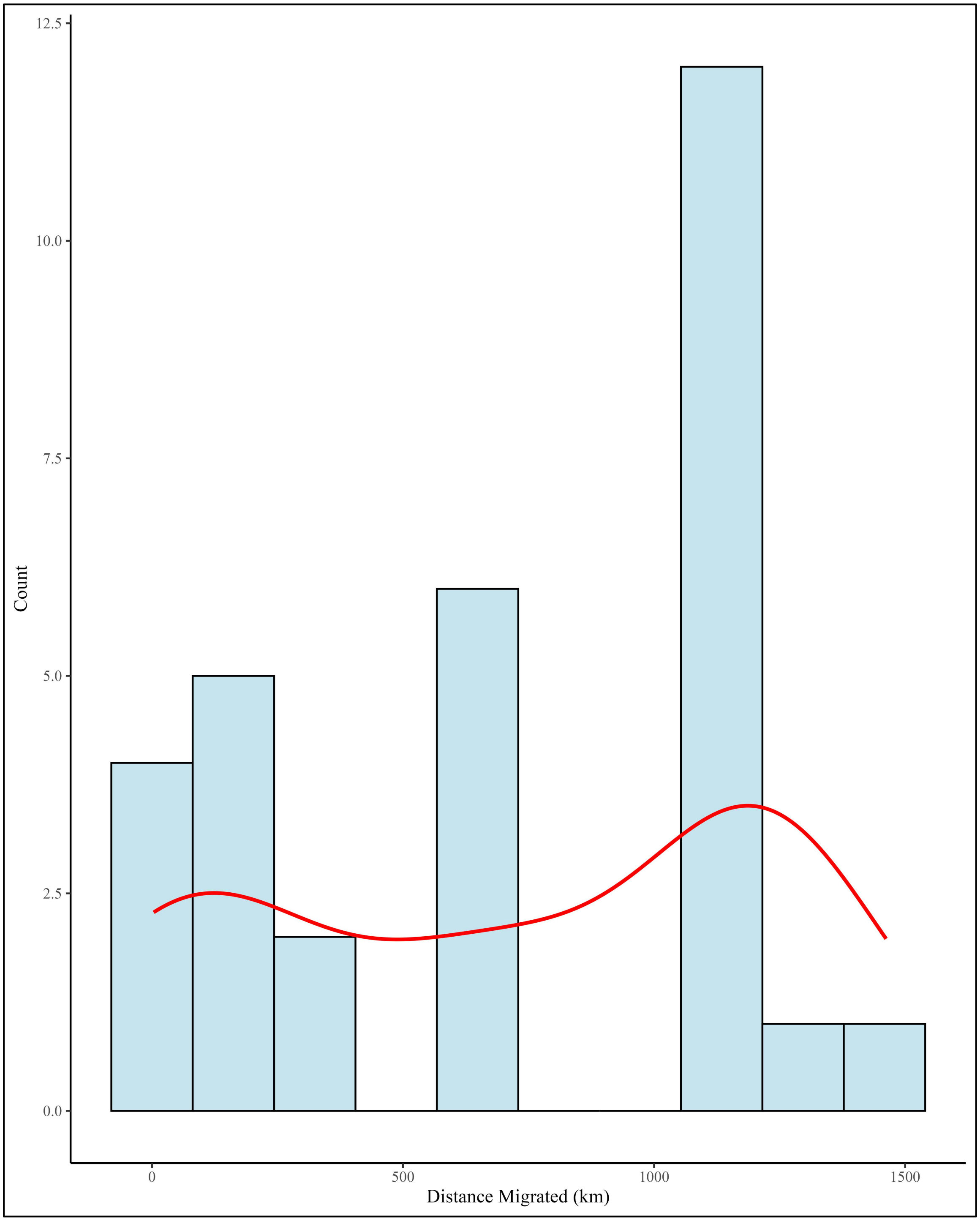


Supplementary Figure 6: Home range of American Oystercatcher (*Haematopus palliatus*) CAT during the non-breeding season while on a stopover event in South Carolina, USA.

