AN ABSTRACT OF THE THESIS OF

Olivia A. Bailey for the degree of Master of Science in Wildlife Science presented on September 5, 2018.

Title: Extrinsic and Intrinsic Factors Associated with Reproductive Success of Caspian Terns (*Hydroprogne caspia*) at East Sand Island, Columbia River Estuary.

Abstract approved: ____

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Declines in wild salmonid (*Oncorhynchus* spp.) populations in the Columbia River basin have resulted in managers identifying that avian predation on juvenile salmonids is an important limiting factor for salmonid recovery. Caspian Terns (*Hydroprogne caspia*), particularly those nesting in the Columbia River estuary, were identified as key avian predators that reduce the survival of juvenile salmonids in the Columbia River basin. To reduce the numbers of juvenile salmonids consumed by Caspian Terns in the Columbia River estuary, the amount of available nesting habitat for Caspian Terns on East Sand Island (ESI) was reduced from 2 ha in 2008 to 0.64 ha in 2012, and then was further reduced to 0.4 ha in 2015. The objective of this management was to reduce the size of the Caspian Tern breeding colony on ESI to about a third of its former size.

Caspian Terns are facultative colonial nesters and generally nest in ephemeral habitats. Caspian Terns nesting at ESI, however, have demonstrated very high colony site fidelity due to the consistent maintenance of nesting habitat, as well as the proximity to an abundant food supply and the paucity of terrestrial predators. Reproductive success for the ESI Caspian Tern colony has, on average, declined since 2001, and in both 2011 and 2017 no young were raised at the colony. The objective of my study was to understand variation in reproductive success of

Caspian Terns at the ESI colony by investigating potential factors associated with nesting success at the scale of the colony and the individual. I investigated both top-down and bottom-up factors that may have affected the average annual reproductive success at the Caspian Tern colony on ESI during 2001-2017, as well as the relative importance of several intrinsic factors that may have affected reproductive success of individual Caspian Terns over two consecutive breeding seasons, 2015 and 2016.

I found that study year and the rate of kleptoparasitism on Caspian Tern bill-load fish by gulls (*Larus* spp.) during the chick-rearing period best explained the inter-annual variation in average annual reproductive success at the ESI colony during 2001-2017. My results suggest that year was acting as a surrogate variable for other factors that were changing in a gradual, consistent manner at or near the tern colony during the study period, such as nesting habitat availability, nest density, Bald Eagle (*Haliaeetus leucocephalus*) disturbance rates, and gull predation rates on tern eggs and chicks. The impact of average Columbia River discharge in May/June as a driving factor for Caspian Tern reproductive success was particularly evident in 2011 and 2017, the two years when river discharge was the highest recorded during the study period, and the only two years when no young were produced at the colony. My results support the hypothesis that both bottom-up factors (e.g., food availability) and top-down factors (e.g., gull kleptoparasitism rates) are drivers of reproductive success at the East Sand Island Caspian Tern colony. The bottom-up factor of average Columbia River discharge in May/June apparently affected the top-down factor of gull kleptoparasitism rates by altering the food supply of nesting gulls, thus prompting them to switch to stealing Caspian Tern bill-loads.

The second study in my thesis sought to gain a better understanding of which factors may influence reproductive success of individual Caspian Terns, based on data collected at the ESI colony in 2015 and 2016. I investigated the relative importance of (1) age, (2) previous breeding experience, (3) timing of breeding, (4) density of nearby conspecific nests, and (5) nest location relative to the colony edge for explaining variation in individual reproductive success. The date when an individual tern initiated its nesting attempt was ranked highest in relative importance among these explanatory variables, with nest success decreasing as the date of nest initiation increased. The density of conspecific nests within 1 meter of an individual's nest was strongly and positively associated with the odds that the nest was successful. Nests located further from the colony edge were more likely to be successful, but only early in the breeding season; later in the season, nest location had no effect on individual reproductive success. Individuals that initiated nests earlier in the breeding season had more time to lay replacement clutches in the event that their earlier nesting attempts failed, and laying more than one clutch per breeding season was common at the ESI colony during the study period. Some individuals attempted to nest as many as four times in a single breeding season.

My study provides a better understanding of those extrinsic and intrinsic factors that are associated with reproductive success of Caspian Terns on two different scales – the breeding colony at ESI as a whole, and the individual Caspian Terns nesting at ESI. Understanding factors influencing reproductive success at each scale increases our knowledge of Caspian Tern breeding ecology at East Sand Island, and can inform managers about which factors likely regulate the size and productivity of the largest Caspian Tern breeding colony in North America. This study can also provide insight into factors that affect other seabird species and organisms that live in seasonal environments, as well as long-lived organisms that may experience considerable variation in overall reproductive success.

Extrinsic and Intrinsic Factors Associated with Reproductive Success of Caspian Terns (*Hydroprogne caspia*) at East Sand Island, Columbia River Estuary

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APPROVED:

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Olivia A. Bailey, Author

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CONTRIBUTION OF AUTHORS

Dr. Daniel D. Roby acquired funding, assisted with study design, data analysis and interpretation of results, and provided editorial comments for all chapters. Dr. Donald E. Lyons assisted with study design, data analysis, and interpretation of results for Chapters 2 and 3. Dr. Yasuko Suzuki provided assistance with study design and interpretation of results in Chapter 3.

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CHAPTER 1. GENERAL INTRODUCTION

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Colony fidelity is thought to have evolved as an adaptation for increased reproductive success. Benefits of returning to the same colony site year after year may include: (1) familiarity with the local environment, such as potential predators and foraging habitat; (2) familiarity with available nest sites, resulting in time and energy savings when finding a quality nest site; (3) familiarity with neighbors; and (4) mate fidelity (McNicholl 1975, Southern and Southern 1982; Shields 1984, Cuthbert 1988, Braby *et al.* 2012). Colony fidelity can be disadvantageous, however, if the nesting habitat deteriorates or no longer supports high nesting success (McNicholl 1975, Cuthbert 1988). High philopatry to a colony site can result in density-dependent reduction in productivity if nesting habitat is reduced and nesting density increases (Tims *et al.* 2004, Matthiopoulos *et al.* 2005, Palestis 2014). For example, for breeding Great Black-backed Gulls (*Larus marinus*), pairs nesting in areas with a high density of nests had lower fledging success (Butler and Trivelpiece 1981). Conversely, a significant positive correlation was found between breeding success and nest density in Common Murres (*Uria aalge*); where pairs nesting at higher densities were better able to defend against gull predation than pairs nesting in sparse areas of the colony (Birkhead 1977). Common Terns (*Sterna hirundo*) nesting centrally in the colony and in areas of higher nest densities had higher nesting success and were better able to defend against predators as a group (Becker 1995).

Colonial nesting waterbirds may respond differently to habitat deterioration or loss. A colony of Ring-billed Gulls (*Larus delawarensis*) whose nesting habitat was greatly altered between breeding seasons showed varied responses to habitat loss. Individuals that lost their specific nest sites on the colony were less likely to nest the year after the habitat was altered (Southern and Southern 1982), but still returned to the colony. Ganter and Cooke (1998) found that Lesser Snow Geese (*Chen caerulescens caerulescens*) exhibited strong fidelity to nest sites, even when the habitat was deteriorating, and other studies had documented an overall decline in fecundity at this colony (Cooch *et al.*1989).

Caspian Terns (*Hydroprogne caspia*), the largest species of tern, can be found on every continent besides Antarctica. This species typically nests in ephemeral habitats, preferring flat sandy or rocky substrates. A facultative colonial nesting species, Caspian Terns may either nest alone or in colonies ranging in size from a few nests to thousands of nests (Cuthbert and Wires 1999). In western North America, the numbers and breeding distribution of the species have expanded in recent decades. Historically, Caspian Terns nested in inland, freshwater habitats, but shifted to breeding grounds on the Pacific coast after loss of habitat due to anthropogenic change (Cuthbert and Wires 1999). Currently, the largest breeding colony (estimated at about 5,000 breeding pairs in 2018) of Caspian Terns in North America is located on East Sand Island in the Columbia River estuary, on the border of Oregon and Washington.

The decline of wild anadromous salmonid (*Oncorhynchus* spp.) in the Pacific Northwest has been attributed to over-harvest, habitat degradation, hydroelectric dams, and large-scale hatchery rearing programs, which are frequently referred to collectively as the “4-H’s” (Lichatowich 1999, Roby *et al.* 2003). In the Columbia River basin, 13 of 20 Evolutionarily Significant Units of salmonids that spawn in the basin are listed under the U.S. Endangered Species Act (ESA) as threatened or endangered (Good *et al.* 2005). Although managers recognize that the aforementioned “4-H’s” are the primary focus for salmonid restoration, predation on salmonids has also been identified as an important limiting factor for salmonid recovery (NOAA 2004).

Among the predators identified as limiting the survival of juvenile salmonids from the Columbia River basin are Caspian Terns, particularly those breeding in the Columbia River estuary. The distribution and abundance of Caspian Terns in the Pacific Flyway of North America changed between the 1960s and the early 2000s. In the late 1970s, only 4% of the Pacific Flyway population nested in Oregon, but by the early 2000s 69% of the population nested in Oregon (Suryan *et al.* 2004), and the majority of the flyway-wide population nested in the Columbia River estuary. In 1984, a large breeding colony of Caspian Terns (~1,000 breeding pairs) formed in the Columbia River estuary for the first time in recorded history; the colony was situated on freshly deposited dredged material on East Sand Island (river km 8), and its formation was concurrent with declines or abandonment of large colonies in Grays Harbor and in Willapa Bay, on the outer coast of Washington. By 1986, the colony on East Sand Island had shifted to Rice Island (river km 34) and, over the next decade, the colony grew due to an abundance of suitable nesting habitat, absence of terrestrial predators, and the existence of a reliable food source during the first half of the breeding season in the form of hatchery-raised juvenile salmonids (Collis *et al.* 2001). Collis *et al.* (2002) found that juvenile salmonids comprised 73% of the diet of Caspian Terns nesting at Rice Island during 1997-1998. To alleviate impacts on juvenile salmonid survival from predation by Caspian Terns nesting at the large colony on Rice Island, the ca. 9,000 pairs of terns nesting at Rice Island were relocated back to East Sand Island (ESI) during 1999-2001, using a combination of habitat enhancement and social attraction (decoys and audio playback systems) on ESI and dissuasion of nesting terns on Rice Island (Roby *et al.* 2002).

The relocation of the Caspian Tern colony from Rice Island to ESI successfully reduced the proportion of juvenile salmonids in tern diets (Roby *et al.* 2002). During 1999 – 2001, the diet of Caspian Terns nesting at East Sand Island averaged 42% salmonids, while that of terns nesting at Rice Island averaged 83% salmonids. During 2001-2013, Caspian Terns nesting at

East Sand Island consumed an average of ca. 5.1 million smolts per year (Bird Research Northwest 2015), which is a significant reduction compared to the estimated 12.4 million smolts consumed by Caspian Terns nesting on Rice Island in 1998 (Roby *et al.* 2003).

Although the average number of salmonid smolts consumed per year by Caspian Terns nesting on ESI was significantly reduced compared to when the colony was located on Rice Island, terns still consumed 5-15% of the smolts that survived to the estuary from some ESA-listed populations of salmonids (Bird Research Northwest 2015). Due to this ongoing impact, management agencies prepared a Caspian Tern management plan for the Columbia River estuary (U.S. Fish and Wildlife Service 2005, 2006), which was implemented starting in 2008. The objective of the management plan was to reduce the size of the Caspian Tern breeding colony on East Sand Island to 3,125 – 4,375 breeding pairs. The reduction in colony size would be accomplished by reducing the area of suitable nesting habitat for Caspian Terns on ESI. In conjunction with reduction in colony area on ESI, terns would be prevented from nesting elsewhere in the Columbia River estuary, and alternative tern nesting habitat (islands) would be constructed elsewhere within the range of the Pacific Flyway population of Caspian Terns. Nine new tern colony sites were constructed by the U.S. Army Corps of Engineers (USACE) in interior Oregon and northeastern California during 2008-2012, and an additional five new colony sites were constructed by the USACE in southern San Francisco Bay in 2015. The colony area at East Sand Island was concomitantly reduced from 6 acres in 2007 to 1.58 acres in 2012, and was then further reduced to 1.0 acre in 2015.

Along with other species in the family Laridae that utilize ephemeral nesting habitat, Caspian Terns generally exhibit low colony site fidelity compared to most species of pelagic seabirds (Cuthbert 1988, Collar 2013). Despite the managed reduction in available nesting habitat on East Sand Island, Suzuki (2012) found that breeding Caspian Terns exhibit very high colony site fidelity to East Sand Island. Similarly, Collar (2013) found unexpectedly high philopatry to the East Sand Island colony despite colony-wide reproductive failure in 2011. Due to the consistent maintenance of nesting habitat for Caspian Terns on ESI and an abundant food supply nearby, ESI has provided a prime and reliable nesting site for Caspian Terns for over 18 years (Collar 2013).

As the amount of available Caspian Tern nesting habitat was gradually reduced from approximately 2.4 ha in 2007 to 0.4 ha in 2015, the nesting density of Caspian Terns at ESI has increased. Average nest density was measured at 0.72 nests/m^2 in 2008, had increased to 1.17 nests/m^2 in 2013 (Bird Research Northwest 2015), and by 2016 average nest density was 1.36 nests/m^2, the highest average nesting density ever recorded at the East Sand Island Caspian Tern colony. Antolos *et al.* (2006) observed a wide range of nest densities within a single Caspian Tern colony on Crescent Island in eastern Washington State (0.25-1.48 nests/m^2). Caspian Tern nesting success was not negatively affected by increasing nest densities, even at the highest nest densities observed on the colony. Although their study did not detect an effect of nest density on productivity, the year the study was conducted (2001) was the year of the highest nesting success and colony size ever recorded for the Crescent Island Caspian Tern colony (Antolos *et al.* 2006). Productivity that year averaged 1.00 fledgling raised per breeding pair, much greater (~35% - 45%) than the productivity observed in subsequent years. Greater overall productivity may have limited the ability to detect density-dependent effects on nest success at the colony on Crescent Island in that particular breeding season. Despite the lack of observed density-dependent effects, the results support the need for additional studies investigating the relationship between nest density and other factors affecting reproductive success of Caspian Terns (Antolos 2002).

In addition to increasing the density at which they nest, Caspian Terns may respond to loss of nesting habitat in several other ways. For example, breeding chronology may become less synchronous across the colony as more pairs attempt to establish nest territories in an already crowded colony, and adult attendance at the colony may decrease. In other seabird species, the ability to adjust breeding chronology in response to changes in the local environment can enhance breeding success at the population level (Perrins 1970). In a population of Gentoo Penguins (*Pygoscelis papua*), for example, the ability to change nesting chronology based on environmental changes helped sustain overall reproductive success (Hinke *et al.* 2012). As changes in nesting habitat occur at the ESI Caspian Tern colony, monitoring the chronology and synchrony of nest initiation may help predict overall nesting success during the breeding season. In conjunction with higher nest densities as the area of nesting habitat has been reduced, the number of breeding pairs on the colony has also decreased. The lack of unoccupied nest sites may drive the dispersal to other nesting sites of individuals that have lost their nests or cannot compete for limited space resources at ESI (Bowler and Benton 2004). Understanding the Caspian Tern colony's overall response to changes in the availability and quality of nesting habitat is not only important for restoration and management, but also for gaining a better understanding of this species' natural history and breeding behavior.

On the individual level, multiple additional factors may affect breeding success. Older individuals generally have higher reproductive success than young conspecifics, perhaps due to greater reproductive effort, more efficient foraging, or more extensive breeding experience (Haymes and Blokpoel 1980, Pyle *et al.* 1991, Forslund and Larsson 1992, Pugesek 1995, Limmer and Becker 2010, Desprez *et al.* 2011). Older and/or more experienced birds may also arrive on the colony earlier, as well as lay eggs earlier. Earlier lay dates have been shown to correlate with higher breeding success in many studies of colonial waterbirds (Haymes and Blokpoel 1980, Perdeck and Cave 1992, Hipfner *et al.* 2010), including in Caspian Terns (Antolos *et al.* 2006).

Timing of nest initiation may also help determine the nest's location on the colony and consequently confer benefits and/or risks to nesting success. Velando and Freire (2001) proposed the "central-satellite" distribution model, where nests are initiated earliest in the center of colonies, and these nests are more successful than nests on the edge of the colony. Antolos *et al.* (2006) demonstrated a strong negative relationship between hatch date and Caspian Tern productivity. In that study, nests that were initiated earlier were more successful, and were established in higher density areas and farther from the edge of the colony than nests initiated later in the season. This is consistent with other studies that have demonstrated that birds that arrive and nest earlier are higher quality breeders (Coulson and White 1958, Dittmann and Becker 2003).

Successful birds are also more likely to exhibit fidelity to a specific nest site or to the area of the colony where they successfully nested previously (Fairweather and Coulson 1995, Boulinier *et al.* 2008). Birds are able to make decisions based on experience and knowledge gained from current and prior breeding attempts. For example, Red-winged Blackbirds (*Agelaius phoeniceus*) moved farther from previous nest sites and were more likely to change marshes if their nests were unsuccessful in the previous year (Beletsky and Orians 1991). This "success-stay/failure-leave" strategy (Schmidt 2004) may be influenced by individual experience and/or by information obtained from the success of conspecifics. Danchin and Cam (2002) found that the breeding probability of experienced Black-legged Kittiwakes (*Rissa tridactyla*) was based more on their own experience than on the average reproductive success of their neighbors.

Young or inexperienced birds cannot rely on past experiences, however, and may instead utilize 'public information' to select breeding sites.

Kittiwakes that failed at breeding in their first year of breeding were more likely to return the subsequent year and attempt to nest on a different cliff, in particular one that had higher breeding success per capita in the first year (Danchin *et al.* 1998). Individual experience had a strong effect on breeding dispersal; birds tended to disperse from cliffs where they failed and their neighboring conspecifics also had low reproductive success. This was not the case for birds that nested and failed on cliffs with high local reproductive success, suggesting that in some cases the success of neighboring birds may override an individual's own breeding experience when deciding whether to move to a different nest site or colony. At some colonies, however, birds that try to choose a more productive nest site may be faced with density-dependent competition with conspecifics. This may lead to birds choosing low quality breeding habitats, nesting later, or skipping breeding altogether (Danchin *et al.* 1998, Kokko *et al.* 2004). The further reduction of available Caspian Tern nesting habitat at East Sand Island in 2015, from 1.5 acres to just 1.0 acre, provides a unique opportunity to look for factors influencing nesting success at both the colony level and at the level of the individual.

Finally, many extrinsic factors may influence the colony and the individual's breeding behavior and nesting success. Due to the dynamic nature of seabird colonies, both top-down and bottom-up factors may limit reproductive success at a colony. Suryan *et al.* (2006) found that an interaction of top-down and bottom-up factors affected Black-legged Kittiwake breeding success. These factors included prey availability and distribution, nest predation, competition with conspecifics for resources, and weather conditions.

Similarly, at the East Sand Island Caspian Tern colony, Collar *et al.* (2017) investigated colony attributes and environmental factors that potentially drove a decline in productivity during 2001-2011. That study found a significant inverse relationship between average Columbia River discharge during the nesting season and average annual reproductive success at the colony. During periods of high freshwater input into the Columbia River estuary, the abundance of marine forage fishes in the estuary is reduced (Loneragan and Bunn 1999), leading to a decline in prey availability for Caspian Terns. A reduction in the availability of marine forage fish in the estuary also likely influenced prey switching by gulls (*Larus* spp.) and Bald Eagles (*Haliaeetus leucocephalus*), and these predators targeted nesting Caspian Terns as a food supply, increasing top-down pressure on the tern colony. Specifically, the 2011 breeding season at ESI represented the lowest annual index of marine forage fish abundance during 2001-2011. During the 2011 breeding season, the frequency and duration of Bald Eagle disturbances increased, facilitating more gull predation on Caspian Tern nests. The interaction of these effects culminated in total breeding failure, with no young terns raised at the colony in 2011. These results present convincing evidence that inferences about the factors affecting nesting success and breeding behavior during the 2015 and 2016 nesting seasons should not be made without factoring in both top-down and bottom-up parameters that have so strongly influenced nesting success at this colony in the past.

Understanding what affects the reproductive success of breeding species is essential when creating successful conservation and management plans for colonial seabirds. My study was undertaken to determine colony-wide and individual factors that influence the reproductive success of breeding seabirds. Chapter 2 investigates which bottom-up and top-down factors are associated with average annual reproductive success of Caspian Terns nesting at East Sand

Island at the level of the colony. Chapter 3 seeks to identify the factors that are associated with the reproductive success of individual banded Caspian Terns nesting at the East Sand Island colony. The results of this study will inform our understanding of the many factors that may interact to limit the nesting success of colonial seabirds.

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CHAPTER 2. TOP-DOWN AND BOTTOM-UP FACTORS ASSOCIATED WITH REPRODUCTIVE SUCCESS OF CASPIAN TERNS (*HYDROPROGNE CASPIA*) AT A LARGE ESTUARINE COLONY

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ABSTRACT

Reproductive success at seabird breeding colonies is generally influenced by both top-down factors (e.g., predators) and bottom-up factors (e.g., food supply). The Caspian Tern (*Hydroprogne caspia*) breeding colony at East Sand Island (ESI) in the Columbia River estuary, failed to produce any young during the 2011 breeding season, primarily due to the impact of high Columbia River discharge on tern food supply and the indirect effect of this bottom-up factor on predators of Caspian Terns and their nests. We investigated whether these factors continued to be closely associated with Caspian Tern reproductive success at ESI during 2012-2017. We found that average annual reproductive success declined from 2001 to 2017, and that top-down factors remained a key driver of reproductive success at the ESI colony. After controlling for year, average reproductive success declined with increasing kleptoparasitism rate on adult terns by gulls (*Larus* spp.). While there was a negative relationship between average annual reproductive success at the tern colony and Columbia River discharge, this explanatory variable was not as predictive of reproductive success as gull kleptoparasitism rate. Columbia River discharge was highly positively correlated with gull kleptoparasitism rate, however, supporting the hypothesis of a strong linkage between top-down and bottom-up factors influencing tern reproductive success. Our results indicate that top-down factors remain important drivers of Caspian Tern breeding success at ESI, particularly in years when high freshwater input to the estuary limits the availability of marine forage fish to both terns and their predators. This complex interaction between bottom-up factors (e.g., Columbia River discharge) and top-down factors (e.g., gull kleptoparasitism) will need to be considered if management to conserve this large and declining colony of Caspian Terns is to be effective.

INTRODUCTION

Marine ecosystems experience considerable variation in ocean conditions, including large-scale climate cycles (e.g., Pacific Decadal Oscillation), short-term climatic fluctuations (e.g., El Niño/Southern Oscillation), as well as local heterogeneity. Seabirds are upper-trophic level predators that utilize extensive areas of marine habitat for foraging during the breeding season; this allows their reproduction to serve as a useful indicator of short- and long-term environmental changes in the marine environment (Ainley and Hyrenbach 2010). To breed successfully, seabirds must adapt to variable forcing from both bottom-up and top-down factors (Suryan *et al.* 2006). Understanding inter-annual variability in reproductive success of colonial nesting seabirds depends on identifying those factors that influence nesting success.

Many studies of seabird reproductive success initially focused on whether top-down or bottom-up factors are more important in determining the breeding success of colonial nesting seabirds (Hairston *et al.* 1960, Floyd 1996, Hunt *et al.* 2002). More recently, research has shifted towards understanding how top-down and bottom-up factors interact, and the relative importance of each factor in driving reproductive success (Suryan *et al.* 2006, Horton 2015, Collar *et al.* 2017). Breeding colonies of seabirds in the California Current System (CCS) are exposed to variable ocean conditions, such as inter-annual variability in sea surface temperatures (SST) and the timing and strength of seasonal coastal upwelling (Abraham and Sydeman 2004). On the scale of multiple years, the El Niño/Southern Oscillation (ENSO) and the North Pacific Gyre Oscillation (NPGO; Abraham and Sydeman 2004) can cause more widespread and longer-term variability in ocean conditions within the CCS. At a longer scale, the Pacific Decadal Oscillation (PDO) can influence marine community structure in the CCS through climatic changes that persist for many years. Changes in ocean conditions can drive variation in primary productivity, prey availability for upper trophic levels, and the aggregation of prey in the CCS (Kaltenberg *et al.* 2010, Gladics *et al.* 2015). This variability can also play a significant role in nesting phenology and fledging success at seabird breeding colonies.

With changing ocean conditions, multiple studies have linked changes in forage fish availability and abundance to variation in nesting success at seabird colonies (Abraham and Sydeman 2004, Anderson *et al.* 2007, Becker *et al.* 2007, Burke and Montevecchi 2009). For Common Murres (*Uria aalge*) nesting on Funk Island, Newfoundland, fledged chicks were in better condition in years when the density and aggregations of capelin (*Mallotus villosus*) were greater. In the CCS, Gladics *et al.* (2015) documented an association between nesting success of Common Murres breeding at Yaquina Head, Oregon, and the availability of forage fish, specifically clupeids (i.e. herring, sardines, and shad). Similarly, the early onset of murre nesting was associated with the abundance and availability of Pacific sand lance (*Ammodytes hexapterus*).

Many seabird species are central place foragers throughout the nesting season, meaning that they must transport resources to the nest site. Breeding adults not only must forage to provide for themselves, but also must provision their mates and young at the breeding colony. Commuting between nest sites and foraging areas can be an important constraint for the budgeting of time and energy resources by breeding adult seabirds (Anderson *et al.* 2007). When forage availability is limited, adult seabirds may compensate by increasing their foraging effort, foraging further from the nest, delaying the initiation of breeding, or abandoning their breeding effort mid-season (Abraham and Sydeman 2004). At Black-legged Kittiwake (*Rissa tridactyla*) colonies over an 11-year study, a large proportion of adults did not breed in years when food resources were not sufficient to raise chicks. Similarly, no kittiwake chicks survived to fledge in a season when adult kittiwakes were foraging at least 40 km from the breeding colony (Harris and Wanless 1997). Therefore, monitoring the breeding success of seabird colonies may provide information about the correlations between food availability and reproductive success.

Spending more time away from the breeding colony to forage may incur costs to reproductive success in multiple ways. If foraging conditions deteriorate, both parents may have to spend more time foraging, instead of one member of the pair attending the nest and provide care to offspring (Harris and Wanless 1997). In a breeding season with lower availability of marine forage fish, Caspian Terns (*Hydroprogne caspia*) nesting at East Sand Island (ESI) in the Columbia River estuary made longer foraging trips, fewer adults attended their nests on-colony, and overall nesting success was lower (Anderson *et al.* 2007).

Changes in the marine environment not only affect seabird reproductive success, but also affect predators of seabirds and their nest contents. Seabird breeding colonies are commonly under pressure from both avian and mammalian predators, and predation on eggs and/or chicks can, in some cases, cause population declines at breeding colonies (Suryan *et al.* 2006), or even colony abandonment (Collar *et al.* 2017). Predators on seabirds and their nest contents may be opportunistic, but predation rates on seabirds can reflect predator switching due to low availability of the predators' primary food sources. Mortality of seabird eggs and chicks due to avian predators can account for the majority of variation in average annual reproductive success at some colonies (Hatch and Hatch 1990). If normal prey for avian predators is scarce, avian predators may key in on seabird colonies as an alternative food source (Collar *et al.* 2017). Since the banning of DDT in 1972, there has been a resurgence of Bald Eagle (*Haliaeetus leucocephalus*) populations in the conterminous United States in general, and in the Columbia River estuary in particular (Isaacs and Anthony 2011). Apex predators, such as the Bald Eagle, have had dramatic top-down impacts on reproductive success at some seabird colonies in the CCS, either directly or indirectly (Hipfner *et al.* 2012, Collar *et al.* 2017). Bald Eagles have been documented to cause direct mortality to breeding adult seabirds, but more often they facilitate secondary avian predators (e.g., gulls and corvids) to take seabird eggs and young by causing massive disturbances to adult seabirds attending nests at a breeding colony (Parrish *et al.* 2001).

Top-down influences on seabird reproductive success may also come in the form of kleptoparasitism (food stealing; Iyengar 2008). This behavior is common among seabird species and, in some cases, occurs among conspecifics (Brockmann and Barnard 1979, Gaglio *et al.* 2018). Many seabird species breed in association with other seabird species, and these associations may provide benefits when the colony associates (e.g., gulls) are more aggressive toward avian predators (e.g., eagles). However, nesting close to another breeding species may come with costs, including kleptoparasitism. High rates of kleptoparasitism by gulls have been documented in some cases to have considerable negative effects on the growth of tern chicks (Stienen *et al.* 2001) and can increase the energetic costs to adult terns of provisioning food to their young (Gaglio *et al.* 2018).

In this study, we sought to enhance understanding of how top-down and bottom-up factors limit the breeding success of Caspian Terns nesting at the breeding colony on East Sand Island (ESI) in the Columbia River estuary. This colony is the largest breeding colony for the species in North America. Breeding success at this colony declined from 2001 to 2011, culminating in the colony failing to produce any fledglings in 2011 (Collar *et al.* 2017). Because ESI is located at the mouth of the Columbia River, it is not only subject to variation in the California Current System, it is also subject to changes in freshwater discharge into the Columbia River estuary. Collar *et al.* (2017) found that the decline in tern breeding success at

ESI between 2001 and 2011 was associated with a significant increase in Columbia River discharge; average Columbia River discharge during May/June was highly negatively correlated with nesting success at the ESI colony. Increased river flows result in more freshwater and less marine water in the estuary, which in turn affects the abundance and species composition of forage fish in the Columbia River estuary. High river flows can physically and physiologically exclude marine forage fish from estuaries, and it has been hypothesized that higher river flows reduce the foraging efficiency of predators that forage at or near the water surface by creating a freshwater lens above marine waters near the mouth of the river (Weitkamp *et al.* 2012). The rate of disturbance to the Caspian Tern colony at ESI by Bald Eagles increased significantly as river discharge increased; eagle disturbance, by causing adult terns to briefly leave their nests unattended, indirectly led to high predation rates on tern eggs and chicks by gulls (Collar *et al.* 2017). Collar *et al.* (2017) also found that the rate of kleptoparasitism on terns by gulls nesting at ESI increased between 2001 and 2011, and there was a positive relationship between kleptoparasitism rates and river discharge. This suggested that in years of relatively high river discharge and poor foraging conditions for gulls, the gulls nesting on ESI relied more on kleptoparasitism of terns as a source of food.

Management agencies developed a Caspian Tern management plan for the Columbia River estuary in order to mitigate the ongoing predation by breeding Caspian Terns on juvenile salmonids (*Oncorhynchus* spp.) listed as threatened or endangered under the U.S. Endangered Species Act (ESA; U.S. Fish and Wildlife Service 2005, 2006). The primary objective of the management plan was to reduce the size of the Caspian Tern breeding colony on ESI from about 10,000 pairs to between 3,125 and 4,375 breeding pairs by limiting the availability of tern nesting habitat. Coinciding with the reduction in area of nesting habitat on ESI, which was initiated in 2008, terns were prevented from nesting elsewhere in the Columbia River estuary. Additionally, alternative nesting habitat was constructed elsewhere in the breeding range of the Pacific Flyway population of Caspian Terns. The area of nesting habitat for Caspian Terns at ESI was gradually reduced from 2.0 ha (5 acres) in 2008 to 0.64 ha (1.58 acres) in 2012, and then further reduced to 0.4 ha (1.0 acre) in 2015. During the 2016 and 2017 breeding seasons, the area of available tern nesting habitat remained at 0.4 ha. The reduction in area of Caspian Tern nesting habitat on ESI was accomplished by erecting visual barriers (landscape fabric fences) around the perimeter of the existing colony area, ensuring that Caspian Terns only nested within the area of habitat designated for their use.

The immediate goal of limiting the available Caspian Tern nesting habitat on ESI was to displace breeding pairs to newly constructed alternative nesting habitat (islands) within the range of the Pacific Flyway population. Establishing colonies outside the Columbia River estuary would accomplish two objectives: (1) reduce Caspian Tern predation on juvenile salmonids listed as threatened or endangered under the ESA, and (2) limit the potential negative effects of a local catastrophic event at the ESI breeding colony, where about two-thirds of the Pacific Flyway population of Caspian Terns nested.

Expanding on previous studies that found an interaction between top-down and bottom-up factors that limit Caspian Tern reproductive success, our study investigated how these factors affected reproductive success at ESI during 2012-2017 and compared findings with those during 2001-2011 (Collar *et al.* 2017). We predicted that Columbia River discharge would continue to have a negative effect on Caspian Tern reproductive success at ESI through its influence on tern food supply. We also predicted that higher Columbia River discharge would cause greater top-down pressure on the Caspian Tern colony by predators (in this case through kleptoparasitism rates by gulls), thereby having a negative effect on average reproductive success at the tern colony.

METHODS

Study Area and Focal Species

East Sand Island (ESI) (46°15’45”N, 123°57’45”W) is a ca. 20-ha island located near the mouth of the Columbia River at river kilometer 8, and it has been the site of the largest breeding colony of Caspian Terns in North America since 2000. The Caspian Tern breeding colony on ESI was re-established after managers restored nesting habitat and deployed social attraction (decoys and audio playback of vocalizations) in 1999 (Roby *et al*. 2002). Limited lethal control of predatory Glaucous-winged/Western Gulls (*Larus glaucescens* X *L. occidentalis*), which also nest in large numbers on ESI, was conducted on the Caspian Tern colony during the 1999 and 2000 breeding seasons, and again during the 2012 breeding season. ESI is owned and managed by the U.S. Army Corps of Engineers (USACE), and annual restoration of tern nesting habitat by the USACE has been required to maintain the Caspian Tern colony at ESI up to the present.

Caspian Terns winter from Southern California to as far south as Nicaragua. They arrive at their Pacific Coast breeding grounds starting in late March and begin nest initiation in April. Caspian Terns lay 1-3 eggs per clutch, and they are incubated for an average of 26 days before hatching. Nesting Caspian Terns exhibit biparental care. Caspian Tern chicks are semi-precocial and become more mobile with age. Finally, on average, chicks fledge when they have reached 45 days old (Cuthbert and Wires 1999).

Colony Data

Number of Breeding Pairs, Density of Nests, and Reproductive Success

The peak number of Caspian Tern breeding pairs nesting at the ESI colony each year during 2001-2017 was estimated from direct counts of adult terns in vertical aerial photography taken late in the incubation period. These counts were corrected for nest attendance rates using simultaneous estimates from the ground of the average ratio of adults sitting on nests to adults not on nests in 36-m^2 sample plots on the colony (Collis *et al.* 2002).

The density of Caspian Tern nests (nests/m^2) on the ESI breeding colony was also estimated using aerial photography. The estimated peak number of breeding pairs in each year was divided by the area of nesting habitat used by terns, based on estimates from controlled vertical aerial photography. The methods for acquiring the controlled aerial photography used in this study were described in detail by Collis *et al.* (2002).

Average annual reproductive success at the ESI colony was estimated each year from the number of fledglings on the colony just prior to the peak of fledging, based on direct counts from aerial photography, corrected using the average ratio of fledglings to adults in the 36-m^2 sample plots (Lyons 2010). Colony reproductive success (average number of young fledged per breeding pair) in each year was estimated by dividing the estimated total number of fledglings by the estimated peak number of breeding pairs.

Nesting Chronology

During each breeding season at the ESI colony, data were collected on multiple measures of tern nesting chronology. These measures included the date when the first tern was observed on the colony, the date the first tern egg was observed, the date when the first chick was observed, and the date when the first fledgling (chick capable of sustained flight) was observed. The dates of each measure of nesting chronology were recorded each year for comparison with the average date of each milestone during the entire study period (2001-2017). We used the date when the first chick was observed as the metric for nesting chronology in this study because first chicks were more readily detectable than the first egg or the first fledgling on-colony. Eggs laid early in the breeding season are more susceptible to predation by gulls, due to the high rate of disturbances by bald eagles early on in the egg-laying period (Collar *et al.* 2017). For this reason, the first chick observed is a more precise and representative indicator of overall nesting chronology for Caspian Terns nesting at ESI. In addition, we used the date of the first observed chick, instead of the first observed fledgling, as a measure of nesting chronology so that we could use the metric for nesting chronology to differentiate the incubation period from the chick-rearing period of the nesting cycle.

Diet Composition Data

Caspian Terns transport a single whole fish in their bills when returning to the breeding colony to feed their mate or chicks. Observations of Caspian Terns returning to the breeding colony with fish in their bills (bill-loads) were conducted twice daily during the breeding season, in all weather conditions, from nest initiation until after the peak of fledging. Twenty-five fish were randomly and visually identified to the taxonomic level of family during each observation session from blinds at the periphery of the colony. Bill-load identification sessions were conducted at high tide and low tide each day to control for potential effects of tide stage and time of day on the taxonomic composition of tern diets.

The average taxonomic composition of the Caspian Tern diet (proportion of each prey type of the total number of identified prey items) was calculated for each breeding season. Bill-load fish were identified to one of the following prey types, based on family: Osmeridae (smelt), Embiotocidae (surfperch), Clupeidae (including Pacific herring [*Clupea pallasi*], Pacific sardine [*Sardinops sagax*], and American shad [*Alosa sapidissima*]), Engraulidae (northern anchovy

[*Engraulis mordax*]), and Salmonidae (*Oncorhynchus* spp., including steelhead [*O. mykiss*], coho salmon [*O. kisutch*], Chinook salmon [*O. tshawytscha*], and sockeye salmon [*O. nerka*]). Prey identification and calculation of average annual taxonomic composition of the tern diet followed standardized methods described in Collis *et al.* (2002) and Collar *et al.* (2017). Average diet composition was calculated for each breeding season during 2001-2017; however, diet data from 2016 were not included in the analysis because of small sample sizes and different data collection techniques in that year (BRNW 2017). Based on results obtained by Collar *et al.* (2017) which found a positive correlation between the average annual reproductive success of Caspian Terns at ESI and the proportion of clupeids in tern diets, only the proportion of clupeids in the annual diet of Caspian Terns nesting at ESI was used in our analysis.

Kleptoparasitism Rates

During each twice-daily bill-load observation session, each tern bill-load observation was assigned to one of the following final fates: (1) eaten by the individual transporting the bill-load fish, (2) fed to an adult tern, (3) fed to a tern chick, (4) stolen by a conspecific, or (5) kleptoparasitized by a gull. Average kleptoparasitism rates for each year were calculated by dividing all bill-load fish that were kleptoparasitized by the total number of fish with assigned final fates, and is thus a minimum measure of kleptoparasitism. Kleptoparasitism rates were calculated for each breeding season during 2001-2017; however, data from 2016 were not included in analyses due to small sample sizes and different data collection techniques used in that year. Finally, average kleptoparasitism rates were divided into two separate rates, one before chick-hatch and one after chick-hatch; the date of the first observation of a chick on-colony in each year was used as the cut-off date between the two periods when kleptoparasitism rates were calculated. Kleptoparasitism rates were calculated separately for these two stages of the nesting cycle to explore whether the intensity of gull kleptoparasitism had more of an effect on tern reproductive success during the incubation period or during the chick-rearing period of the nesting cycle.

Climate Data: Columbia River Discharge

Data on daily Columbia River discharge were downloaded from the U.S. Geological Survey website (http://waterdata.usgs.gov) for river km 86 (site number 14246900). This site is downstream from the confluence of all major tributaries to the Columbia River. We calculated average monthly river discharge (thousands of cubic feet per second, *kcfs*) for the months encompassing the Caspian Tern breeding season (April, May, June, July) for each year during 2001-2017. We chose to only include river discharge data from May and June in our analyses because these months include the periods when most Caspian Terns nesting at ESI are incubating eggs and provisioning young chicks. The average river discharge for the months of May and June in each year were combined following the methods used by Collar *et al.* (2017) in order to further investigate the relationship between May/June river discharge and average annual reproductive success that was demonstrated in that study.

Data Analysis

The response variable used in our data analyses was the annual Reproductive Success (average number of young raised per breeding pair) at ESI. All potential correlations between explanatory variables were explored using Pearson's correlation in R (R Development Core Team 2011). Explanatory variables with Pearson's correlation coefficients (R) greater than 0.7 were not included in the same regression model. Due to the small sample size of the time series ($n = 17$ y), no more than two explanatory variables were included in a model to avoid overparameterization. Generalized linear models with a Gaussian distribution and log link were created based on *a priori* biologically relevant hypotheses (Burnham and Anderson 2010).

Models were ranked using Akaike's Information Criterion adjusted for small sample sizes (AIC_c) to determine which explanatory variables best explained the inter-annual variability in (log-transformed) Caspian Tern reproductive success at the ESI colony over the study period. Models were compared using the ΔAIC_c value, which is the difference between a model's AIC_c score and the lowest (most probable) AIC_c score of the candidate models. All statistical analyses were performed using program R (version 3.4.4), packages *nlme*, *MuMIn*, and *ggplot2* (R Development Core Team 2011).

RESULTS

Reproductive Success

Caspian Tern reproductive success at the colony on East Sand Island averaged 0.53 (95% CI: 0.32 – 0.75) chicks fledged per breeding pair during the 17-year study period (Table 2.1). Average annual reproductive success ranged from a high of 1.39 chicks fledged per breeding pair in 2001 to a low of 0.00 chicks fledged per breeding pair in both 2011 and 2017; in both 2011 and 2017, the entire tern breeding colony at ESI failed, with no young terns raised to fledging in either year. The average annual reproductive success at the ESI Caspian Tern colony declined from 2001 to 2017 ($r^2 = 0.72$, $F_{1,15} = 18.5$, $p < 0.001$; Figure 2.1); annual reproductive success decreased by an average of 3.9% per year elapsed (95% CI: 2.0% - 5.8%) during the study period.

Nest Density

The density of Caspian Tern nests on the East Sand Island colony averaged 0.81 nests/m^2 (95% CI: 0.66 – 0.96) during the 17-year study period. Average annual nest density ranged from a low of 0.45 nests/m^2 in 2005 to a high of 1.36 nests/m^2 in 2016 (Table 2.1). Average nest density increased during the study period ($r^2 = 0.79$, $F_{1,15} = 56.2$, $p < 0.001$). Nest density was highly inversely correlated with the area of nesting habitat prepared for the tern breeding colony ($R = -0.92$, $p < 0.001$).

There was a negative correlation between nest density and colony size (Pearson's correlation coefficient $R = -0.67$, $p = 0.005$; Table 2.2), and a positive correlation between nest density and nest chronology (date of first chick hatch; $R = 0.61$, $p = 0.01$; Table 2.2).

Colony Size

The size of the Caspian Tern breeding colony on ESI averaged 7,978 breeding pairs (95% CI: 7,011 – 8,944) during the study period and ranged from a low of 3,500 pairs in 2017 to a high of 10,668 pairs in 2008 (Table 2.1). Colony size decreased during 2001-2017 ($r^2 = 0.64$, $F_{1,15} = 26.9$, $p < 0.001$). Average reproductive success increased with increasing colony size ($r^2 = 0.38$, $F_{1,15} = 9.13$, $p = 0.009$); reproductive success increased by an estimated 8.93% (95% CI: 2.63% - 15.2%) with each increase of 1,000 breeding pairs in the size of the tern colony. There was a strong positive correlation between colony size and the area of tern nesting habitat prepared for the breeding colony ($R = 0.80$, $p < 0.001$). There was also a negative correlation between colony size and nesting chronology (Day of Year of first observed chick; $R = -0.50$, $p = 0.01$, Table 2.2); the larger the colony was, the earlier nesting chronology tended to be.

Nesting Chronology

The date when the first Caspian Tern chick was observed on the ESI colony averaged 145 day of year (25 May in non-leap years) (95% CI: 141 – 148) during 2001–2017. The date of first chick-hatch ranged from 134 day of year (14 May) in 2004 to 155 day of year (4 June) in 2017 (Table 2.1). There was an increase in the date when the first chick was observed during the study period ($r^2 = 0.57$, $F_{1,15} = 20.3$, $p < 0.001$). There was a highly positive correlation between nest chronology (date of first observed chick) and average Columbia River discharge during May/June ($R = 0.75$, $p < 0.001$; Table 2.2); first hatching tended to be delayed in years with high river discharge. Similarly, there was a highly negative correlation between nest chronology and the proportion of clupeids in the diet ($R = -0.75$, $p < 0.001$; Table 2.2); first hatching tended to be delayed in years with low proportions of clupeids in the diet. There was a positive correlation between nest chronology and gull kleptoparasitism rate after hatch ($R = 0.61$, $p = 0.01$; Table 2.2); years with higher kleptoparasitism rates also tended to be years when nesting chronology was delayed.

Diet Composition

The proportion of clupeids (i.e. herring, sardines, and shad) in the diet of Caspian Terns nesting at ESI during 2001–2017 (excluding data from 2016) averaged 11.8% (95% CI: 8.0 – 15.5%) of all identified prey items in bill-loads. The proportion of clupeids in the tern diet ranged from a low of 1.9% in 2012 to a high of 29.3% in 2004 (Table 2.1, Figure 2.2). The proportion of salmonids in the diet of ESI Caspian Terns during 2001–2017 (excluding 2016) averaged 31.9% of identified prey items and ranged from a low of 16.8% in 2004 to a high of 37.4% in 2017 (Figure 2.2). The proportion of clupeids in the tern diet was negatively correlated with the proportion of salmonids in the tern diet during 2001-2017 ($R = -0.49$, $p = 0.05$).

There was a decline in the proportion of clupeids in the diet of Caspian Terns during the study period ($r^2 = 0.41$, $F_{1,14} = 9.87$, $p = 0.007$). There was a corresponding increase in the proportion of salmonids in the diet of Caspian Terns during the study period ($r^2 = 0.49$, $F_{1,14} = 13.3$, $p < 0.001$). There was a negative correlation between the average proportion of clupeids in the diet and Columbia River discharge during May/June ($R = -0.58$, $p = 0.02$, Table 2.2); higher river discharge was associated with lower proportions of clupeids in the diet. There was a highly negative correlation between nest chronology and the proportion of clupeids in the diet ($R = -0.75$, $p < 0.001$; Table 2.2); earlier nesting was associated with higher proportions of clupeids in the diet.

We chose to exclude the proportion of salmonids in the Caspian Tern diet at ESI as a prospective explanatory variable for average tern reproductive success because there was not a significant correlation between the proportion of salmonids in the diet and reproductive success ($R = 0.22$, $p = 0.07$).

River Discharge

Columbia River discharge during May/June in 2001–2017 averaged 329.8 kcfs (95% CI: 279.7 – 379.9). Average May/June river discharge ranged from a low of 163.2 kcfs in 2001 to a high of 518.1 kcfs in 2011 (Table 2.1). There was little evidence of a linear trend in average May/June river discharge as a function of year during the study period ($r^2 = 0.13$, $F_{1,15} = 2.14$ $p = 0.16$).

Kleptoparasitism Rate

Gull kleptoparasitism rates of terns before hatch averaged 8.8% (95% CI: 6.8 – 10.8%) of all bill-loads whose fate was determined during 2001–2017, excluding 2016 data. Kleptoparasitism rates before hatch ranged from a low of 4% of bill-loads in 2002 to a high of

16% of bill-loads in 2003 (Table 2.1). There was no trend in kleptoparasitism rates before hatch as a function of year ($r^2 = 0.01$, $F_{1,14} = 0.14$, $p = 0.72$).

Gull kleptoparasitism rates of terns after hatch averaged 3.3% (95% CI: 2 – 4.6%) of all bill-loads whose fate was determined during 2001–2017, excluding 2016 data. Kleptoparasitism rates after hatch ranged from a low of 1% in 2015 to a high of 9% in both 2011 and 2017 (Table 2.1). There was a trend of increasing kleptoparasitism rate after hatch as a function of year ($r^2 = 0.20$, $F_{1,14} = 3.54$, $p = 0.08$).