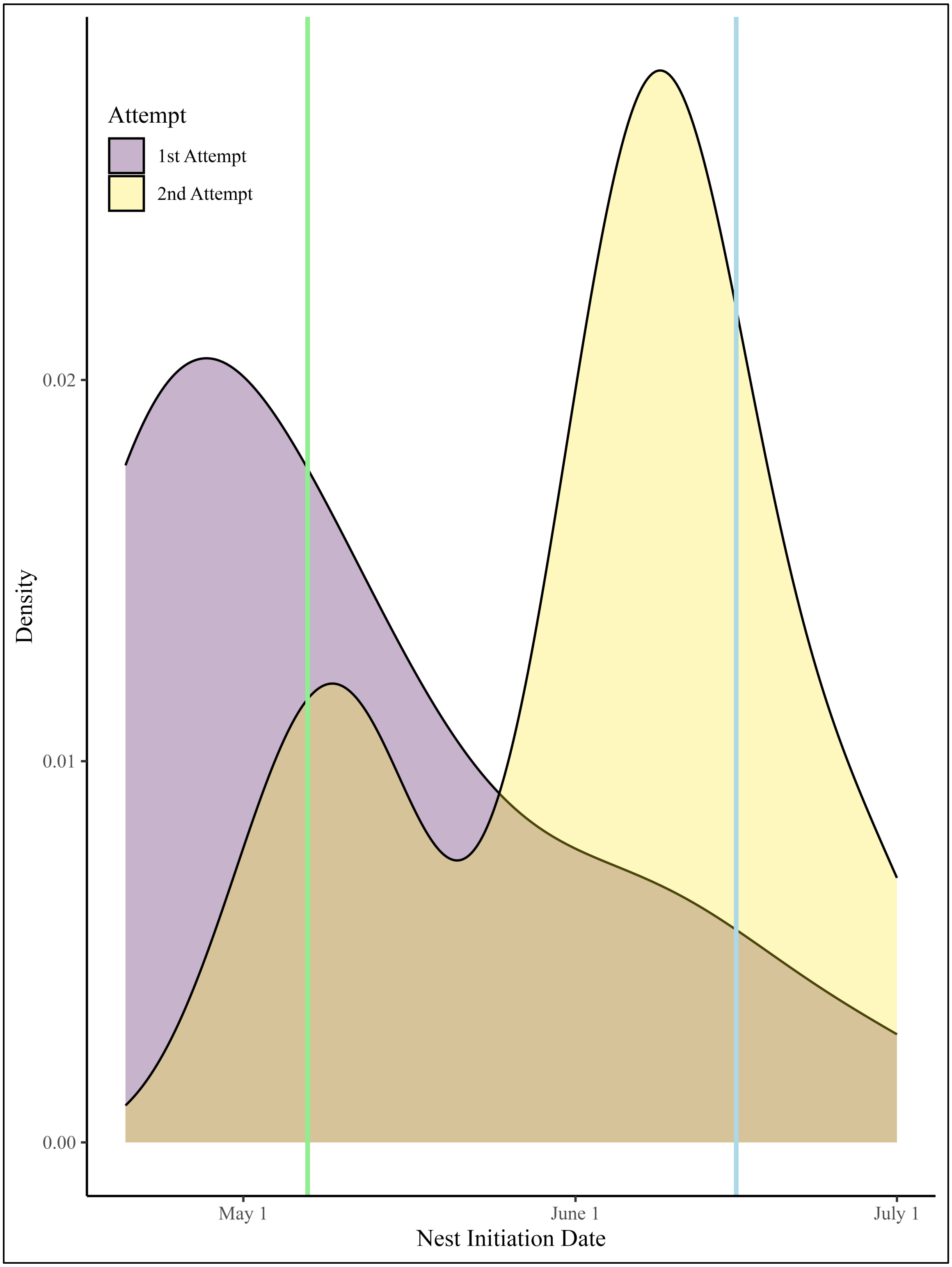
Supplementary Figure 7: Home range of American Oystercatcher (*Haematopus palliatus*) CKT during the non-breeding season in Virginia, USA.



Supplementary Figure 8: Home ranges of non-breeding American Oystercatchers (*Haematopus palliatus*) in South Carolina, USA. Green represents CEJ and pink represents CCK.



Supplementary Figure 9: Distribution of haversine distance migrated for 31 migration events across 20 American Oystercatchers (*Haematopus palliatus*). No distance migrated represents a non-migrant remaining in Chincoteague National Wildlife Refuge year-round.



Supplementary Figure 10: Distribution of Piping Plover (*Charadrius melodus*) nests attempts during the summer of 2023 at Chincoteague National Wildlife Refuge. Green vertical line represents the date in which 95% of secondary nests are excluded, removing 75% of primary nest attempts. Blue vertical line represents the date in which the last 5% of primary nests are excluded.