Gull kleptoparasitism rate before hatch was not correlated with any other explanatory variable. Kleptoparasitism rate after hatch, however, was highly correlated with average Columbia River discharge during May/June ($R = 0.85$, $p < 0.001$; Table 2.2); when river discharge was high, kleptoparasitism rates after hatch were also high (Figure 2.5). In addition, kleptoparasitism rate after hatch was correlated with nest chronology ($R = 0.61$, $p = 0.01$; Table 2.2); early nest chronology was associated with low kleptoparasitism rates after hatch. There was no correlation between kleptoparasitism rates before hatch and kleptoparasitism rates after hatch ($R = 0.11$, $p = 0.69$; Table 2.2).

Model Selection

When each the *a priori* models to explain variation in average annual reproductive success of the ESI Caspian Tern colony (n = 13 models; Table 2.3) were ranked using ΔAIC_c scores, there was only one competitive model ($\Delta AIC_c < 2$) given the data (Table 2.4). The top model contained the explanatory variables of Year and Kleptoparasitism Rate After Hatch ($W_i = 0.68$). After controlling for Year, average Reproductive Success decreased by about 8.3% (95% CI: 6.9% - 9.7%) with every 0.1 percentage point increase in Kleptoparasitism Rate After Chick Hatch.

DISCUSSION

We found that inter-annual variation in Caspian Tern reproductive success at ESI during the study period was primarily associated with the rate of gull kleptoparasitism of tern bill-loads during chick-rearing, after accounting for Year. The model that included Year and Kleptoparasitism Rate After Hatch as explanatory variables was the only competitive model in the model set and had a much higher weight (*Wi*) then the next best model. Because river discharge was not present in the only competitive model in this study, our results are different from those of Collar *et al.* (2017), who found that average Columbia River discharge in May/June best explained the decline in Caspian Tern breeding success from 2001 to 2011. Collar *et al.* (2017) also found positive correlations between river discharge in May/June and the rate of disturbances to the Caspian Tern colony by Bald Eagles, the rate of gull predation on tern eggs and chicks, and the rate of gull kleptoparasitism on terns.

Gull kleptoparasitism rates were highly positively correlated with average Columbia River discharge during May/June in the present study (Figure 2.5). Because river discharge and kleptoparasitism rates were so highly correlated, the effect of gull kleptoparasitism rates on tern reproductive success could in large part reflect the influence of river discharge on food availability to gulls. This supports the hypothesis that there is a strong association between bottom-up factors (e.g., river discharge), top-down factors (e.g., gull kleptoparasitism rates of terns during chick-rearing), and Caspian Tern reproductive success at ESI. The decline in tern reproductive success was likely not caused by gull kleptoparasitism rate *per se*, but rather kleptoparasitism rate was a surrogate for Columbia River discharge and those top-down factors that we were unable to measure in this study (i.e. eagle disturbance rates, gull predation rates).

Year was also one of the most important variables explaining variation in average reproductive success of the Caspian Tern colony at ESI, appearing in the sole competitive model and all of the top five models. Average reproductive success declined over the study period, suggesting that other factors influencing reproductive success were changing in a gradual, linear fashion during the 2001-2017 period. The density of nests on the tern colony increased over the study period, while colony size (number of breeding pairs) decreased during the study period. These two trends were expected, and can be attributed to active management on ESI to reduce the available nesting habitat for Caspian Terns and the size of the tern colony during the study period; the available tern nesting habitat on ESI was gradually reduced from 2.4 ha in 2007 to 0.4 ha in 2015.

Reduction in the area of habitat available for the ESI Caspian Tern colony is unlikely to explain the gradual decline in reproductive success during 2001-2017, however. In Chapter 3 of this thesis, we found a positive relationship between density of nests within 1-m of a tern nest and reproductive success, indicating that the negative trend in average annual reproductive success during the study period was not caused by increasing average nest density at ESI. Furthermore, in 1999 and 2000, a total of 228 Glaucous-winged/Western Gulls were lethally removed from the Caspian Tern colony on ESI to enhance the prospects of terns nesting successfully at the newly restored colony site (Roby *et al.* 2002). Also, in 2012 a total of 50 Glaucous-winged/Western Gulls were lethally removed from the Caspian Tern colony on ESI, following the 2011 breeding season when the tern colony failed to produce any young. Lethal control of depredating gulls is commonly used in association with other methods (e.g., social attraction techniques) to establish or restore seabird breeding colonies (Kress 1983). Harassment and lethal control of gulls can reduce the number of gulls nesting on islands where tern colonies are being restored, and can reduce the number of gulls that utilize a newly restored tern colony as a source of food in subsequent years, thereby giving a new tern colony a chance to become well-established (Kress 1983, Anderson and Devlin 1999).

Lethal control of predatory gulls at the ESI Caspian Tern colony during the first two years of colony restoration likely resulted in higher tern reproductive success in those and subsequent years. Similarly, lethal control of gulls conducted on the tern colony at ESI in 2012 likely enhanced reproductive success in 2012 and again in 2013, when reproductive success partially recovered from the low levels of 2010 and 2011. Because we did not collect data that provided a representative measure of the magnitude of gull predation pressure on Caspian Tern nests during 2012-2017, we cannot quantify how gull control (or the lack thereof) may have influenced gull nest predation rates and inter-annual variation in tern reproductive success.

Disturbance rates to the ESI Caspian Tern colony by Bald Eagles also likely increased gradually during the study period. After passage of the U.S. Endangered Species Act (ESA) in 1973, populations of Bald Eagles in Oregon increased 400% by 2007 (Isaacs and Anthony 2011). Subsequent studies have shown that the density of Bald Eagle nests within the state were highest along the north coast of Oregon (Horton *et al.* 2015). The number of Bald Eagles roosting and foraging at ESI likely increased during the study period; however, survey data on Bald Eagle numbers at ESI during the study period are not available. Although data were collected throughout the study period on the frequency and magnitude of Bald Eagle disturbances to the tern colony, these data were only collected systematically during sessions when tern diet composition was sampled. Those sessions were usually conducted during the day, yet large, high-impact disturbances to the tern colony by Bald Eagles frequently occurred at dawn and dusk (Collar 2013). Therefore, the eagle disturbances that had the greatest direct impact on Caspian

Tern reproductive success at ESI were not captured by this data collection protocol. Because the dataset could not provide unbiased estimates of eagle disturbance rates, we were not able to test the hypothesis the eagle disturbance rates to the tern colony gradually increased during the study period.

Bottom-Up Factors

Collar *et al.* (2017) concluded that the increase in Columbia River discharge was a proxy for a decline in abundance and availability of marine forage fish to Caspian Terns nesting in the estuary, and it was this decline in availability of prey that caused lower reproductive success. The lack of marine forage fish, such as clupeid species, in the Columbia River estuary during years of high river discharge would be costly not only for breeding Caspian Terns, but also for other piscivorous predators in the estuary, such as gulls and Bald Eagles. Decreased availability of marine forage fish likely caused Bald Eagles and gulls to prey-switch, which in turn led to increased pressure on the Caspian Tern colony from these predators.

Weitkamp *et al.* (2012) found that fish assemblages in the Columbia River estuary were influenced by river discharge, as well as seasonal climate change. High river discharge rates can change the properties of the water column and circulation within the estuary and reduce maximum surface salinity (Weitkamp *et al.* 2012). Changes in salinity and mixing of estuarine waters likely limits the entry of marine forage fish in the estuary during high discharge years; Weitkamp *et al.* (2012) reported lower numbers of marine forage fish, including northern anchovy and Pacific herring, in estuary survey trawls during high discharge years. The inverse relationship between the proportion of clupeids in the diet of Caspian Terns and the proportion of salmonids in the diet that we demonstrated during our study period is consistent with the hypothesized changes in forage fish assemblages in the Columbia River estuary based on these dynamic physical processes. The inverse relationship between the proportion of marine forage fish and the proportion of salmonid smolts in Caspian Tern diets is also consistent with previous studies that linked high river discharge with a corresponding increase in Caspian Tern predation on salmonids in the Columbia River estuary (Lyons 2010, Collar *et al.* 2017).

In addition to the effects on abundance and availability of forage fish prey in the estuary, river discharge can also influence the salinity of the Columbia River estuary. The salinity of water at a depth of 1 meter in the Columbia River estuary is most susceptible to changes in river flow, and high flows can change the stratification of the water column at this depth (Weitkamp *et al.* 2012). The stratification of water up to a depth of 1 meter can create a "freshwater lens" in the estuary and would result in fish with lower salinity tolerance (e.g., salmonid smolts) being present in the top meter of the water column. Marine forage fish, on the other hand, would be pushed to depths below 1 meter, and thus out of reach of plunge-diving and surface-foraging avian predators, such as terns, gulls, and eagles (Weitkamp *et al.* 2012, Collar *et al.* 2017).

Our results support the conclusion by Collar *et al.* (2017) that exceptionally high river discharge during May/June in 2011 (518.1 kcfs) resulted in low availability of marine forage fish to Caspian Terns and other piscivores in the Columbia River estuary and the failure of the tern colony to produce any young in that year. The Caspian Tern colony at ESI also failed to fledge any young in 2017, when average river discharge during May/June averaged 476.3 kcfs, well above the 17-year average of 329.8 kcfs. Thus, we can infer that the availability of marine forage fish was reduced due to high river discharge during the 2017 breeding season as well. The link between food availability and seabird reproductive success has been extensively demonstrated (Hall and Kress 2004, Anderson *et al.* 2005, Suryan *et al.* 2006). Low food availability can lead to reduced survival in both adults and chicks, longer duration and distance of foraging trips, reduced adult attendance at the nest, and ultimately higher rates of nest predation or nest abandonment (Anderson *et al.* 2005).

Top-Down Factors

East Sand Island is home to large breeding colonies of Glaucous-winged/Western Gulls and Ring-billed Gulls. Individual Glaucous-winged/Western Gulls, in particular, may specialize in kleptoparasitizing fish from Caspian Terns and/or depredating Caspian Tern eggs and chicks from nests during disturbances to the tern colony (Collar *et al.* 2017). We found that the only competitive model to explain annual variation in average Caspian Tern reproductive success included the explanatory variable of gull kleptoparasitism rate after hatch. Kleptoparasitism is a foraging strategy that has been documented in a variety of taxa, such as invertebrates, birds, and mammals (Morand-Ferron *et al.* 2007). Animals can utilize kleptoparasitism opportunistically, commonly, or exclusively in meeting their energy needs. In order for individuals to utilize kleptoparasitism rather than foraging for their own food, there must be significant time and energy benefits from the practice. Individuals may benefit from kleptoparasitism, for example, when the quality of forage declines (Flower *et al.* 2012). Individual Roseate Terns (*Sterna dougallii*) and Common Terns (*Sterna hirundo*) that kleptoparasitized conspecifics were found to have chicks with higher growth rates and higher overall reproductive success than individuals that did not kleptoparasitize (Flower *et al.* 2012, García *et al.* 2013).

Kleptoparasitism has been documented frequently in seabird colonies, especially in those where gull and tern species are nesting alongside one another (Stienen *et al.* 2006, Gaglio *et al.* 2018). While inter- and intra-specific kleptoparasitism have been documented as being beneficial to those utilizing this foraging strategy, the individuals that lose the food items they are bringing back to the colony to kleptoparasites likely incur a significant cost, but that cost has not been quantified. Stienen *et al.* (2006) concluded that chick provisioning and reproductive success of Sandwich Terns (*Thalasseus sandvicensis*) decreased with increased frequency of kleptoparasitism by Black-headed Gulls (*Chroicocephalus ridibundus*). Similarly, Greater Crested Terns (*Thalasseus bergii*) nesting in association with Hartlaub's Gulls (*Chroicocephalus hartlaubii*) experienced a higher rate of kleptoparasitism than Greater Crested Terns nesting in a single-species colony (Gaglio *et al.* 2018). Terns nesting at the mixed species colony took longer to deliver fish to their chicks, likely increasing the reproductive effort of those adults. Adult Greater Crested Terns also likely incurred higher energetic costs just from avoiding gulls in order to deliver food to their young (Gaglio *et al.* 2018). In the present study, kleptoparasitism rate was found to have an effect on Caspian Tern reproductive success only during chick-rearing. The chick-rearing period requires greater food resources and higher adult foraging efficiencies than during the incubation period, and parent Caspian Terns may be provisioning multiple chicks in a brood at one time (Anderson *et al.* 2005). A successful kleptoparasitism attempt by a gull would require the host tern to embark on another foraging trip to provision its chick(s), and in years when prey availability is low, this would be even more costly.

Although kleptoparasitism by gulls imposes a cost on nesting adult terns, it is unlikely that at ESI the rate of kleptoparasitism, especially after chicks had hatched, was high enough to cause major declines in tern reproductive success. Average annual kleptoparasitism rates after hatch ranged from a low of only 1% of bill-load fish delivered to the colony by adult terns to a high of only 9%. Therefore, the explanatory variable of kleptoparasitism rate after chick hatch apparently served as a surrogate for other factors with high impacts on tern reproductive success. These high-impact factors probably included top-down factors that we were unable to measure, in particular gull predation rates on tern eggs and chicks and Bald Eagle use of the Caspian Tern colony as a food source. These top-down factors have direct and synergistic effects on tern reproductive success, because gulls take large numbers of tern eggs and chicks during Bald Eagle disturbances to the tern colony (Collar *et al.* 2017). In years when eagle disturbances occur at high frequencies, gulls may be more focused on the tern colony as a food source in general – both to take eggs and chicks, and to kleptoparasitize adult terns. Further research should attempt to measure these factors in order to quantify the direct causes of reduced reproductive success in years of high river discharge.

CONCLUSIONS

The results of our study indicate that variation in Caspian Tern reproductive success at the East Sand Island colony is driven by both bottom-up and top-down factors, but the relative strength of prospective causative factors is obscured by difficulties in measuring some factors and the complexity of interactions among factors. Reproductive success decreased on average by 3.9% per year during the study period, and this consistent decline reflects gradual change at the East Sand Island colony that does not favor tern productivity. The rate of gull kleptoparasitism on adult terns was associated with an 8.3% decline in average reproductive success at the tern colony with every 0.1 percentage point increase in kleptoparasitism rate.

The rate of gull kleptoparasitism on adult terns after chick hatching, while likely not a strong causative factor itself, clearly served as a surrogate for factors that have a high impact on tern reproductive success irrespective of the factors causing the gradual decline with year. These include Columbia River discharge during May/June, gull predation rates on tern eggs and chicks, and the frequency and intensity of Bald Eagle disturbances to the Caspian Tern colony. The two years during 2001-2017 when freshwater input into the Columbia River estuary was highest were also the only two years when no young were raised on the ESI Caspian Tern colony – 2011 and 2017. High levels of river discharge are associated with lower abundance and availability of marine forage fish in the estuary, which in turn affects food availability for terns and the availability of alternative prey for predators of terns. Columbia River discharge was highly correlated with gull kleptoparasitism rates on terns during the chick-rearing period, providing a strong link between bottom-up and top-down controls on colony-wide reproductive success.

Finally, this study indicates that unmeasured factors influencing reproductive success at the Caspian Tern colony on East Sand Island were changing gradually during the study period and placing increasing constraints on tern nesting success. These unmeasured factors probably included changes in the numerical and functional responses of tern predators, especially gulls and Bald Eagles, at the colony on East Sand Island.

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Table 2.1. Summary statistics of variables included in regression models based on *a priori* hypotheses of the factors associated with reproductive success of Caspian Terns at East Sand Island during 2001-2017. Data from 2016 were excluded from the last 3 variables due to differences in data collection effort and methodology.

	Mean ± SD	**Median**	**Range**
Reproductive Success (average number of young fledged/breeding pair)	0.53 ± 0.42	0.57	0.00 – 1.39
Nest Density (average number of nests/m^2)	0.81 ± 0.29	0.72	0.45 – 1.36
Colony Size (number of breeding pairs on-colony at the peak)	7,978 ± 1,879	8,325	3,500 – 10,668
Nest Chronology (date of first observed chick)	144.9 ± 6.87	147	134 - 155
River Discharge (average river discharge [kcfs] during May-June)	329.8 ± 97.4	323.8	163.2 – 518.1
Clupeids in Diet (average proportion of clupeids in the tern diet)	11.8 ± 7.03	10.5	1.9 – 29.3
Kleptoparasitism Rate Before Hatch (proportion of bill-load fish kleptoparasitized by gulls before first observed chick)	8.8% ± 3.7%	8.2%	3.5% – 16%
Kleptoparasitism Rate After Hatch (proportion of bill-load fish kleptoparasitized by gulls after first observed chick)	3.3% ± 2.4%	2.3%	0.7% – 8.5%

Table 2.2. Pearson's correlation matrix showing the correlation between all explanatory variables used in model selection to explain variation in reproductive success of Caspian Terns at East Sand Island in the Columbia River estuary during 2001-2017. The top number in each cell is the Pearson's correlation coefficient, and the bottom number is the *p*-value, representing the significance of the correlation for each pair of explanatory variables, as well as the response variable. Bolded values represent correlations significant at the $\alpha = 0.05$ level.

	Year	**Nest Density**	**Colony Size**	**Nest Chronology**	**River Discharge**	**Clupeids in Diet**	**Kleptoparasitism Rate Before Hatch**
Nest Density	**0.89**	--	--	--	--	--	--
	<0.001	--	--	--	--	--	--
Colony Size	**-0.80**	**-0.67**	--	--	--	--	--
	<0.001	**0.005**	--	--	--	--	--
Nest Chronology	**0.76**	**0.61**	**-0.50**	--	--	--	--
	<0.001	**0.01**	**0.01**	--	--	--	--
River Discharge	0.35	0.21	-0.36	**0.75**	--	--	--
	0.16	0.45	0.17	**<0.001**	--	--	--
Clupeids in Diet	**-0.64**	**-0.58**	0.39	**-0.75**	**-0.58**	--	--
	0.007	**0.02**	0.13	**<0.001**	**0.02**	--	--
Kleptoparasitism Rate Before Hatch	-0.10	-0.20	0.33	0.14	0.14	-0.27	--
	0.72	0.47	0.20	0.60	0.60	0.31	--
Kleptoparasitism Rate After Hatch	0.45	0.15	-0.44	**0.61**	**0.85**	-0.31	-0.11
	0.08	0.59	0.09	**0.01**	**<0.001**	0.24	0.69

Table 2.3. List of 13 generalized linear models with a Gaussian distribution and log link developed using *a priori* hypotheses for the variation in average annual reproductive success of Caspian Terns nesting at East Sand Island. These models were included in analyses using Akaike's Information Criterion adjusted for small sample sizes (AIC_c), and are not ranked in this table.

	Model
1	Intercept Only
2	Year
3	Density of Nests
4	Colony Size
5	Nest Chronology
6	River Discharge
7	Clupeids in Diet
8	Kleptoparasitism Rate Before Hatch
9	Kleptoparasitism Rate After Hatch
10	River Discharge + Year
11	Clupeids in Diet + Year
12	Kleptoparasitism Rate Before Hatch + Year
13	Kleptoparasitism Rate After Hatch + Year

Table 2.4. The top five regression models selected from the set of 13 models based on *a priori* hypotheses of the factors associated with reproductive success at the Caspian Tern colony on East Sand Island in the Columbia River estuary during 2001-2017. Models were ranked using Akaike's Information Criterion adjusted for small sample sizes (AIC_c). No models in the model set included explanatory variables that had a Pearson's correlation coefficient ≥ 0.70. Models are ranked in ascending order based on the ΔAIC_c value. Only the first model was competitive ($\Delta AIC_c < 2.0$).

Rank	**Model**	**AIC_c**	**ΔAIC_c**	**W_i**	**r^2**
1	Year + Kleptoparasitism Rate After Hatch	0.2	0.00	0.68	0.83
2	Year	3.5	3.24	0.13	0.72
3	Year + River Discharge	4.6	4.39	0.08	0.76
4	Year + Clupeids in Diet	5.1	4.87	0.06	0.78
5	Year + Kleptoparasitism Rate Before Hatch	5.3	5.11	0.05	0.77

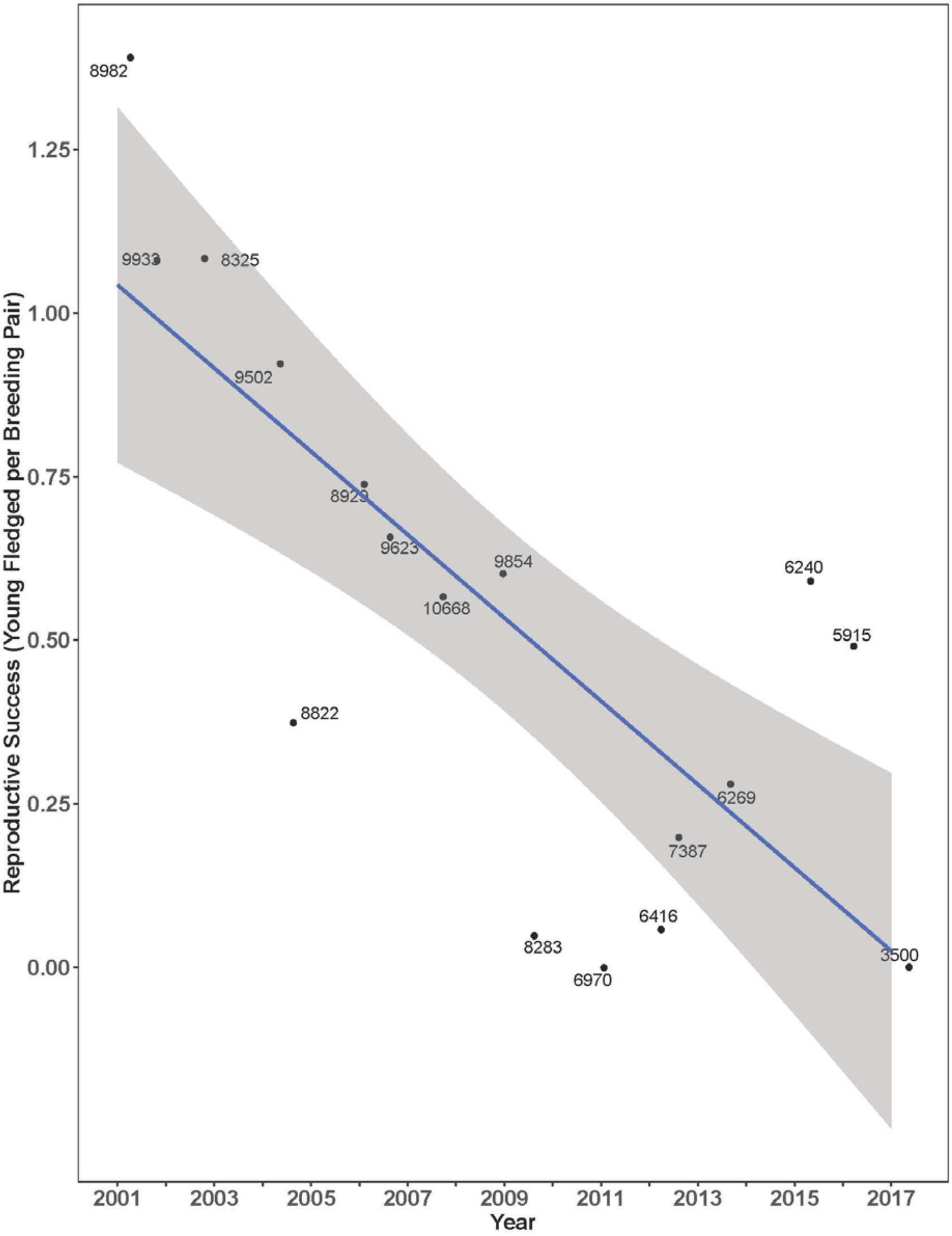

Figure 2.1. Annual reproductive success (average number of young fledged per breeding pair) of the Caspian Tern colony at East Sand Island in the Columbia River estuary as a function of year during 2001-2017 ($r^2 = 0.72$, $F_{1,15} = 39.2$, $p < 0.001$). Data points are labeled by the size of the tern breeding colony (number of breeding pairs) at East Sand Island in that year.

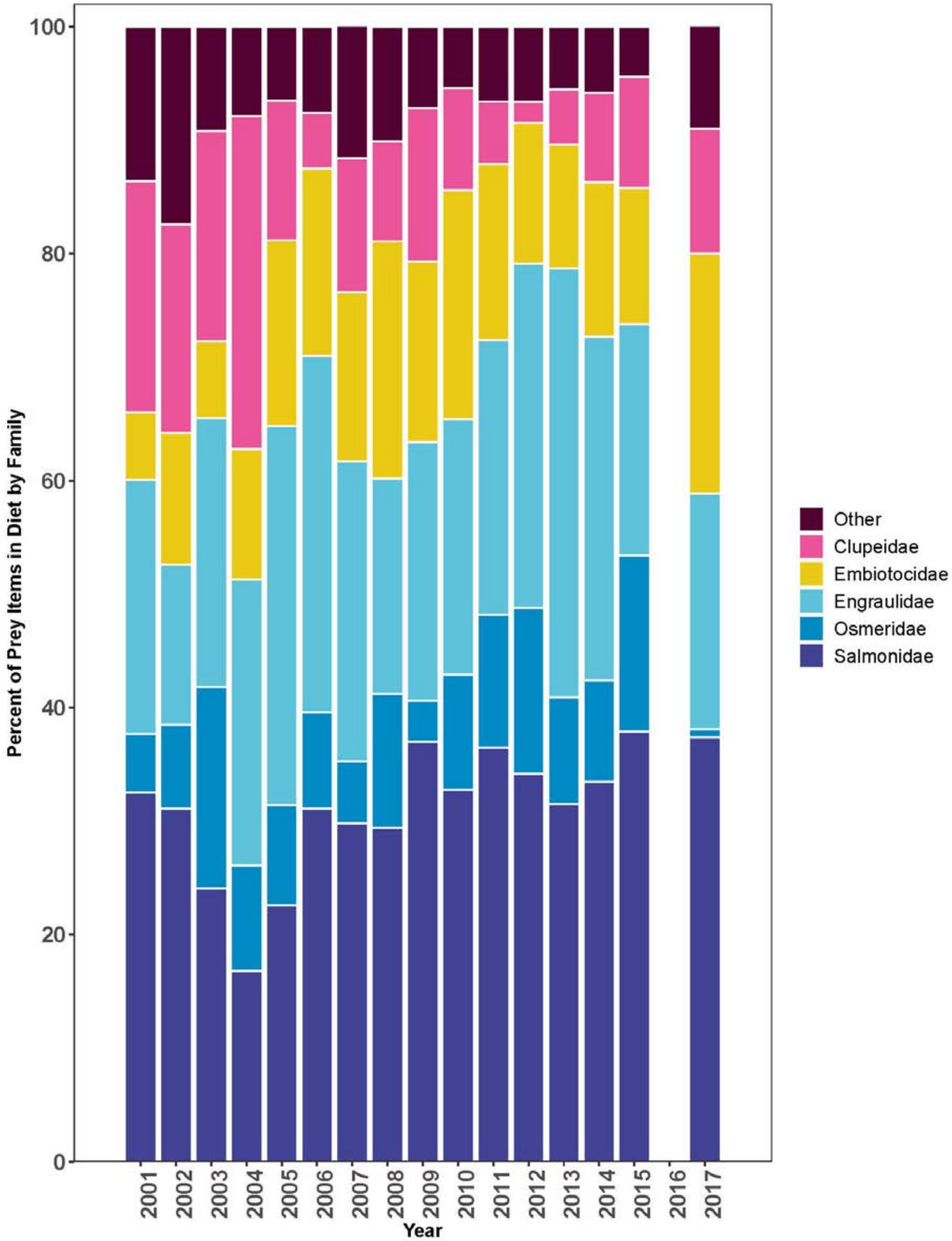

Figure 2.2. Taxonomic composition (based on numbers of identified prey items in bill-loads) of the Caspian Tern diet at East Sand Island in the Columbia River estuary during 2001-2017. Dominant prey types were identified to family. Data from 2016 were not included due to differences in data collection methodology and sample size.

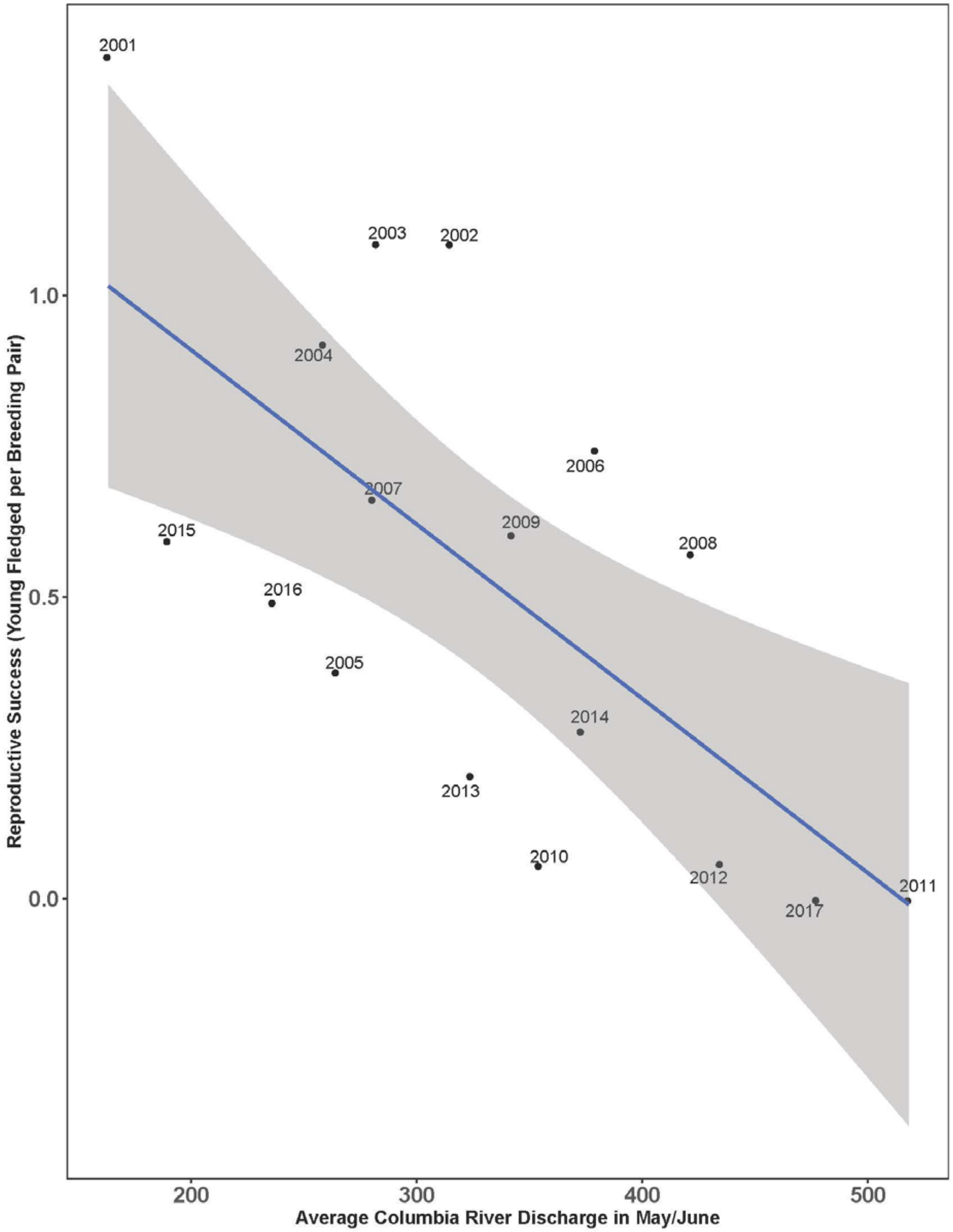

Figure 2.3. Annual reproductive success (average number of young fledged per breeding pair) at the Caspian Tern breeding colony on East Sand Island in the Columbia River estuary as a function of average river discharge during May/June in 2001-2017 ($r^2 = 0.43$, $F_{1,15} = 11.3$, $p = 0.004$). Data points are labeled by the year.

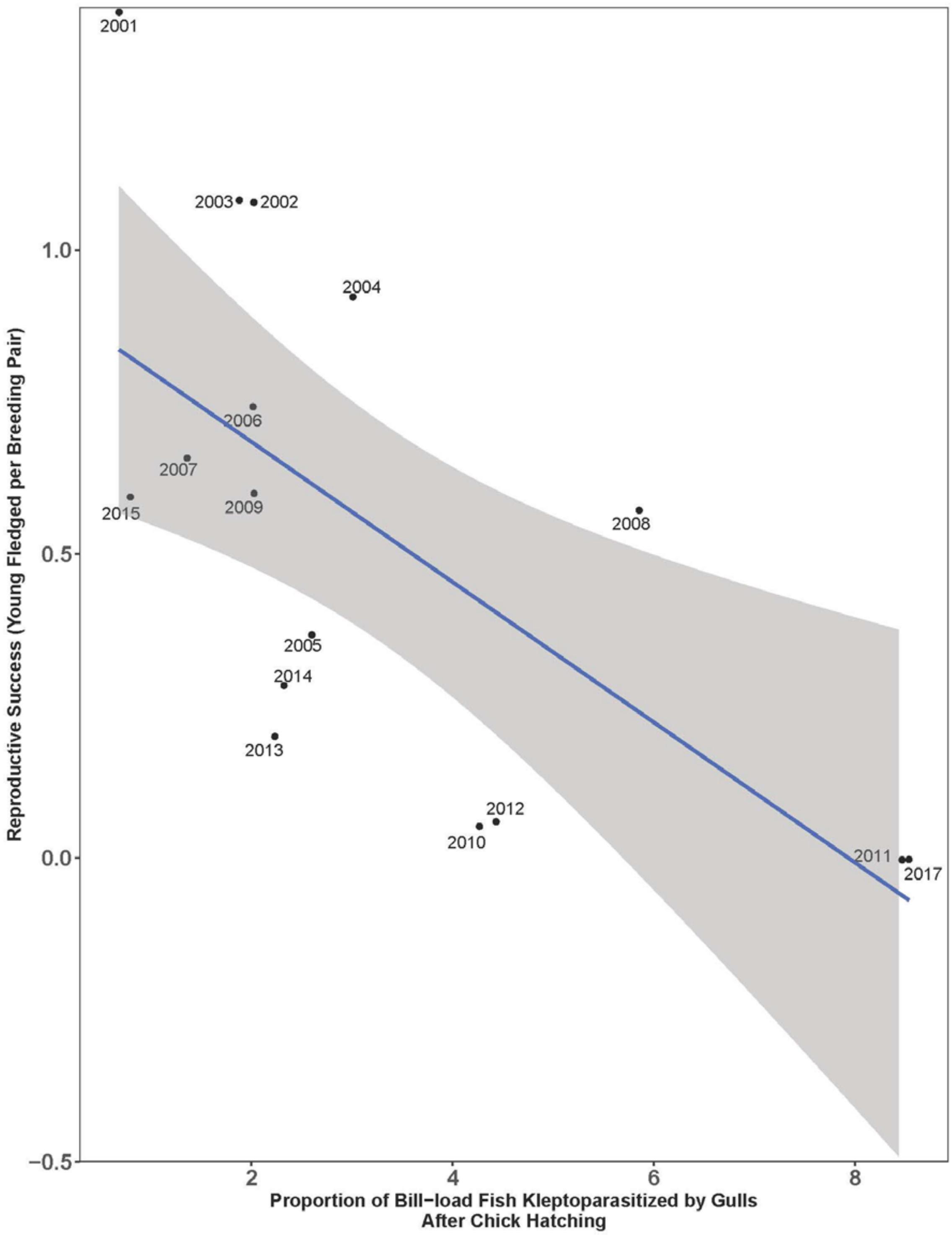

Figure 2.4. Annual reproductive success (average number of young fledged per breeding pair) of the Caspian Tern breeding colony on East Sand Island in the Columbia River estuary as a function of gull kleptoparasitism rate after hatch (proportion of bill-load fish kleptoparasitized/all recorded bill-load fish observed on-colony after observation of the first tern chick) during 2001-2017 ($r^2 = 0.48$, $F_{1,14} = 13.0$, $p = 0.003$). Data points are labeled by the year; data from 2016 were excluded.

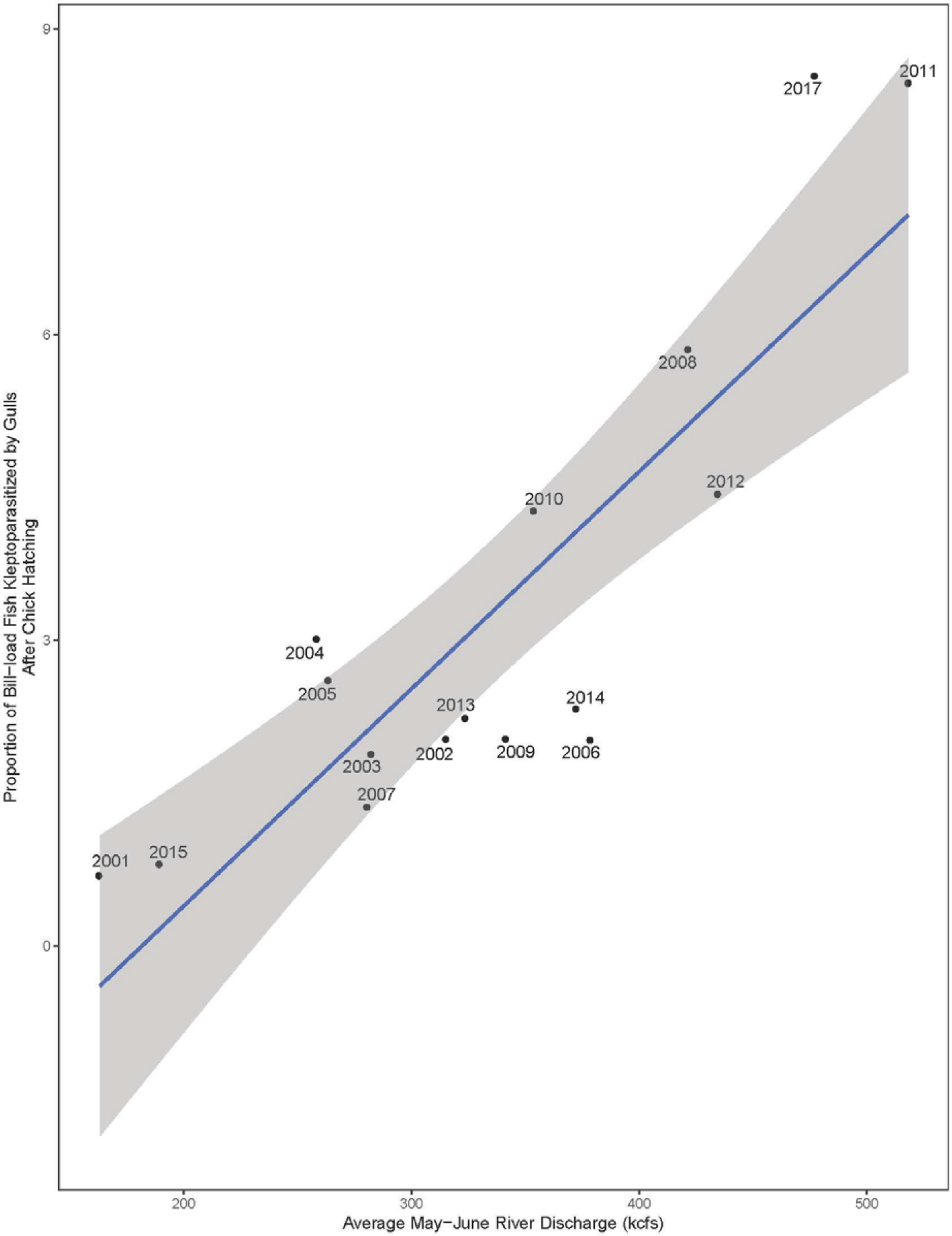

Figure 2.5. Gull kleptoparasitism rate after hatch (proportion of tern bill-load fish kleptoparasitized by gulls/all recorded bill-load fish observed on-colony after observation of the first tern chick) at the Caspian Tern colony on East Sand Island in the Columbia River estuary as a function of average Columbia River discharge during May/June (kcfs) in 2001-2017 ($R = 0.85$, $p < 0.001$). Data points are labeled by year.

CHAPTER 3. A MATTER OF TIMING: NEST INITIATION DATE EXPLAINS MUCH OF THE VARIATION IN INDIVIDUAL BREEDING PERFORMANCE OF CASPIAN TERNS (*HYDROPROGNE CASPIA*) AT A LARGE ESTUARINE COLONY

Olivia Bailey, Daniel D. Roby, Donald E. Lyons, and Yasuko Suzuki

ABSTRACT

A number of factors may explain differences in reproductive success among individual colonial nesting seabirds, including age, experience, nest site location, and nest initiation date. We investigated the relative strength of effects of these factors on the reproductive success of Caspian Terns (*Hydroprogne caspia*) at East Sand Island (ESI) in the Columbia River estuary. We monitored the nesting attempts of a sample of individually recognizable, marked terns during the 2015 and 2016 breeding seasons and used a precise surveying instrument (Leica Total Station) to measure the location of each nesting attempt of marked birds on the breeding colony. Date of nest initiation (egg-laying date) was the variable ranked highest in relative importance for explaining variation of individual reproductive success over the two breeding seasons (W_i = 0.96). Reproductive success was strongly negatively associated with nest initiation date and was strongly positively associated with the density of other tern nests nearby, although neighborhood nest density was ranked below nest initiation date as an explanatory variable (W_i = 0.31). Nests located closer to the center of the colony were more likely to be successful than those located near the edge (W_i = 0.25), but the location of nests initiated later in the season had no influence on reproductive success. Age, previous breeding experience at the ESI colony, and nesting attempt number during the breeding season each helped explain variation in reproductive success (W_i = 0.21, 0.13, and 0.09, respectively), but less so than the aforementioned variables. Individuals that initiated nests earlier had more opportunities to re-nest if their initial nesting attempt failed, and the success rate of those re-nesting attempts did not decline throughout the breeding season, suggesting that early nesters are higher quality compared to those initiating nests later in the season. Overall, the timing of nest initiation explained most of the variation in individual reproductive success.

INTRODUCTION

Individual reproductive success within a breeding season can vary widely among colonial nesting seabirds (Coulson and Porter 1985). Within colonies and years there is variation in the rate of energy acquisition by individuals, leading to differences in reproductive success, and a number of hypotheses have been proposed for how this variation relates to life history traits. Variability in reproductive success may be due to heterogeneity in the quality (fitness) of individuals, as well as age- or experience-related processes (Lescroël *et al.* 2009). For example, the positive effect of age on reproductive success has been well documented in some colonial nesting seabirds (Pyle *et al.* 2001). Such differences in reproductive performance are critical factors for the evolution of life history traits in long-lived species.

Older individuals generally have higher reproductive success than younger conspecifics (Sydeman *et al.* 1991), and a number of different factors may be responsible for age-related improvements in reproductive success. One potential factor is increasing reproductive effort with increasing age, known as the effort or restraint hypothesis (Williams 1966, Limmer and Becker 2010). This hypothesis posits that older individuals expend higher reproductive effort because of declining residual reproductive value with age, and are therefore more likely to be successful. Aging individuals may also experience senescence, however, which may cause a decline in reproductive output and survival later in life (McCleery *et al.* 2008). Thus, this hypothesis presupposes that as reproductive efficiency declines with age, the effort an individual expends for reproduction increases. Effort may also increase because of skills gained with age and experience that may be required for successful reproduction, such as foraging behaviors. This assumes that older and more experienced individuals are more competent breeders, investing more effort to raise young, resulting in a higher rate of success (Mauck *et al.* 2004). Alternatively, older individuals may have more extensive breeding experience – leading to greater familiarity with nest territories, mates, and parental care (Limmer and Becker 2010, Desprez *et al.* 2011). Older and/or more experienced birds may also arrive on the colony earlier, as well as lay eggs earlier. Earlier egg-laying dates have been shown to correlate with higher reproductive success in a number of seabird studies (Haymes and Blokpoel 1980, Perdeck and Cave 1992, Hipfner *et al.* 2010), including studies of Caspian Terns (*Hydroprogne caspia*; Antolos *et al.* 2006).

The positive correlation between age and reproductive success can also be attributed to fitness differences among individuals. This is also known as the selection hypothesis, and it assumes that there are phenotypic differences among individuals that relate to both survival and reproductive output (Mauck *et al.* 2004). These differences can result in higher average annual reproductive success in some long-lived individuals, while less-fit individuals exhibit lower average reproductive success over shorter lifespans. For example, in Leach's Storm-petrels (*Oceanodroma leucorhoa*), individuals that were unsuccessful in their early breeding attempts were less likely to survive than individuals that nested successfully (Mauck *et al.* 2004). Although Mauck *et al.* (2004) found that individuals that lived longer were also more productive, they were not able to determine whether increased experience or effort contributed more to the reproductive success of longer-lived individuals.

Timing of nest initiation may influence the location of a nest on the colony and, consequently, confer benefits and/or risks to subsequent reproductive success. Velando and Freire (2001) proposed the "central-satellite" distribution model, where nests initiated earliest in the center of the colony experience higher success rates than nests on the edge of the colony.

Antolos *et al.* (2006) found a strong negative relationship between hatch date and Caspian Tern reproductive success. In that study, nests initiated earlier were more successful, were established in areas of the colony with higher nest densities, and were further from the colony edge than nests initiated later in the season. This is consistent with other studies that have demonstrated that colonial seabirds that arrive and initiate nesting earlier are higher quality breeders (Coulson and White 1958, Dittmann and Becker 2003).

Many species of terns nest in proximity to breeding colonies of gulls (*Larus* spp.). Associating with breeding gulls may negatively affect tern reproductive success, whether through increased gull predation on tern eggs or chicks, or through gull kleptoparasitism of fish brought to the nest site by terns provisioning their mates and young. In some cases, predation on tern nest contents by gulls can result in total failure of a tern breeding colony (Cabot and Nisbet 2013). Timing of egg-laying, the location of the nest site within the tern colony, and the density of tern nests are all factors that can influence the susceptibility of a tern nest to gull predation (Hatchwell 1991, Becker 1995, Hernández-Matís and Ruiz 2003). Becker (1995) documented that Common Tern (*Sterna hirundo*) nests on the periphery of the colony were more likely to be depredated by Herring Gulls (*L. argentatus*) than nests near the center of the colony. Thus nests that were initiated earlier and located toward the center of the colony, where nest densities were higher, tended to be more successful. Nesting Little Terns (*S. albifrons*) are subject to high rates of egg loss during the breeding season, whether from predation or flooding, and have evolved the adaptation of laying three or more replacement clutches during a single breeding season. Laying replacement clutches is more likely when Little Terns lose their eggs early in the season (Cabot and Nisbet 2013), suggesting that initiating nests earlier provides more opportunities for nesting successfully during a breeding season.

Successful breeders are also more likely to exhibit fidelity to a specific nest site on the breeding colony, or to an area of the colony where they successfully nested previously (Fairweather and Coulson 1995, Boulinier *et al.* 2008). Birds are able to make nest site selection decisions based on experience and knowledge gained from current and prior breeding attempts. For example, Red-winged Blackbirds (*Agelaius phoeniceus*) moved farther from previous nest sites and were more likely to change nesting marshes if their nesting attempts were unsuccessful in the previous year (Beletsky and Orians 1991). This “success-stay/failure-leave” strategy (Schmidt 2004) may be influenced by individual experience and/or by information obtained from the reproductive success of neighboring conspecifics. Danchin and Cam (2002) found that the probability of breeding in experienced Black-legged Kittiwakes (*Rissa tridactyla*) was based more on their own nesting experience than on the average reproductive success of their neighbors.

Young or inexperienced birds that cannot rely on their own previous experience, however, may instead utilize ‘public information’ to select breeding sites. Kittiwakes that failed in their first year of breeding were more likely to attempt to nest on a different cliff the subsequent year and, in particular, one that had higher reproductive success per capita in the first year (Danchin *et al.* 1998). Individual experience had a strong effect on breeding dispersal; birds tended to disperse from cliffs where they had failed and their neighboring conspecifics experienced low reproductive success. This was not the case for birds that nested and failed on cliffs with high local reproductive success, suggesting that in some cases the success of neighboring birds may override an individual’s own breeding experience when deciding whether to move to a different nest site or colony (Danchin *et al.* 1998). At some colonies, however, birds that attempt to procure a nest site in a more productive neighborhood of the colony may encounter intense competition with conspecifics, which can result in birds ultimately using low quality breeding habitat, nesting later, or skipping breeding altogether (Danchin *et al.* 1998; Kokko *et al.* 2004).

In this study, we examined the reproductive success of individual Caspian Terns during the 2015 and 2016 breeding seasons at the breeding colony on East Sand Island in the Columbia River estuary. The objectives of this study were to determine whether there is a relationship between an individual's reproductive success and its age, breeding experience, timing of breeding, density of conspecific nests in the neighborhood, and nest location within the colony relative to the colony edge. We predicted that the reproductive success of Caspian Terns would be higher in older birds, based on studies of other seabird species and the theory that older birds may expend more reproductive effort or may have better reproductive skills. Similarly, we predicted that birds with more previous breeding experience at the East Sand Island colony would have higher reproductive success than breeders with little or no previous experience nesting at this colony. In addition, we predicted that Caspian Terns that initiated nests earlier in the season would have higher reproductive success than birds that initiated nests later in the breeding season. We predicted that nests in areas of the colony with higher densities of nests would have higher reproductive success due to reduced susceptibility to nest predation by gulls. We also predicted that nests located closer to the edge of the colony would be less successful than more centrally located nests because the main predators on Caspian Tern nest contents at this colony, Western/Glaucous-winged Gulls (*Larus occidentalis* X *L. glaucescens*), tend to nest at the periphery of the Caspian Tern colony on East Sand Island. Finally, we predicted that birds that nested unsuccessfully in 2015 would seek new nest locations in 2016 in order to enhance prospects for successful nesting. These predictions are not mutually exclusive, however, and individuals may experience interactions between these factors that influence the likelihood of reproductive success. We accounted for this by investigating these interactions between factors.

METHODS

Study Area

East Sand Island (ESI) (46°15’45”N, 123°57’45”W) is located near the mouth of the Columbia River and is the site of the largest breeding colony of Caspian Terns in North America. ESI is a semi-natural, low-lying island that has been reinforced with rocky revetment and deposits of dredged material. ESI is owned and managed by the U.S. Army Corps of Engineers (USACE), which also maintains the available nesting habitat (bare sand) for Caspian Terns on the island. ESI has been the site of a large breeding colony of Caspian Terns since 2000, the year after managers restored suitable nesting habitat and deployed social attraction (Caspian Tern decoys and audio playback of vocalizations) on the habitat.

Caspian Terns nesting at the ESI colony depredate millions of juvenile salmonids (*Oncorhynchus* spp.) annually, some of them listed as threatened or endangered under the U.S. Endangered Species Act. Consequently, fisheries management agencies prepared a Caspian Tern management plan for the Columbia River estuary (U.S. Fish and Wildlife Service 2005, 2006), which was implemented starting in 2008. One objective of the management plan was to reduce the size of the Caspian Tern breeding colony on East Sand Island from about 10,000 breeding pairs to within the range of 3,125 – 4,375 breeding pairs. The reduction in colony size would be accomplished by reducing the area of suitable nesting habitat provided for Caspian Terns on ESI. In conjunction with the reduction in colony area on ESI, terns would be prevented from nesting elsewhere in the Columbia River estuary, and alternative tern nesting habitat would be constructed elsewhere within the range of the Pacific Flyway population of Caspian terns. The area of nesting habitat for Caspian Terns at ESI was concomitantly reduced from 2.0 ha (5 acres) in 2008 to 0.64 ha (1.58 acres) in 2012, and was then further reduced to 0.4 ha (1.0 acre) in 2015. During the 2016 breeding season, the available nesting habitat remained at 0.4 ha.

Focal Individual Observations

Since 2005, Caspian Terns have been banded at the ESI colony with engraved, field-readable plastic leg bands, each with a unique alphanumeric code to identify individuals. Some of the Caspian Terns banded at the ESI colony were banded as fledglings, and therefore their age in years was known, whereas others were banded as adults, and therefore their age was not known precisely. Consequently, terns banded as adults were assumed to be 6 years post-hatching, the average age at first reproduction, when they were banded. Therefore, this measure of age was a minimum estimate of an individual's age, as many were likely older than 6 years when they were banded.

The banding and resighting database maintained by Bird Research Northwest contains records of each bird banded by the project (www.birdresearchnw.org), as well as observations and behaviors of banded birds resighted during the breeding season on colonies within the Pacific Flyway. This database was used to obtain information about an individual's observed breeding attempts at the ESI colony before 2015. Prior breeding experience on ESI for a banded individual that nested on ESI in 2015 and/or 2016 ("focal bird") was determined by that individual's record of resightings on the ESI colony during 2010-2015, including any records of breeding behavior. A banded tern was classified as a breeder at the ESI colony during a particular breeding season if it was observed incubating eggs, brooding chick(s), attending chick(s), or feeding chick(s) during that breeding season. If a banded adult was observed repeatedly on the ESI colony, but was not observed performing the aforementioned breeding behaviors, it was not classified as a breeding individual.

All of the terns that were banded as adults on ESI were banded during 2005-2010. For this sample of banded terns, only resighting records during 2010-2014 were used so that, regardless of the year when an adult tern was banded, each banded bird had the same opportunity to be resighted on the colony. The age in years of focal birds banded as chicks was based on the year when the individual was banded. Because the exact age of focal birds banded as adults was not known, the age of these banded individuals was estimated by adding 6 years to the number of years since the bird was banded. Using this procedure, the age of some focal birds that were banded as adults may have been underestimated by a substantial amount (Caspian Terns are known to live at least 26 years in the wild; DDR, unpubl. data). It is unlikely, however, that the age of focal birds banded as adults was overestimated by more than one year because individuals rarely nested when they were less than 5 years of age (YS, unpubl. data).

Observations of banded adult Caspian Terns on the breeding colony at ESI in 2015 and 2016 were conducted from three different observation blinds located at the periphery of the colony. Observers used binoculars and spotting scopes to scan the colony for prospecting terns with alphanumeric leg bands. Banded individuals that demonstrated persistent commitment to prospective nest sites were designated as a "focal bird," and their nest site was designated as a "focal nest." Each "focal nest" included at least one banded bird in the breeding pair, and the nest was monitored at least once every three days throughout the nesting season or until the nest failed. All banded terns that were observed to be nesting at the ESI colony in 2015 or 2016 were included as focal birds in this study. If both members of a breeding pair at a focal nest were banded, only one focal bird was included in the analysis due to the lack of independence between members of the same breeding pair. Breeding chronology, including lay dates and hatch dates, was recorded for each focal nest. Chicks in focal nests were tracked until they were 30 days old post-hatching, after which they were considered to have successfully fledged. After this age, chicks are large and quite mobile, so accurate identification of individual chicks becomes quite difficult.

When lay-date or hatch-date were not directly observed for a given focal nest, chick ages were estimated based on comparison with photos of known-age chicks. Hatch-date was then estimated by back calculating from estimated chick age. Lay dates were assumed to be 26 days earlier than hatch dates, based on the average incubation period for this species (Cuthbert and Wires 1999).

A focal bird's nest was considered to have failed if the nest was observed unattended for three consecutive days. If focal terns attending older, more mobile chicks moved out of their original nest scrape before the chick was 30 days old, the focal tern and its chick were monitored using the banded focal bird to identify the chick it was attending. When possible, focal birds were monitored after their nests failed in order to identify potential re-nesting attempts. Re-nesting attempts by focal birds were monitored, regardless of whether the location of the focal nest had changed or not. Each time a focal bird re-nested, the nesting attempt was numbered chronologically through that breeding season.

Nest Mapping

Each focal nest was mapped on the tern colony using a high-precision surveying instrument (Leica TPS 1200+ total station), which assigned specific GPS coordinates to each focal nest that are accurate to ± 2 mm. These data were collected following the methods outlined by Antolos *et al.* (2006), as well as by Collar (2013). All mapping with the total station was conducted from observation blinds adjacent to the colony.

Data from the Leica total station were downloaded into the Leica GeoOffice program, version 8.4 (Leica Geosystems, Heerbrugg, Switzerland) at the end of each breeding season, and the GPS coordinates for each focal nest and all tern nests in the neighborhood within 1 m of each focal nest were determined. These coordinates were overlaid onto geo-referenced aerial photography of the East Sand Island colony using ArcMap 10.2.2 (ESRI 2011). The distance from the colony edge of each focal nest was determined by drawing a line feature around the colony area and then using the Near tool in ArcMap 10.2.2 to measure the distance between the focal nest and the closest point on the colony edge. The Near tool was also used to calculate the distance between each focal bird's nests in the two years of the study, if the focal bird nested at the ESI colony in both years. The Near tool was also used to measure the distance between each focal bird's nesting attempts within a season for both 2015 and 2016, if a focal bird attempted to nest more than once at the ESI colony in either 2015 or 2016.

When mapping a focal nest, measurements were taken in the four cardinal directions from the nest. These measurements were used to establish a circle of 1-m radius around each focal nest on a photo of the nest area taken from the nearest observation blind. The nest status of each focal bird's "neighbors" within this 1-m radius circle were monitored at least once every two weeks. If the focal bird's nest failed and it moved and re-nested, the new focal nest and 1-m radius neighborhood were mapped using the methods described above.

Characterizing a Nest's Social Environment

After mapping the location and 1-m radius neighborhood of each focal nest, a photograph was taken of the neighborhood area for each focal nest from an observation blind. The photographs were uploaded onto a field tablet, and the focal nest and 1-m radius neighborhood were marked on each photograph. The ‘neighbor’ nests inside the 1-m radius neighborhood were then numbered on each photograph. Initial photographs of each focal nest’s neighborhood were used as a reference during each monitoring session of a nest’s neighborhood. Monitoring sessions were conducted for each focal nest neighborhood at least once every two weeks for a half-hour. At the beginning of each monitoring session, a new photograph of the neighborhood area was taken, and the neighboring nests within 1 m of the focal nest were identified and numbered to be consistent with the original photograph. Newly initiated nests in the neighborhood area were numbered consecutively. During each monitoring session, we attempted to identify the nest contents of the focal nest and all neighborhood nests within 1 m. If contents could not be determined, or eggs or chicks could not be confirmed, the posture of the tern attending the focal nest was used to determine whether the tern was incubating eggs or brooding chicks. If a focal bird failed in its nesting attempt, moved to a new nest scrape, and re-nested, a new photograph of the neighborhood area was taken and the above process was repeated.

After each breeding season, the density of active tern nests in the 1-m radius neighborhood of each focal nest was calculated for each monitoring session. The average neighborhood nest density across monitoring sessions was also calculated. Nest densities of neighborhoods were calculated first using the photographs from each monitoring session. These calculations were verified by overlaying focal nest location data on georeferenced vertical aerial photography from throughout the nesting season. A 1-m buffer was placed around each focal nest point, allowing for the calculation of neighborhood nest densities in nests/m^2.

Data Analysis

Models were created corresponding to *a priori* biologically relevant hypotheses to determine the relative influence on individual reproductive success of (1) the age of focal adults, (2) their previous breeding experience at ESI, (3) the distance of their nest from the colony edge, (4) their egg-laying date, (5) the density of nests in their neighborhood, and (6) whether it was the first, second, third, or fourth nesting attempt during that season. All potential correlations between explanatory variables were explored using Pearson's correlation in R (R Development Core Team 2011).

We used generalized linear mixed models (GLMMs) with a binomial distribution to assess the effects of age, previous breeding experience at ESI, distance of nest to the colony edge, timing of nest initiation, neighborhood nest density, and nesting attempt number on a focal bird's chances of reproductive success. We used GLMMs to account for multiple measurements of some explanatory variables for many focal individuals (e.g., lay date, distance to edge). Each model included the random effects of year and individual bird. Models were ranked using Akaike's Information Criterion adjusted for small sample sizes (AICc) to investigate which explanatory variables best explained the likelihood that a focal individual would reproduce successfully during the two study years. Models were compared using the ΔAICc value, which is the difference between a model's AICc score and the lowest – and most probable – AICc score of the candidate models, given the data. Each explanatory variable was scaled to make interpretation consistent across variables. Explanatory variables with Pearson's correlation coefficients (R) greater than 0.7 were not included in the same model. All models were fit using the R package "lme4" (Bates *et al.* 2015). To estimate the relative importance of each explanatory variable, we summed the Akaike weights (W_i) for each model in which an explanatory variable occurred, as described by Burnham and Anderson (2010).

Linear mixed effects models were used to assess relationships between the inter-annual distance between nests of focal individuals and the explanatory variables of age, breeding experience at ESI, reproductive success in 2015 and 2016, timing of nest initiation (lay date) in each year, distance of the nest from the colony edge in each year, and neighborhood nest density in each year. Mixed effects models with a random effect of individual were used to account for repeated measures for some individuals. To correct for unequal variances and non-linearity, the data for inter-annual distance between nests were log-transformed and tests were performed on the log-transformed data; log-transformed data met the assumptions of normality and equal variance. Reported estimates and confidence intervals are back-transformed. For focal birds that nested more than once in a breeding season, I compared each nesting attempt to the corresponding nesting attempt in the other breeding season. For example, first nesting attempts in each year were compared, as were second nesting attempts. Finally, for individuals that nested in both years, a separate means model was used to answer whether there were differences in the distance moved by birds that moved either away from the colony edge or towards the colony edge.

All statistical analyses were performed using program R (version 3.4.1), packages *lme4, ggplot2, MuMIn, standardize, geoR,* and *Mass* (R Development Core Team 2011).

RESULTS

Reproductive Success

A total of 146 unique banded individuals were monitored at the ESI colony during the 2015 breeding season, the 2016 breeding season, or both; a total of 76 banded individuals were monitored during both the 2015 and the 2016 breeding seasons. During the 2015 breeding season, 47.2% of all focal birds that attempted to nest at ESI did so successfully, fledging at least one chick (n = 58 of 123 focal birds). During the 2016 breeding season, 48.5% of all focal birds that attempted to nest at ESI fledged at least one chick (n = 48 of 99 birds). There was no evidence that reproductive success was different between the 2015 and 2016 breeding seasons (Fisher's Exact Test, $p = 0.89$).

In 2015, a total of 24 focal birds (19.5% of focal birds in that year) attempted to nest (laid a clutch of eggs) more than once at the ESI colony; in 2016, a total of 50 focal birds (50.5% of focal birds in that year) attempted to nest more than once at the ESI colony. The between-year difference in the number of birds that re-nested was significant (Fisher's test, $p < 0.001$). Of the 24 focal birds that re-nested in 2015, 5 successfully fledged a chick (20.8%). Of the 50 focal birds that re-nested in 2016, 20 individuals (40.0%) successfully fledged a chick; however, this inter-annual difference in success of re-nesting attempts was not significant (Fisher's test, $p = 0.34$). In 2015, there were 27 distinct re-nesting attempts made by the 24 individual birds - three individuals made a third attempt (Figure 3.1). In 2016, there were 72 distinct re-nesting attempts made by the 50 individual birds; each individual made a second attempt, while 16 made a third attempt, and 6 made a fourth attempt (Figure 3.1). These results indicate that the conditions for nesting were more favorable early in the 2015 nesting season compared to the 2016 nesting season, while the conditions for nesting were more favorable late in the 2016 nesting season compared to the 2015 nesting season (Figure 3.2).

Prospective Explanatory Variables

The number of years of documented previous breeding experience on ESI for focal Caspian Terns in 2015 ranged from 0 to 4 years, with a mean of 1.93 years (n = 123 focal terns; Table 3.1). In 2016, breeding experience on ESI for focal terns ranged from 0 to 5 years, with a mean of 2.71 years (n = 103 focal terns; Table 3.2). The age of known-age focal individuals that were monitored during the 2015 breeding season ranged from 4 to 16 years, with a mean age of 11.2 years (Table 3.1). The age of known-age focal birds monitored in 2016 ranged from 6 to 17 years, with a mean of 11.6 years (Table 3.2). Of the 147 unique focal individuals monitored during this study, 94 were banded as adults on ESI and 53 were banded as chicks on ESI.

In 2015, the distance from each focal bird's nest to the colony edge ranged from 1.13 m to 25.81 m, with a mean of 11.2 m (Table 3.1). In 2016, the distance from each focal bird's nest to the colony edge ranged from 0.50 m to 26.32 m, with a mean of 11.9 m (Table 3.2). Neighborhood nest densities in 2015 ranged from 0.21 to 1.59 nests/m^2, with a mean density of 0.91 nests/m^2 (Table 3.1); neighborhood nest densities in 2016 ranged from 0.32 to 1.59 nests/m^2, with a mean of 0.92 nests/m^2 in 2016 (Table 3.2).

Egg-laying dates for focal individuals, measured in days since January 1, ranged from 111 (21 April) to 209 (28 July) in 2015, with a median lay date of 135 (15 May; Table 3.1). In 2016 (a leap year), egg-laying dates ranged from 111 (20 April) to 225 (12 August), with a median lay date of 138 (17 May; Table 3.2). There was a difference in median lay date between the two years of the study, 2015 and 2016 (Wilcoxon Rank-Sum test, $p = 0.032$); however, when lay dates in 2016 were adjusted for the leap year, there was no difference in median lay dates between years (Wilcoxon Rank-Sum test, $p = 0.09$).

Inter-annual distance between nest locations

The distance between an individual's nest in the two years of the study ranged from 0.48 m to 39.6 m, with a median of 4.65 m (n = 83; Figure 3.3). Linear mixed models found no evidence that inter-annual distance between nest locations was associated with reproductive success in 2015 ($F_{1,79}$, $p = 0.12$), or with reproductive success in 2016 ($F_{1,79}$, $p = 0.93$). There was no evidence that the distance between nest locations of corresponding nesting attempts during the two breeding seasons of the study was associated with an individual's age ($F_{1,79}$, $p = 0.35$) or breeding experience on ESI ($F_{1,79}$, $p = 0.2$). There was no evidence that inter-annual distance between nest locations was associated with a focal individual's egg-laying date in 2015 ($F_{1,79}$, $p = 0.16$). There was also no evidence that the inter-annual distance between nesting locations was associated with the density of neighborhood nests in 2015 ($F_{1,79}$, $p = 0.50$) or with the density of neighborhood nests in 2016 ($F_{1,79}$, $p = 0.92$). There was, however, evidence that inter-annual distance between nest locations was associated with the distance of a focal individual's nest from the colony edge in 2015 ($F_{1, 79}$, $p = 0.029$); terns that nested closer to the edge of the colony in 2015 were more likely to move farther from their nest location in 2015 when choosing a nest location in 2016.

To determine whether birds that nested in 2015 were moving to a different zone within the colony in 2016, the nest location of each focal individual in each year was placed into one of three zones: "EDGE" nests (locations < 5 meters from the colony edge), "MID" nests (locations 5 – 10 meters from the colony edge), and "CENTER" nests (locations > 10 m from the colony edge). We then examined whether an individual changed between these zones from 2015 to 2016. If an individual remained in the same zone in each season, they were categorized as "No Change." If individuals changed zones and moved to a zone closer to the center of the colony, they were categorized as "To Center" nests. Finally, if an individual changed zones between the

2015 and 2016 breeding seasons and moved to a zone closer to the edge of the colony, they were categorized as moving "Away from Center." We compared the average distance moved between each of these three categories: No Change, To Center, and Away from Center. There was no significant difference in the average distance moved between seasonal nest sites of birds that remained in the same zone (No Change) and those that moved to a zone closer to the edge (Away from Center) ($F_{2,80} = 12.68$, $p = 0.067$). There was a significant difference in average distance moved between seasonal nest sites of birds that remained in the same zone (No Change) and those that moved to a zone further from the colony edge in 2016 (To Center) ($F_{2,80} = 12.68$, $p < 0.001$). Finally, there was not a significant difference in the average distance moved between seasonal nest sites of birds that moved to a zone closer to the center of the colony (To Center) and birds that moved to a zone closer to the edge (Away from Center) ($F_{2,80} = 12.68$, $p = 0.085$).

Logistic Regression – success of all reproductive attempts

A total of 37 models to explain variation in reproductive success were investigated, including an intercept only model (Table 3.3). Covariates included in each model were selected *a priori*. The best-fit model explaining variation in reproductive success, given the data, included two explanatory variables: (1) Date of Nest Initiation, and (2) Neighborhood Nest Density. For every 7-day increment in Date of Nest Initiation (or one standard deviation from the mean), the odds of reproductive success decreased by 12.2% (95% CI: 6.23% - 16.7%) in this model (Table 3.5, Figures 3.4 and 3.5). As Neighborhood Nest Density increased by 0.27 nests/m^2 (one standard deviation from the mean), the odds of reproductive success increased by 31.6% (95% CI: 2.74% – 68.7%; Figures 3.4 and 3.5).

Four other models were competitive with the best-fit model (ΔAIC_c value less than 2; Table 3.4), and the set of competitive models included all of the prospective explanatory variables with the exception of Nesting Attempt number. The explanatory variable Date of Nest Initiation, however, was included in each of the five competitive models. When using the Burnham and Anderson (2010) method to determine relative importance of explanatory variables, Date of Nest Initiation was the variable with the greatest weight ($W_i = 0.96$), while the weights of Neighborhood Nest Density ($W_i = 0.31$), Distance to Colony Edge ($W_i = 0.25$), Age ($W_i = 0.21$), and Breeding Experience on ESI ($W_i = 0.13$) were considerably less. Nesting Attempt number had the lowest weight among the explanatory variables ($W_i = 0.09$).

The second most competitive model included the explanatory variables (1) Date of Nest Initiation and (2) Distance to Colony Edge, as well as (3) an interaction term between Date of Nest Initiation and Distance to Colony Edge (Table 3.4). Date of Nest Initiation and the interaction term were the only significant explanatory variables in this model. For every 7-day increment in Date of Nest Initiation (standard deviation of the mean), the odds of reproductive success decreased by 12.2% (95% CI: 5.72% - 17.0%). Although Distance to Colony Edge by itself did not explain a significant proportion of the variation in reproductive success, it was a significant explanatory variable in combination with Date of Nest Initiation. The odds of reproductive success were highest for birds that initiated nests early in the season and when their nest was located further from the colony edge (Figures 3.6 and 3.7).

The third most competitive model included the explanatory variables (1) Date of Nest Initiation and (2) Age (Table 3.4). For every increase in Age by 2.86 years (one standard deviation from the mean), the odds of reproductive success increased by 29.8% (95% CI: 0.95% - 67.0%). Similar to the other competitive models, the odds of reproductive success decreased by 12.1% (95% CI: 6.23% - 16.6%) with every increase in Date of Nest Initiation by 7 days (Figures 3.8 and 3.9).

The fourth most competitive model included the explanatory variables of (1) Date of Nest Initiation and (2) Breeding Experience on ESI; however, Date of Nest Initiation was the only significant explanatory variable in the model (Table 3.4). As in the previous models, as Date of Nest Initiation increased by 7 days, the odds of reproductive success decreased by 11.9% (95% CI: 5.96% - 16.4%).

Finally, the fifth most competitive model included the explanatory variables of (1) Date of Nest Initiation, (2) Neighborhood Nest Density, and (3) an interaction term between Date of Nest Initiation and Neighborhood Nest Density (Table 3.4). This model is the same as the top model, but with the addition of the interaction term; however, the interaction term was not significant in this model. With every 7-day increment in Date of Nest Initiation, the odds of reproductive success decreased by 12.3% (95% CI: 6.51% - 16.7%). For every increase in Neighborhood Nest Density by 0.27 nest/m^2 (one standard deviation from the mean), the odds of reproductive success increased by 30.0% (95% CI: 1.17% - 67.1%).

DISCUSSION

Timing of Reproduction

Our results revealed that, during the 2015 and 2016 breeding seasons, an individual's odds of reproducing successfully declined the later in the season its first nesting attempt was initiated. These results were similar to those of Antolos *et al.* (2006) for Caspian Terns nesting at Crescent Island in central Washington State. Antolos *et al.* (2006) found a negative relationship between reproductive success and hatch date. There were some differences, however, between the findings of Antolos *et al.* (2006) and those of the present study. The individual tern nests that were monitored at Crescent Island were not only more productive if initiated earlier in the season, but also earlier nests were generally located further from the edge of the colony than nests initiated later in the breeding season. While this relationship between reproductive success and distance to the colony edge was observed in our study, it was limited to nests that were also initiated early in the breeding season. In the present study, as the breeding season progressed the distance of a nest from the colony edge had less and less influence on the likelihood of a nest being successful.

The negative relationship between reproductive success and nest initiation date may be explained by younger, less experienced, and less fit individuals that tend to nest later in the breeding season, in accordance with the 'parental quality' hypothesis (Arnold *et al.* 2004), which may explain the high levels of re-nesting that we observed in 2016. The relationship between reproductive success and nest initiation date could also be explained by a decline in resource availability throughout the breeding season – the 'timing' hypothesis (Arnold *et al.* 2004). Similarly, the inverse relationship between nest initiation date and reproductive success could reflect higher nest predation rates as the season progresses. The earliest nesters may have more intrinsic reproductive capability, may have more nesting experience, or are nesting during a time when ambient environmental conditions are most favorable (Arnold *et al.* 2004, Verhulst and Nilsson 2008). Without experimentally manipulating groups to investigate measures of individual quality that may explain variation in reproductive success, we may not be able to distinguish among these three hypotheses.

Our results, however, are similar to those of Arnold *et al.* (2004) with Common Terns (*Sterna hirundo*), whose experimental results suggested that both the timing and parental quality hypotheses were supported. Reproductive success declined throughout the season due to external factor(s) in the environment, in accordance with the timing hypothesis. In Arnold *et al.*'s (2004) study, the external factors were mainly an increase in intraspecific aggression and kleptoparasitism as the season progressed. At East Sand Island, nesting Western/Glaucous-winged Gulls are in the chick-rearing stage of breeding as the majority of Caspian Terns are preparing for their chicks to fledge. Some of these pairs of gulls specialize specifically in kleptoparasitizing fish from Caspian Terns, as well as depredating Caspian Tern nest contents (Collar *et al.* 2017). Collar *et al.* (2017) found a significant negative relationship between the average reproductive success of the colony at East Sand Island and increased kleptoparasitism rates by gulls. These findings support the hypothesis that, towards the end of the Caspian Tern breeding season, gulls are increasing their efforts to obtain food to feed their chicks, resulting in a decline in the success of Caspian Tern nests later in the season.

Although we found that Date of Nest Initiation was the explanatory variable with the highest relative influence on reproductive success, the explanatory variables of Age and Breeding Experience on ESI were each included in one of the five competitive models. The two interaction terms between Date of Nest Initiation and Age or Breeding Experience, however, were not included in the set of competitive models. There were also no significant correlations between Date of Nest Initiation and either Age or Breeding Experience, plus the explanatory variable of Breeding Experience was not significant in the only competitive model that included Breeding Experience. While these results did not support the parental quality hypothesis in the way we predicted, the amount of re-nesting observed in the study indicates that higher quality individuals were those that nested early, giving them time to lay replacement clutches if earlier nesting attempts failed. Also, we did not observe a negative relationship between Reproductive Success and Nesting Attempt number, suggesting that the individuals that nested early had relatively high odds of breeding successfully throughout the breeding season, compared to individuals that initiated their first nesting attempt later in the season.

In the best-fit model, we observed a positive relationship between Neighborhood Nest Density and individual reproductive success, and Neighborhood Nest Density was the explanatory variable with the second highest weight, after Date of Nest Initiation. Antolos *et al.* (2006) did not observe a significant difference in reproductive success between groups of Caspian Terns nesting in areas of relatively high nest densities vs. relatively low nest densities on the colony at Crescent Island. Although results of the present study differed somewhat from those of Antolos *et al.* (2006), both studies did not find a negative relationship between reproductive success and nest density. This supports the hypothesis that nesting at higher densities can provide Caspian Terns and other colonial birds more protection from nest predators. It also supports the finding by Antolos *et al.* (2006) that density-dependent intraspecific adult aggression did not cause significant mortality to neighboring chicks at the Crescent Island colony, even at the highest nest densities. A related hypothesis is that Caspian Terns nesting at East Sand Island have an ‘optimal nest density’ that maximizes reproductive success, above which reproductive success declines due to density-dependent factors, such as intraspecific adult-chick aggression. We found no support for this hypothesis in our results, however; even at the highest nest densities observed at East Sand Island (1.59 nests/m^2) there was not an appreciable decline in Caspian Tern reproductive success.

The results of this study are seemingly in conflict with the results of Chapter 2, where there was a negative correlation between the average annual reproductive success of the Caspian Tern colony at ESI and the average density of nests on the colony during 2001-2017. There are several possible explanations for these conflicting results. First, conditions on the ESI Caspian tern colony at the beginning of study period were quite different compared to the two years when the present study was conducted. For example, predatory gulls were lethally controlled on the ESI tern colony during 1999-2000. With reduced risk of gull predation on tern nests, there would have been little benefit for terns to nest at high densities. Tern nest densities increased later in the 2001-2017 time series, when the amount of disturbance and nest predation by predators like Bald Eagles and Western/Glaucous-winged Gulls had also increased. Had the present study been conducted in years with lower nest densities and lower predation risk, we likely would have found a different relationship between neighborhood nest density and individual reproductive success.

In the second most competitive model, an interaction term between Date of Nest Initiation (egg-laying date) and a nest's Distance from the Colony Edge was significant in explaining variation in reproductive success. This result is similar to that of Antolos *et al.* (2006), where early nesters were more successful and whose nests were more centrally located on the colony. In the present study, however, an increase in the distance of a nest from the colony edge only increased the likelihood of reproductive success for individuals that laid eggs during the early part of the breeding season (Figure 3.7). This was an unexpected result because our observations in the field suggested that there was a high risk of nest failure to the earliest initiated tern nests due to high nest predation rates and the asynchrony of nest initiation at the outset of the breeding season, despite these early nests being located near the center of the colony.

Data collected in the field for this study perhaps did not capture the earliest nest predation events for focal birds, because early in the breeding season there were many disturbances to the colony, resulting in gulls depredating tern eggs soon after they were laid. Our data may not include failed nesting attempts for the earliest nesters if their egg(s) were depredated during the egg-laying period, before their clutch was completed and incubation had commenced. Caspian Terns typically lay 1-3 eggs per clutch (Cuthbert and Wires 1999), and if the entire clutch is depredated then the next clutch is not laid until 9 or 10 days later, once the female is ovulating again (Cabot and Nisbet 2013). If the female member of a focal pair had not laid the entire clutch when the predation event occurred, the nesting attempt would not have been classified as failed, because we had no way to distinguish whether a focal bird was in the midst of egg-laying or not. Therefore, our study is likely biased towards detecting eggs in focal nests where the incubation period has already started and the adults are committed to that nest, because we were unlikely to have detected nests where the eggs were depredated before the adults began incubation.

The large number of re-nesting attempts detected in 2016 was another unexpected result, particularly because a few focal individuals re-nested as many as three times during a single breeding season after their initial nesting attempt failed. Although re-nesting by Caspian Terns at East Sand Island had been documented anecdotally, we did not expect the frequency and extent of re-nesting that we observed in 2016. Further, the proportion of re-nesting attempts that were successful in 2016 did not decline significantly compared to initial nesting attempts (Figure 3.2). Laying replacement clutches is not unusual in seabird species, especially those that may experience nest failure due to weather or predation early in the nesting season (Wendeln *et al.* 2000). Because Caspian Terns exhibit biparental care, however, both individuals must weigh the costs and benefits associated with laying replacement clutches. Wendeln *et al.* (2000) found that Common Terns that re-nested were more likely to be older, laid their first clutch earlier, and were more likely to have successful replacement clutches than birds that were laying their first clutch at the same time, which is consistent with what we observed in 2016. In some studies, birds that re-nest must balance the increased energy allocated toward multiple clutches in one season with subsequent survival and future reproduction.

Although nesting early, in the center of the colony, and in areas with greater nest densities is clearly beneficial to Caspian Terns nesting at East Sand Island, nesting early also gives individuals that are unsuccessful in their first nesting attempt more time to re-nest. In Common Terns, laying replacement clutches did not result in negative effects on survival or future reproductive success, and instead was associated with high individual quality (Becker and Zhang 2010), results similar to those observed in the present study. Common Terns that arrived early and laid their initial clutches earlier were older and higher quality individuals that were able to buffer against losing the first clutch by re-nesting (Becker and Zhang 2010).

Age and Previous Breeding Experience

Our results support our prediction that reproductive success of Caspian Terns at East Sand Island increases with age, but not necessarily with greater previous breeding experience at the site. We found that these variables had low relative importance weights in explaining variation in individual reproductive success in this study, compared to other explanatory variables (i.e. Date of Nest Initiation, Neighborhood Nest Density). Although Age did not rank high in variable weight, it was an explanatory variable in the third most competitive model, and there appears to be a trend of increasing reproductive success with increasing age (Figures 3.8 and 3.9), after accounting for Date of Nest Initiation.

Contrary to our predictions, Breeding Experience on ESI did not have a significant effect on reproductive success, although there was a positive trend. The positive trend is consistent with the hypothesis that individuals become more competent breeders with the added experience obtained from previous nesting attempts at a colony (Lewis *et al.* 2006). Some studies have found that reproductive success increased only when previous nesting attempts were successful (Lewis *et al.* 2006). Because we do not have information on the reproductive success of monitored individual's during their previous nesting attempts at East Sand Island, we cannot evaluate the effects of reproductive success during previous nesting attempts at East Sand Island on reproductive success during the present study. Our results do suggest that after a few years of nesting experience at a breeding site, the advantages of additional nesting experience at the site no longer significantly increases the probability of nesting successfully. This is similar to results from Western Gulls (*L. occidentalis*), where reproductive success increased the most between the first and second nesting attempts at a particular colony site (Pyle *et al.* 1991); however, because some focal individuals were banded as fledglings in the present study, we assumed that an individual banded as a fledgling was a first-time breeder if we had not observed it breeding in previous years at the ESI colony.

Nest Location and Inter-annual Distance Between Nests

We hypothesized that we would see a pattern of younger or less experienced Caspian Terns nesting further from the center of the breeding colony at ESI (closer to the edge), because this relationship has been documented in Ring-billed Gulls (*L. delawarensis*; Haymes and Blokpoel 1980). Haymes and Blokpoel (1980) assumed that younger birds either could not compete for the best territories or were arriving on the colony later in the breeding season than older birds. While the interaction between the distance of a nest from the colony edge and either age or previous breeding experience did not explain a significant proportion of the variation in reproductive success in our study, there was a positive but non-significant trend between reproductive success and distance of the nest from the colony edge. In our analyses, distance of a nest from the colony edge was only important in explaining variation in nesting success when interacting with nest initiation date, because distance of a nest from the colony edge only influenced nesting success early in the breeding season.

The results of our study were different from those of Antolos *et al.* (2006), who observed a significant negative relationship between reproductive success and the proximity of nests to the colony edge. Antolos *et al.* (2006) found that location of a tern nest on the colony at Crescent Island was more important in explaining reproductive success than the individual's nest initiation date, whereas nest initiation date was the explanatory variable with the greatest weight for predicting reproductive success in the present study.

In colonial nesting birds, there are multiple hypotheses for how individuals select nesting territories and how birds are distributed throughout the colony. The central-periphery model assumes that centrally located nests in a colony are less susceptible to predation, will likely be more successful, and that individuals of higher quality occupy these nest sites. The central-satellite model suggests that lower-quality individuals chose their nest sites near high-quality birds, and that this may not necessarily occur at the center of the colony. In the Antolos *et al.* (2006) study, Caspian Terns at Crescent Island generally followed the central-periphery model; the earliest birds nested closest to the center of the colony and were more successful. Although not all early nesting birds at ESI chose nest sites at the center of the colony, those that both nested early and further from the edge were the most successful; therefore, our results also provide support for the central-periphery model.

Although we expected birds that were unsuccessful nesters in 2015 to have a higher probability of moving their nest site in 2016, as per the "win-stay, lose-switch" strategy, we did not find a significant relationship between nesting success in 2015 and distance between nest sites in 2015 and 2016. Birds that nested closer to the colony edge in 2015, however, were more likely to move further from that nest site in 2016. Birds that moved greater distances between their nest sites from one year to the next were more likely to move their nest location closer to the center of the colony. Regardless of their reproductive success in 2015, individuals that nested closest to the edge of the colony were motivated to move in the subsequent breeding season to find higher quality nest sites. Caspian Terns are also considered a species with low nest site fidelity, due to the tendency of breeding sites to be ephemeral. ESI, however, is a relatively stable colony site that has existed for over a decade, within close proximity of quality foraging habitat. Our results are similar to those of Collar (2013), who found that Caspian Terns nesting at ESI have a high degree of fidelity not only to the colony as a whole, but also to certain areas of the colony, despite nesting failure or the loss of their former nest site.

CONCLUSIONS

In this study, we found that Caspian Terns breeding at the large colony on East Sand Island in 2015 and 2016 were more successful at raising young when individuals initiated nesting early in the breeding season. While reproductive success also increased with increasing neighborhood nest density, the date of nest initiation was the single most important factor for explaining variation in reproductive success. This supports the hypothesis that older birds tend to arrive at the breeding colony first, nest earlier in the season, and are more successful. Our data from the East Sand Island Caspian Tern colony support the central-periphery model of nest distribution, whereby higher quality individuals select nest sites near the center of the colony and experience higher reproductive success. Terns that were among the earliest nesters chose nest sites in neighborhoods with higher nest densities, occupied nest sites near the center of the colony, and were more likely to reproduce successfully. Individual birds that nested close to the colony edge in 2015 were not only more likely to move greater distances to choose a nest location within the colony in 2016, but also were more likely to move away from the edge of the colony and thereby obtain a more centrally located nest site on the colony. Finally, those individuals that nested earlier had more time to lay replacement clutches if eggs or chicks were lost to predation in initial nesting attempts. Thus, they were able to increase their chances of reproducing successfully by arriving and initiating nesting earlier, despite having to allocate additional resources toward laying replacement clutches if their first nesting attempt failed.

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Table 3.1. Summary statistics of characteristics of Caspian Tern nesting attempts monitored during the 2015 breeding season on East Sand Island (ESI) in the Columbia River estuary (n = 150 attempts by 123 different individuals).

	Mean ± SD	**Median**	**Range**
Breeding Experience on ESI (years)	1.91 ± 1.33	2	0 - 4
Age (years)	11.22 ± 2.80	11	4 - 16
Distance to Colony Edge (m)	11.20 ± 6.19	10.46	1.13 – 25.81
Date of Nest Initiation (egg-laying date)	143.09 ± 21.37	135.5	111 - 209
Neighborhood Nest Density (nests/m^2)	0.91 ± 0.29	0.96	0.21 – 1.59

Table 3.2. Summary statistics of characteristics of Caspian Tern nesting attempts monitored during the 2016 breeding season at East Sand Island in the Columbia River estuary (n = 171 attempts by 99 different individuals).

	Sample Size	**Mean ± SD**	**Median**	**Range**
Breeding Experience on ESI (years)	171 attempts	2.71 ± 1.46	3	0 - 5
Age (years)	171 attempts	11.60 ± 2.92	12	6 - 17
Distance to Colony Edge (m)	171 attempts	11.88 ± 6.24	11.67	0.50 – 26.32
Date of Nest Initiation (egg-laying date)	171 attempts	149.87 ± 24.16	148	119 - 225
Neighborhood Nest Density (nests/m^2)	171 attempts	0.92 ± 0.26	0.96	0.32 - 1.59
Distance of nest from 2015 nest location (m)	81 individuals	7.43 ± 8.49	4.65	0.48 – 39.6

Table 3.3. List of 37 generalized linear mixed models developed using *a priori* hypotheses for the odds of reproductive success for individual Caspian Terns nesting at East Sand Island. These models are not ranked, but were included in analyses using Akaike's Information Criterion adjusted for small sample sizes (AIC$_c$). ESI = East Sand Island.

	Model
1	Intercept Only
3	Breeding Experience on ESI
4	Age
5	Distance to Colony Edge
6	Date of Nest Initiation
7	Neighborhood Nest Density
8	Nesting Attempt
9	Age + Age^2
10	Breeding Experience on ESI + Date of Nest Initiation
11	Breeding Experience on ESI + Age
12	Age + Date of Nest Initiation
13	Distance to Colony Edge + Date of Nest Initiation
14	Breeding Experience on ESI + Nesting Attempt
15	Age + Nesting Attempt
16	Distance to Colony Edge + Nesting Attempt
17	Neighborhood Nest Density + Nesting Attempt
18	Breeding Experience on ESI + Distance to Colony Edge
19	Age + Distance to Colony Edge
20	Breeding Experience on ESI + Neighborhood Nest Density
21	Age + Neighborhood Nest Density
22	Date of Nest Initiation + Neighborhood Nest Density
23	Distance to Colony Edge + Neighborhood Nest Density
24	Breeding Experience on ESI + Distance to Colony Edge + (Breeding Experience on ESI * Distance to Colony Edge)
25	Age + Distance to Colony Edge + (Age * Distance to Colony Edge)
26	Age + Date of Nest Initiation + (Age * Date of Nest Initiation)
27	Breeding Experience on ESI + Date of Nest Initiation + (Breeding Experience on ESI * Date of Nest Initiation)
28	Distance to Colony Edge + Date of Nest Initiation + (Distance to Colony Edge * Date of Nest Initiation)
29	Distance to Colony Edge + Neighborhood Nest Density + (Distance to Colony Edge * Neighborhood Nest Density)
30	Breeding Experience on ESI + Neighborhood Nest Density + (Breeding Experience on ESI * Neighborhood Nest Density)
31	Age + Neighborhood Nest Density + (Age * Neighborhood Nest Density)
32	Date of Nest Initiation + Neighborhood Nest Density + (Date of Nest Initiation * Neighborhood Nest Density)

33	Distance to Colony Edge + Nesting Attempt + (Distance to Colony Edge * Nesting Attempt)
34	Nest Density + Nesting Attempt + (Nest Density * Nesting Attempt)
35	Date of Nest Initiation + Nesting Attempt + (Date of Nest Initiation * Nesting Attempt)
36	Breeding Experience on ESI + Nesting Attempt + (Breeding Experience on ESI * Nesting Attempt)
37	Age + Nesting Attempt + (Age * Nesting Attempt)

Table 3.4. The top six generalized linear mixed models explaining variation in reproductive success of all nesting attempts by focal Caspian Terns nesting on East Sand Island (ESI) in 2015 and 2016. The models were ranked using Akaike's Information Criterion adjusted for small sample sizes (AIC_c). Models were compared using the ΔAIC_c value, the difference between an individual model's AIC_c score and the lowest AIC_c score of all the candidate models. Each model included a random effect of both Individual Bird and Year. The top five models were competitive ($\Delta AIC_c \leq 2.0$).

Rank	**Model**	**AICc**	**ΔAICc**	W_i
1	Date of Nest Initiation + Neighborhood Nest Density	395.97	0.00	0.196
2	Distance to Colony Edge + Date of Nest Initiation + (Distance to Colony Edge * Date of Nest Initiation)	395.27	0.31	0.168
3	Age + Date of Nest Initiation	395.57	0.60	0.145
4	Breeding Experience on ESI + Date of Nest Initiation	396.56	1.59	0.089
5	Date of Nest Initiation + Neighborhood Nest Density + (Date of Nest Initiation * Neighborhood Nest Density)	396.61	1.64	0.086
6	Date of Nest Initiation + Distance to Colony Edge	397.28	2.31	0.062

Table 3.5. Results of the best fit generalized linear mixed model explaining variation in reproductive success for all nesting attempts by focal Caspian Terns at the East Sand Island breeding colony during the 2015 and 2016 nesting seasons, with a binomial logit link output. The model includes fixed effects of (1) Date of Nest Initiation, and (2) Neighborhood Nest Density. *P*-values are approximate two-sided values derived from Wald's tests for single coefficients.

Coefficients	**Estimate**	**SE**	**Z-statistic**	***P*-value**
(Intercept)	-1.702	0.457	-3.73	< 0.0001
Date of Nest Initiation	-0.512	0.144	-3.54	0.0004
Neighborhood Nest Density	1.012	0.466	2.17	0.0297

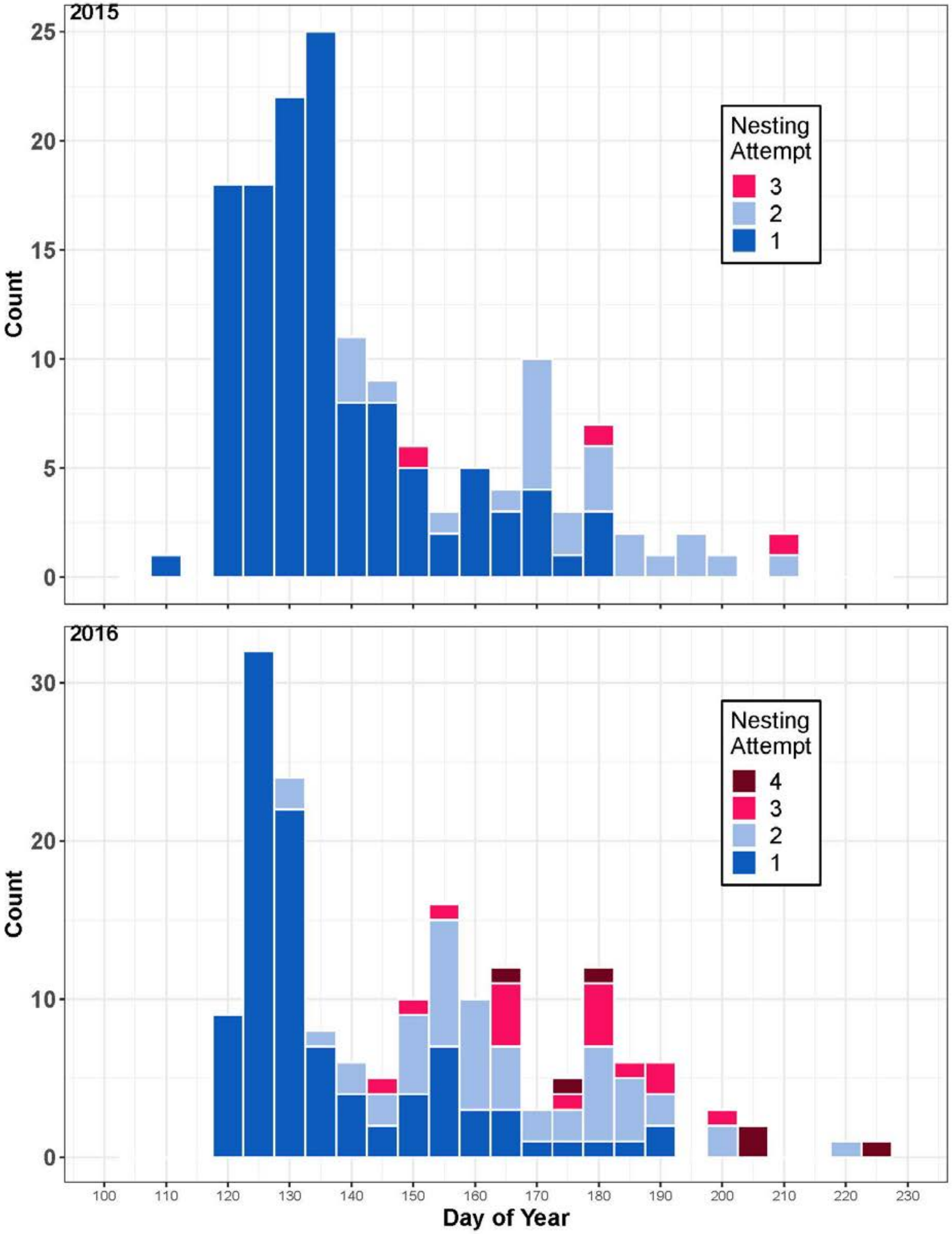

Figure 3.1. Frequency histograms of the total number of nesting attempts by individual Caspian Terns nesting at the East Sand Island colony per 5-day interval during the 2015 and 2016 breeding seasons. The number of attempts in each 5-day interval is broken down by the total number of first, second, third, and fourth nesting attempts by individual Caspian Terns.

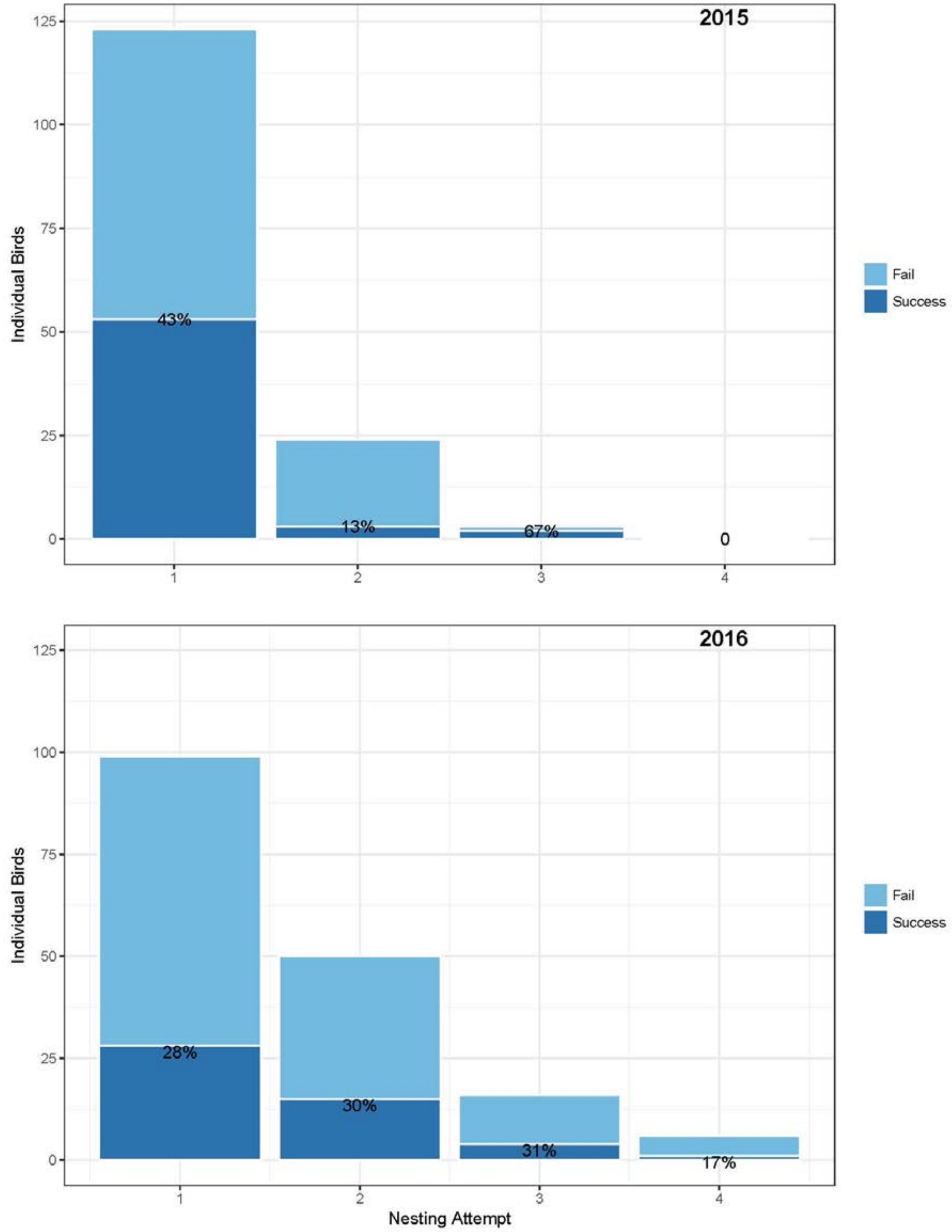

Figure 3.2. Bar graph of the number of banded Caspian Terns with successful (at least one fledgling raised) and failed (no young raised to fledging) nesting attempts on the East Sand Island colony as a function of nesting attempt number in 2015 and in 2016.

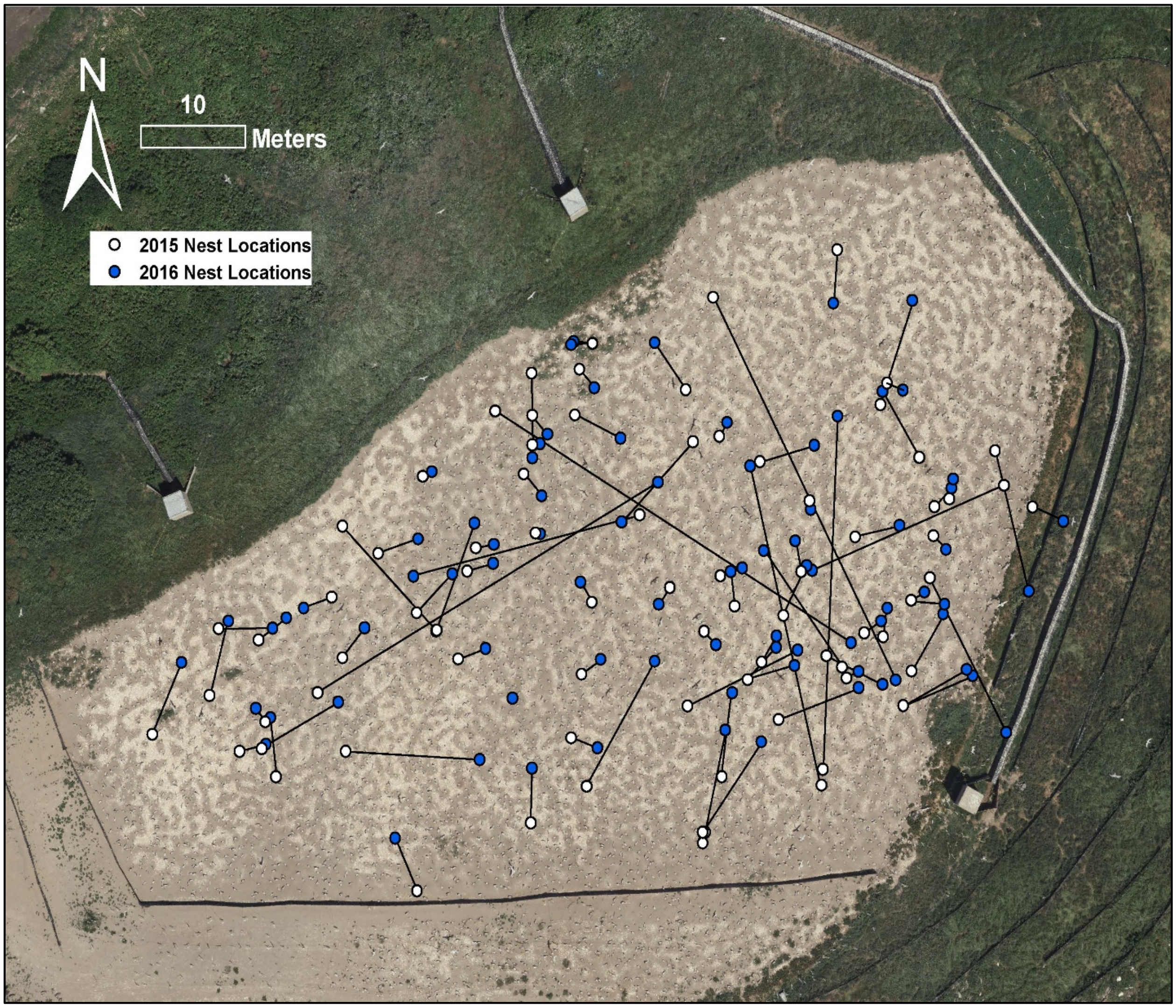

Figure 3.3. Vertical overhead aerial photography of the East Sand Island Caspian Tern colony in 2015, showing the inter-annual differences in nest site locations for focal individuals that nested on the colony in both 2015 and 2016 (n = 81 nesting attempts). The nest site of each focal bird in 2015 (white circle) and in 2016 (blue circle) are connected by a solid black line.

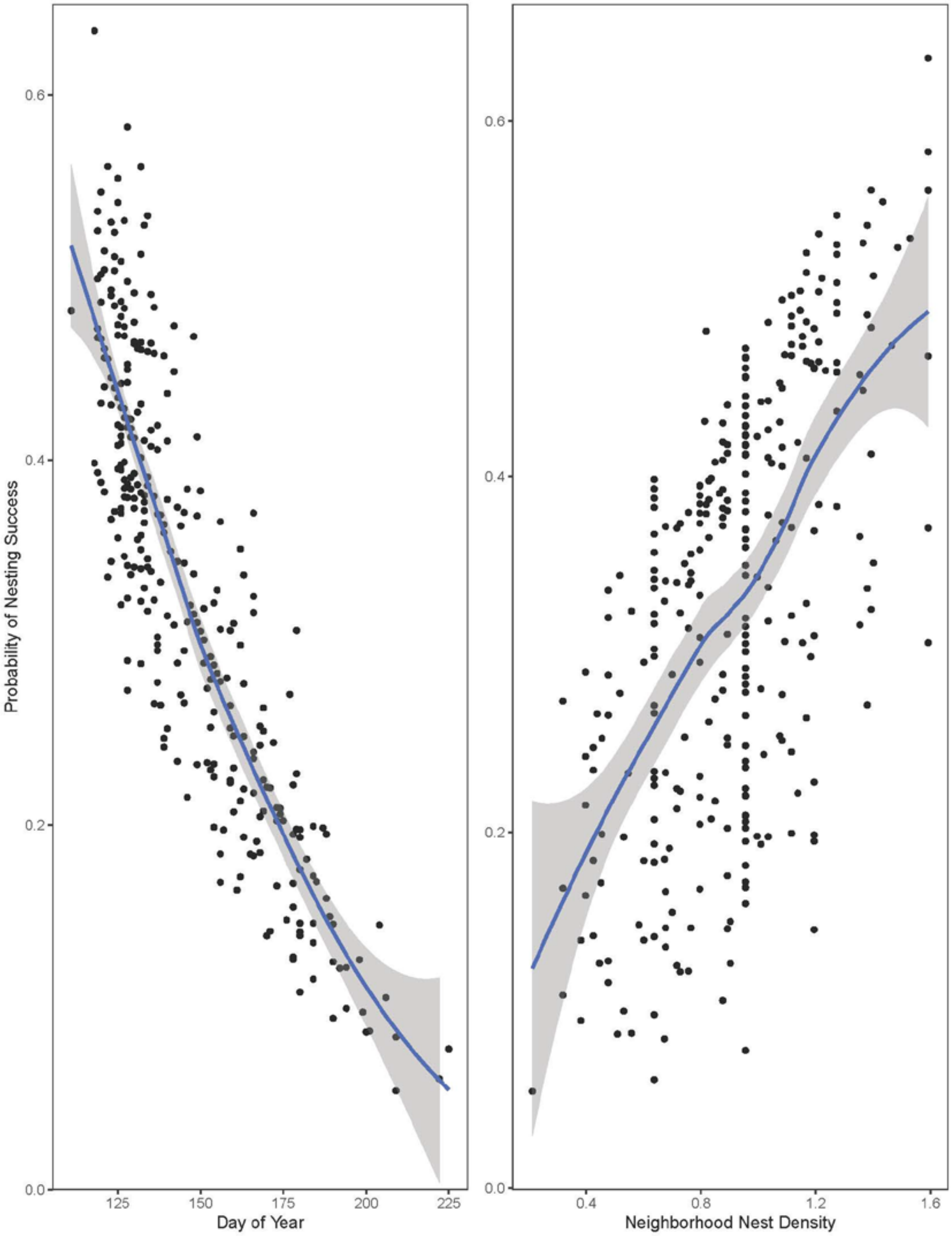

Figure 3.4. Graphical representation of the GLMM model coefficients in the best-fit model (see Table 3.5) predicting Caspian Tern reproductive success at East Sand Island as a function of the Date of Nest Initiation and Neighborhood Nest Density for all nesting attempts by focal birds during the 2015 and 2016 breeding seasons. Each graph depicts the relationship between an explanatory variable in the model (x-axis) and the probability of nesting successfully, after accounting for all other explanatory variables in the model. The prediction line (blue line), 95% confidence intervals (shaded grey), and partial residuals are displayed for each explanatory variable.

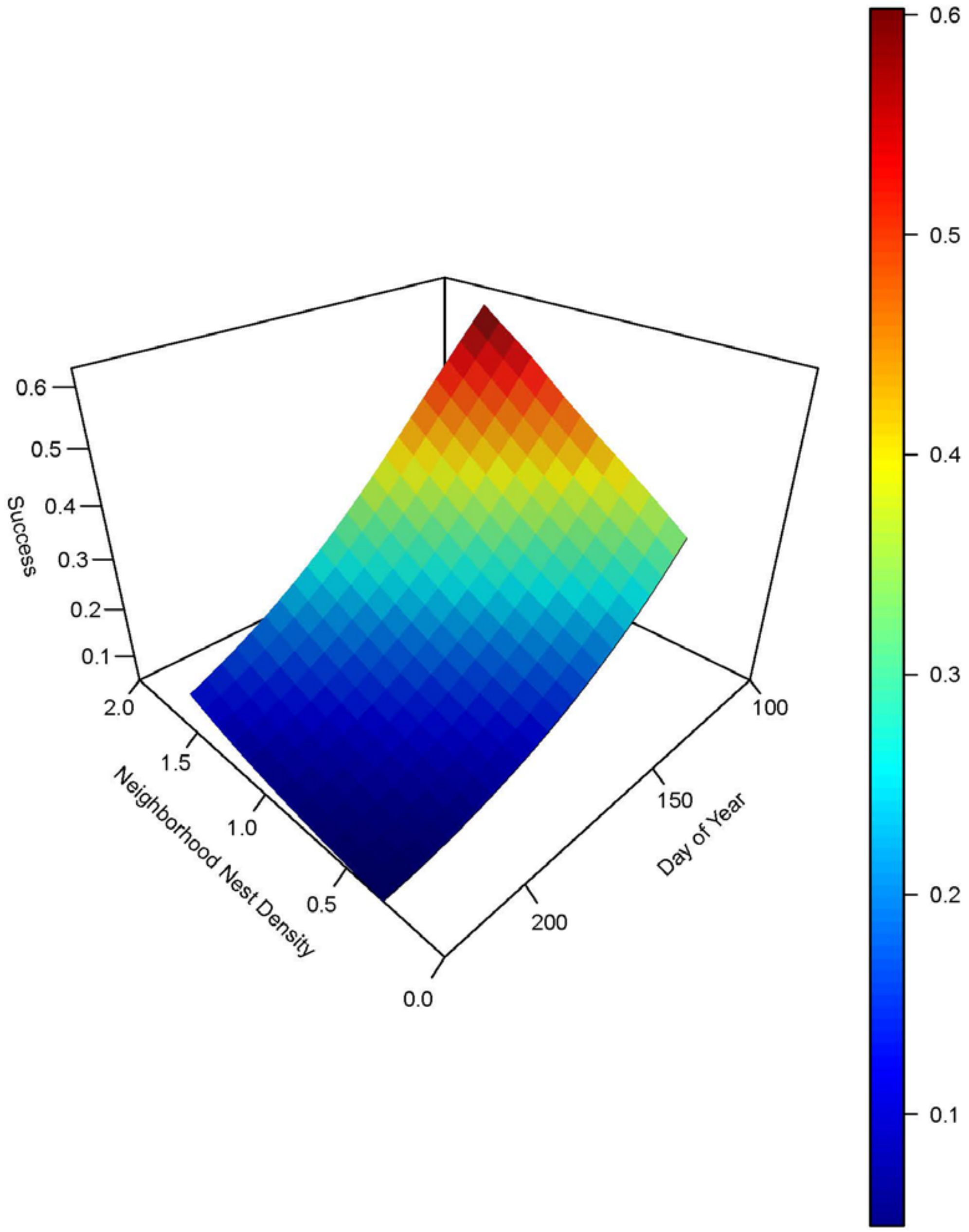

Figure 3.5. Three-dimensional graphical representation of the probability of reproductive success for Caspian Terns nesting at East Sand Island as a function of Date of Nest Initiation and the Neighborhood Nest Density. All nesting attempts by focal birds during the 2015 and 2016 breeding seasons were used in this analysis.

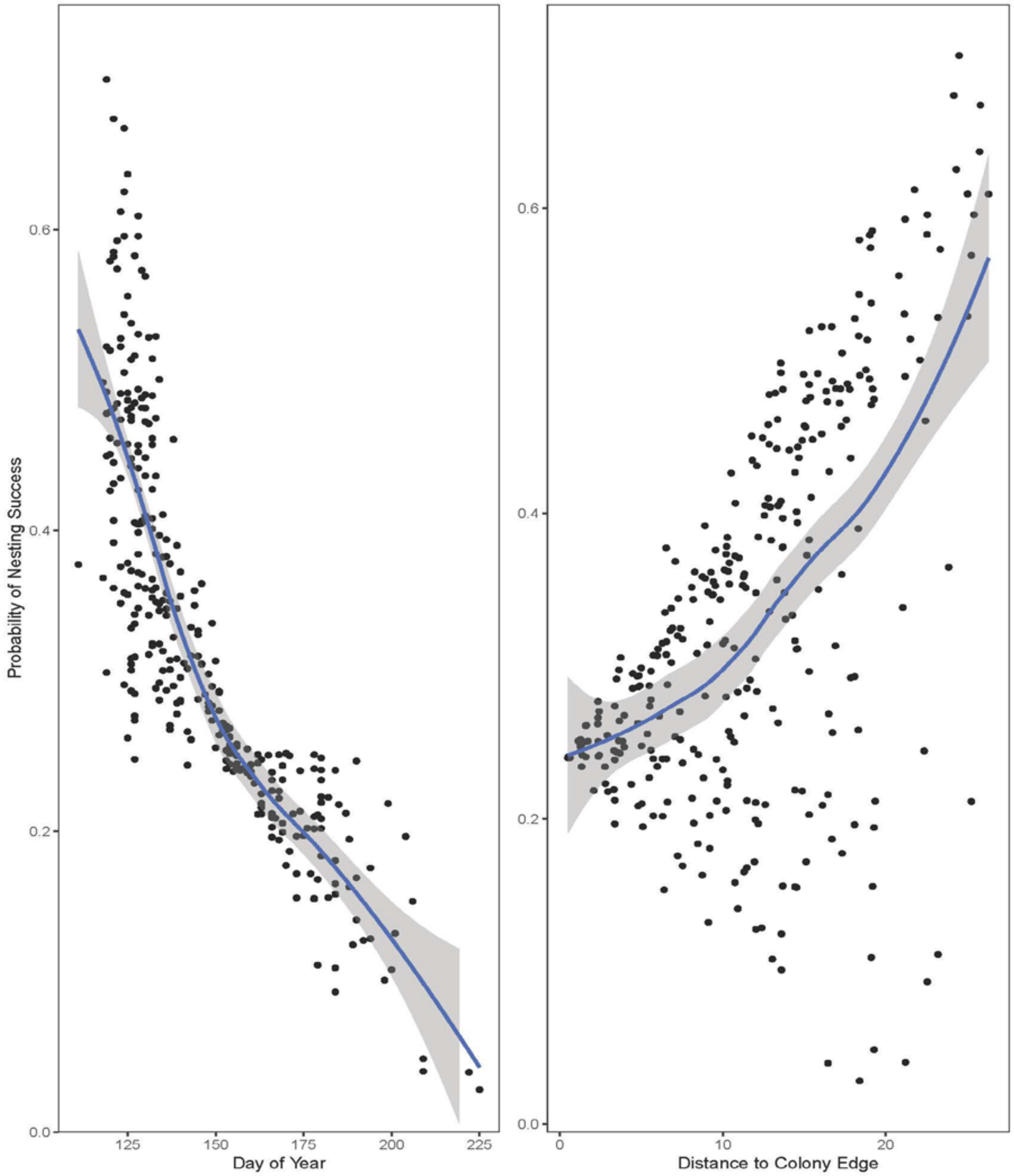

Figure 3.6. Graphical representation of the GLMM model coefficients in the second most competitive model in the model set (see Table 3.4) predicting Caspian Tern reproductive success at East Sand Island as a function of the Date of Nest Initiation and Distance to Colony Edge of the nest for all nesting attempts by focal birds during the 2015 and 2016 breeding seasons. Each graph depicts the relationship between an explanatory variable in the model (x-axis) and the probability of nesting successfully, after accounting for all other explanatory variables in the model. The prediction line (blue line), 95% confidence intervals (shaded grey), and partial residuals are displayed for each explanatory variable.

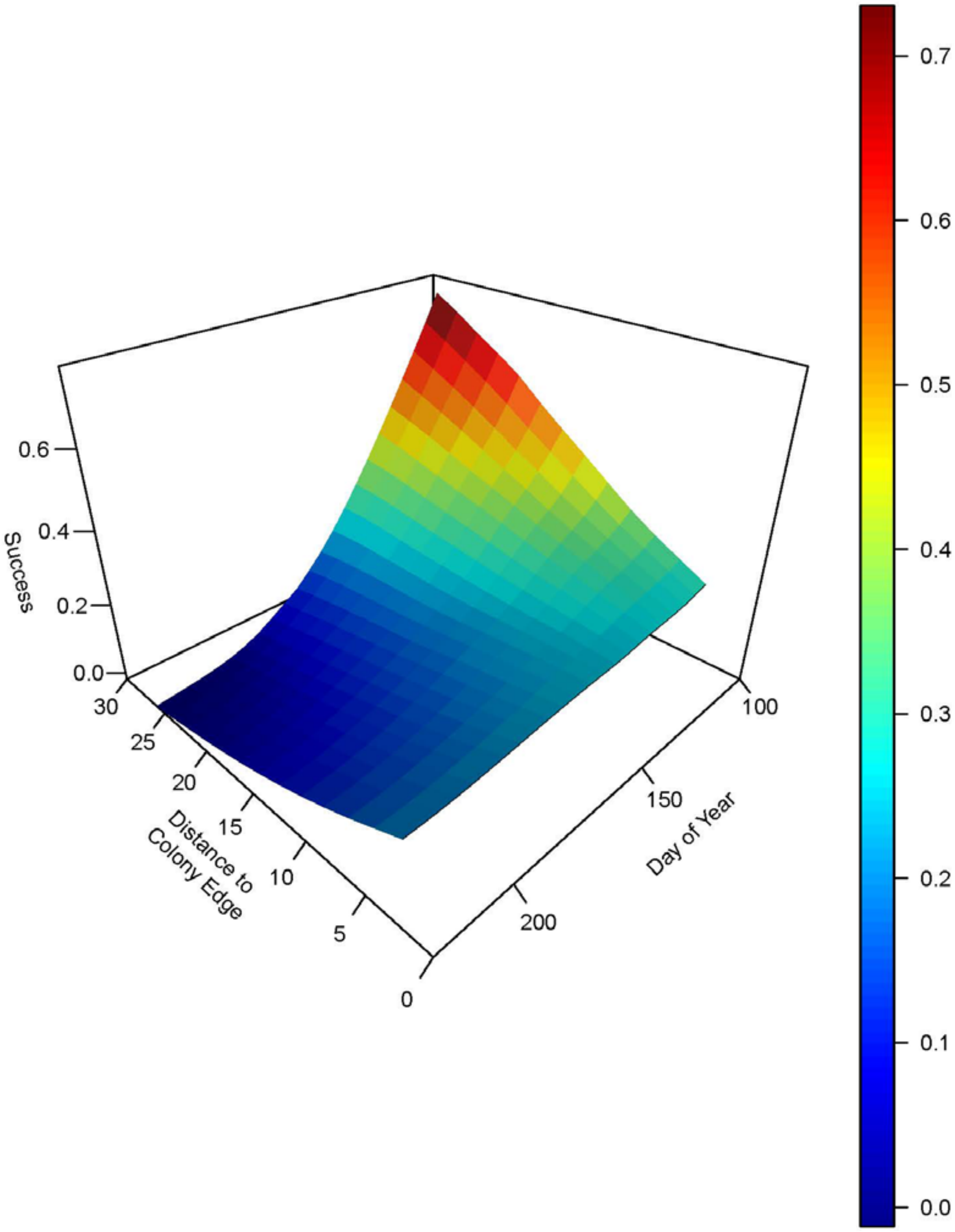

Figure 3.7. Three-dimensional graphical representation of the probability of reproductive success for Caspian Terns nesting at East Sand Island as a function of Date of Nest Initiation and Distance to Colony Edge of the nest. All nesting attempts by focal birds during the 2015 and 2016 breeding seasons were used in this analysis.

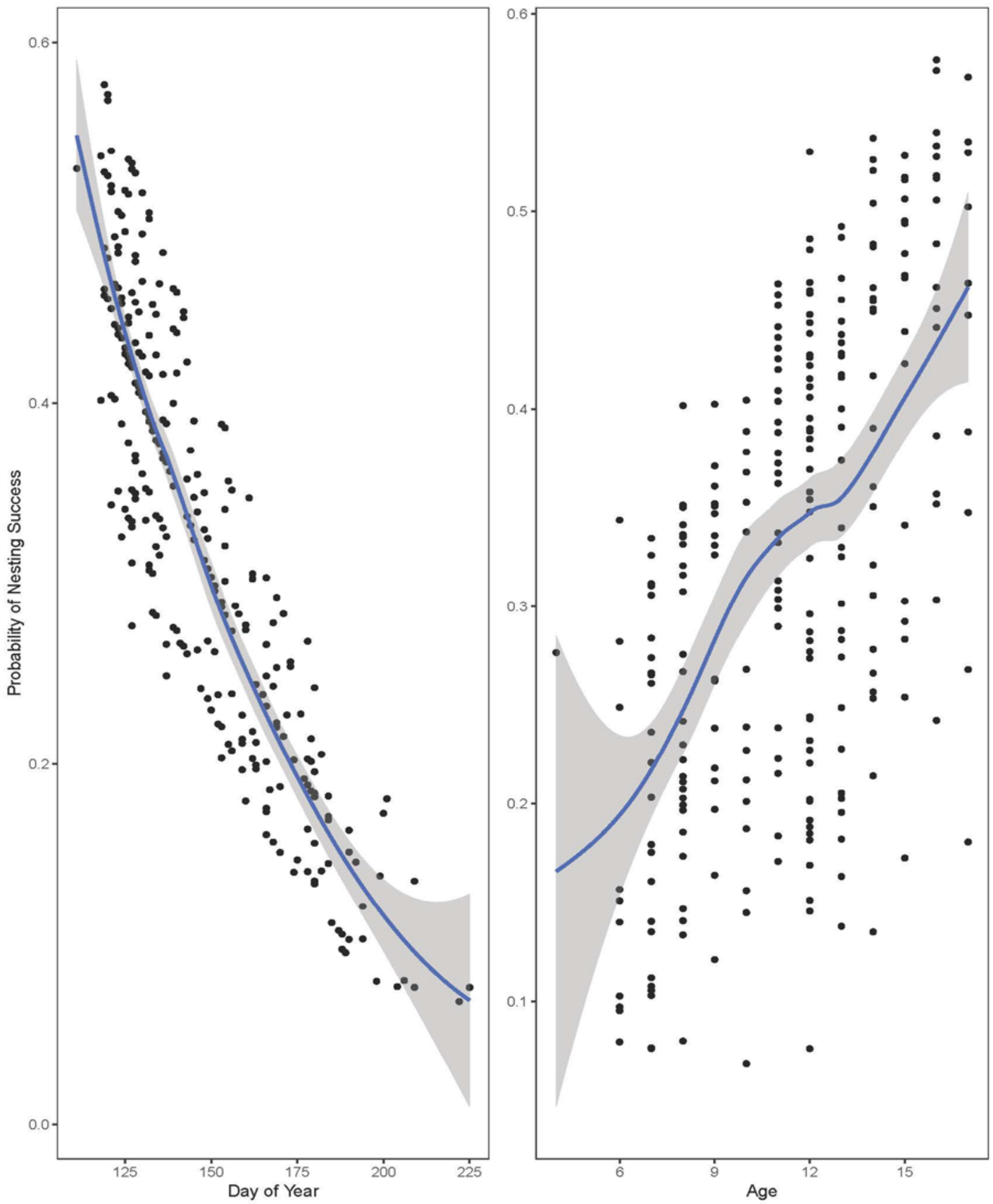

Figure 3.8. Graphical representation of the GLMM model coefficients in the third most competitive model in the model set (see Table 3.4) predicting Caspian Tern reproductive success on East Sand Island as a function of the Date of Nest Initiation and Age (in years) of the focal member of the breeding pair for all nesting attempts by focal birds during the 2015 and 2016 breeding seasons. Each graph predicts the relationship between an explanatory variable in the model (x-axis) and the probability of nesting successfully, after accounting for all other explanatory variables in the model. The prediction line (blue line), 95% confidence intervals (shaded grey), and partial residuals are displayed for each explanatory variable.

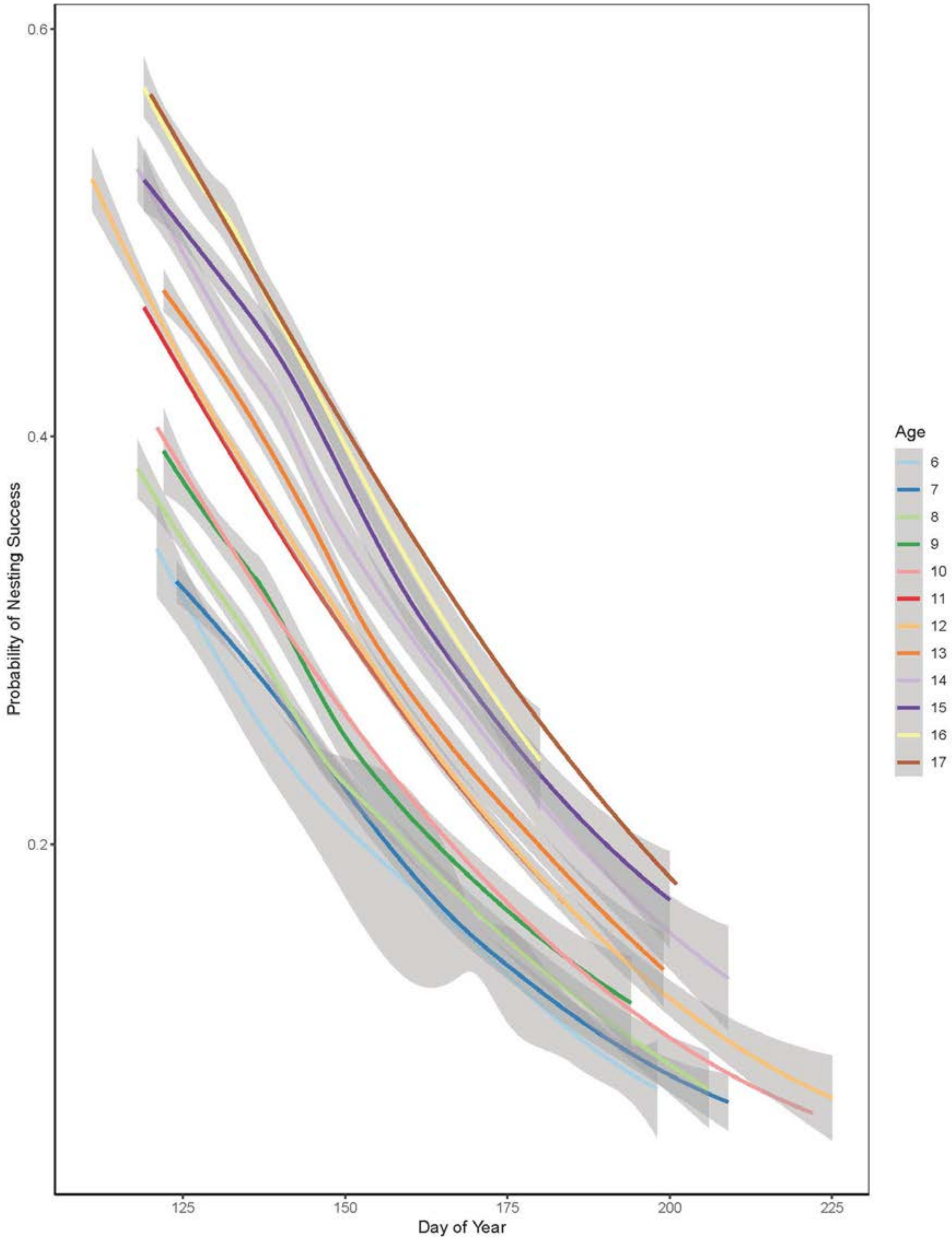

Figure 3.9. GLMM response curves for the probability of nesting successfully in Caspian Terns nesting on East Sand Island as a function of Age and Date of Nest Initiation (egg-laying date), with 95% confidence intervals for all nesting attempts by focal birds during the 2015 and 2016 breeding seasons.

CHAPTER 4. SYNOPSIS AND CONCLUSIONS

Olivia Bailey

The objective of my study was to understand the factors that affect Caspian Tern (*Hydroprogne caspia*) reproductive success at East Sand Island (ESI) in the Columbia River estuary. I was interested in the relative importance of factors that may affect reproductive success at the level of the individual Caspian Tern over two breeding seasons, as well as the top-down and bottom-up factors that may affect the reproductive success of the Caspian Tern colony at ESI as a whole, over a 17-year period. A better understanding of what drives reproductive success at these two different scales increases the knowledge of Caspian Tern breeding ecology at East Sand Island and can inform managers of the factors that may be regulating the size and productivity of the colony.

At the colony level, my results demonstrate that Year and gull kleptoparasitism rates after chick hatching Columbia River discharge (kcfs) are key factors in determining the reproductive success of Caspian Terns nesting at ESI. Reproductive success declined significantly over the 17-year study period. This demonstrates that Year was acting as a surrogate for other variables that were changing in a gradual, consistent manner during the study period. One possible factor that contributed to changes in the colony over time is the managed reduction in available nesting habitat for Caspian Terns on ESI. At the beginning of the study period (2001), 2.6 ha (6.5 acres) of bare sand habitat were available for Caspian Tern nesting. This area of available habitat was gradually reduced during implementation of the Caspian Tern Management Plan for the Columbia River Estuary, which began in 2008 and culminated in 0.4 ha (1.0 acre) of available bare sand nesting habitat from 2015 to the present. This managed reduction in available nesting habitat was responsible for the decline in colony size (number of breeding pairs) during the latter half of the study period, as well as the increase in density of Caspian Tern nests on the colony.

Less understood, however, is what was driving the gradual delay in Caspian Tern nesting phenology on the ESI colony during the study period, as evidenced by the increase in the day of the year when the first tern chick was observed on-colony. Management cannot be directly linked to this colony-level change during the study period since the delay in phenology began before the first reduction in colony size and continued to fluctuate throughout the latter half of the study period. Thus; thus, I can assume that there were other factors at play besides nesting habitat reduction. One possibility is the timing of lethal gull control on the tern colony during the study period. Over 220 Glaucous-winged/Western Gulls (*Larus glaucescens* x *L. occidentalis*) were lethally removed from the tern colony on ESI in 1999 and 2000 (Roby *et al.* 2002), which may have accounted for, at least in part, the high level of reproductive success during the early part of the study period. Another 50 gulls were lethally removed from the tern colony in 2012, and this likely contributed to increased reproductive success of the tern colony in 2012 and 2013, and perhaps in later years. Although lethal gull control is a common technique for restoration of seabird breeding colonies, gull management is typically conducted continuously, rather than intermittently, because singular efforts at gull control have been shown to have little effect in the long-term (Kress 1983).

Another factor that likely changed gradually during the study period is the number of Bald Eagles (*Haliaeetus leucocephalus*) present on ESI during the tern nesting season, as well as the effect this had on the level of Bald Eagle disturbance to the Caspian Tern colony. Bald Eagle populations have increased significantly since the banning of DDT in 1972 and passage of the U.S. Endangered Species Act in 1973, and Bald Eagle numbers increased 400% in the lower Columbia River by 2007 (Isaacs and Anthony 2011). Horton (2015) found that in Oregon, the north coast had the highest densities of breeding Bald Eagles. At ESI in 2011, the total failure of the Caspian Tern colony on ESI was indirectly caused by repeated disturbances by bald eagles over a period of two weeks (Collar *et al.* 2017).

Unfortunately, in my study I was not able to collect data that provided an unbiased estimate of Bald Eagle disturbance rates or gull predation rates on Caspian Tern nest contents to assess their impact on Caspian Tern reproductive success at the ESI colony. I determined that data that had been collected to quantify gull predation rates on tern nest contents did not provide an unbiased measure of the impact that gulls had on Caspian Tern reproductive success. High rates of gull predation on tern nests occur on the Caspian Tern colony when adult terns are flushed off their nests during disturbances to the tern colony, which are typically caused by Bald Eagles. These eagle disturbance events are short-lived, but the loss of tern nest contents to gull predation during these large flushes were only captured in the rare event that data collection sessions for gull predation rates coincided with eagle disturbance events. Three hours of gull predation rate data were collected each week from two observation blinds, which was not a sufficient sampling period to capture the impact of gull nest predation on Caspian Tern reproductive success. Finally, gull predation rate was not an explanatory variable that accounted for a significant amount of the variation in tern reproductive success in Collar *et al.*'s (2017) study, likely for the same reasons just described. Consequently, I did not include data on gull predation rates in my analyses. Data on Bald Eagle disturbance rates, although a significant explanatory variable in Collar *et al.*'s (2017) analyses of factors affecting tern reproductive success, was not included as an explanatory variable in this study due to concerns about discrepancies in data collection effort and quality among years. Furthermore, these data were sampled in a way that did not fully represent the frequency or intensity of eagle disturbances to the Caspian Tern colony.

The inter-annual variability in river discharge rates (freshwater input to the Columbia River estuary) can significantly affect the reproductive success of the ESI tern colony. This was particularly evident in the total failure to produce any young on the colony in both 2011 and 2017, the years with the highest levels of river discharge during the study period. High rates of river discharge in the estuary was associated with a reduction in the numbers of marine forage fish in the estuary (Weitkamp *et al.* 2012), leading to shortages in food availability to piscivorous predators that consume marine forage fish, such as Caspian Terns. This bottom-up mechanism was found to also influence top-down factors that directly affect tern reproductive success at ESI, in particular the rate of gull kleptoparasitism of Caspian Tern adults during chick-rearing. Changes in the assemblages and abundances of forage fish in the Columbia River estuary apparently also influenced the rate at which gulls targeted Caspian Tern nest contents as a food source.

Years with high river discharge rates are associated with changes in the properties of the water column and circulation in the estuary (Weitkamp *et al.* 2012). These changes in salinity and currents likely limit the entry of marine forage fish into the Columbia River estuary during years of high river discharge. Supporting this hypothesis, Weitkamp *et al.* (2012) reported reduced numbers of marine forage fish, particularly northern anchovy (*Engraulis mordax)* and Pacific herring (*Clupea pallasi*), in surveys conducted in years with high river flows. An increase in river discharge can also result in increased salinity stratification of the water column to a depth of at least 1 meter. This stratification can result in a "freshwater lens," which pushes fish species with lower salinity tolerance, like salmonid smolts, to the top of the water column, while pushing marine forage fish to depths greater than 1 meter. This places marine forage fishes out of reach of avian surface-feeding piscivores in the Columbia River estuary, such as Caspian Terns, Bald Eagles, and various gull species (Weitkamp *et al.* 2012, Collar *et al.* 2017).

The results of my study provided some support for the hypothesis that Caspian Tern reproductive success at ESI is strongly influenced by Columbia River discharge, despite river discharge not appearing in the best model explaining variation in reproductive success (Collar *et al.* 2017). Collar *et al.* (2017) also found a link between high levels of river discharge and an increase in the rate of Bald Eagle disturbances to the Caspian Tern colony at ESI. The high rate of Bald Eagle disturbances in 2011 was considered to be the proximate cause of the colony failure in that season, likely intensified by reductions in availability of marine forage fish in that year (Collar *et al.* 2017). Although eagle disturbance rates were not measured in my study, eagle disturbance is linked to the rate that secondary predators (i.e. gulls) are able to depredate Caspian Tern nests on the ESI colony. The rate of gull kleptoparasitism of adult terns was also an important factor associated with tern reproductive success at the ESI colony in Collar *et al.*'s (2017) study, which supports the results presented here.

Caspian Terns commonly nest in association with species of gulls, and gull predation on Caspian Tern nest contents, as well as kleptoparasitism of fish from terns, have been considered potential limiting factors for multiple Caspian Tern colonies on the Columbia River basin (Collar *et al.* 2017). California Gulls (*L. californicus*) nesting at Crescent Island in the mid-Columbia River were documented to kleptoparasitize nesting Caspian Terns at a high rate in 2001, and likely contributed indirectly to chick mortality (Antolos *et al.* 2005, 2006). It is likely that individual gulls specialize in kleptoparasitizing or depredating nests of Caspian Terns, and because the mixed Caspian Tern and Glaucous-winged/Western Gull colony on ESI has persisted for over 17 years, this longevity allows these specialized behaviors to be passed on to multiple generations of gulls (Collar *et al.* 2017).

An interesting and novel result of my study was that only gull kleptoparasitism rates on adult terns after the first Caspian Tern chick was observed on-colony were a driving factor for Caspian Tern reproductive success. Conversely, gull kleptoparasitism rates before the first tern chick hatched explained very little of the variation in Caspian Tern reproductive success at ESI. This suggests that the cost of kleptoparasitism to breeding Caspian Terns is much more significant during the chick-rearing period than during the incubation period. This is consistent with other research, which has demonstrated a reduction in chick provisioning and increased time between meal deliveries to chicks as a result of high kleptoparasitism rates (Stienen *et al.* 2006, Gaglio *et al.* 2018). In studies by Stienen *et al.* (2006) and Gaglio *et al.* (2018), high kleptoparasitism rates were also associated with reduced reproductive success at tern colonies, likely due to the higher energetic costs of provisioning chicks after losing fish to gulls. This interpretation, however, assumes that kleptoparasitism is the factor directly limiting reproductive success. The importance of gull kleptoparasitism after chick hatching likely represents the years in which predators, such as Bald Eagles and gulls, were more focused on the Caspian Tern colony and directly caused reproductive failure.

My study expanded on previous research and it supports earlier findings that gull kleptoparasitism is a top-down mechanism that is related to Columbia River discharge. The results of my study demonstrate that continuing to monitor annual diet composition, gull kleptoparasitism rates, and Columbia River discharge levels is important for understanding inter-annual variation in the reproductive success of Caspian Terns at ESI. Continuing this research would better inform understanding of the trends and patterns that were observed in my study.

Furthermore, the difference in the effect of gull kleptoparasitism rates during the incubation and chick-rearing periods on tern reproductive success suggests that further research should be conducted to parse out the mechanisms that are driving tern reproductive success on ESI during each phase of the breeding cycle. Finally, more research should be done to identify the factors limiting tern reproductive success that changed gradually during the study period. While the reduction in tern nesting habitat on ESI follows the pattern of gradual decline in reproductive success at the ESI colony that I observed during the study, I was unable to attribute causality of the longitudinal decline in reproductive success to habitat management without exploring other factors that might have gradually changed over the study period as well (e.g., gull nest predation rates, Bald Eagle disturbance rates).

This study also investigated the relative importance of factors that affected individual reproductive success of Caspian Terns at the ESI colony during the 2015 and 2016 breeding seasons. I found that the date when an individual tern initiated its nesting attempt ranked highest in relative importance of the explanatory variables that I studied. Reproductive success of focal birds included in the study was strongly negatively associated with nest initiation date. Nest initiation date was included in each of the competitive models explaining variation in individual reproductive success in my study. Neighborhood nest density was an explanatory variable that was also included in the most competitive model, and was strongly positively associated with reproductive success. I also found that nests located farther from the edge of the ESI colony were more likely to be successful, but this was only the case early on in the breeding season; nest location had no influence on success of nests initiated later in the season. Overall, I found that tern that initiated nests earlier in the season had more time to lay replacement clutches in the event that an early nesting attempt failed. Individuals that initiated their first nesting attempt later in the season were much less likely to succeed, in part because of the lack of re-nesting opportunities.

In 2015 and 2016, the odds of an individual Caspian Tern nesting successfully significantly declined the later it initiated a nest in the breeding season. This result was supported by previous research that found that, for Caspian Terns nesting at Crescent Island in the mid-Columbia River, there was a negative relationship between nesting success and hatch date (Antolos *et al.* 2006). There are many possible explanations for this result from my study, including the 'parental quality' hypothesis, which predicts that younger, less experienced birds tend to nest later in the season (Arnold *et al.* 2004). The relationship between nesting success and nest initiation date could also be explained by the 'timing' hypothesis, which proposes that resources for reproduction decline throughout the breeding season (Arnold *et al.* 2004). The success of re-nesting attempts, however, failed to support the 'timing' hypothesis, because the success of replacement clutches did not decline during the season. Although I was not able to determine whether my results support one of these hypotheses over the other, the results are similar to those of Arnold *et al.* (2004), who suggested that reproductive success in their experimental study could be explained by a combination of these hypotheses. In particular, their study found increases in intraspecific aggression as well as kleptoparasitism as the season progressed, which supports my result in Chapter 2 of a negative relationship between reproductive success and kleptoparasitism rate after chick hatch. The increased kleptoparasitism rate coincides with the chick-rearing period of gulls nesting on ESI, late in the breeding season of Caspian Terns.

Age and Previous Breeding Experience were each included in one of the five competitive models explaining variation among individual terns in reproductive success, yet there was no correlation between either of these two explanatory variables and nest initiation date. I could not definitively support the parental quality hypothesis based on these data, even though the relative success of re-nesting attempts seemed to support the hypothesis. Future research with larger sample sizes of known-age birds may be able to produce clearer results, however. Research that includes more data on the history of reproductive success of individuals in previous years may also better inform how prior nesting experience can affect success in a particular breeding season.

Although my study found that certain demographic and behavioral traits of individuals are important for explaining the variation in reproductive success among Caspian Terns nesting at East Sand Island, the scope of inference for my study is limited to East Sand Island and to the two years when I monitored the nesting success of individual Caspian Terns. Due to the small sample size of terns with alphanumeric bands that nested on East Sand Island in both 2015 and 2016, my study was limited to investigating the factors affecting breeding success of individuals; however, because Caspian Terns exhibit biparental care, the individual quality of each parent adult in a pair likely contributes to the success of a nesting attempt. Future research should investigate how the behavior, characteristics, and quality of both members of breeding pairs are related to Caspian Tern nesting success at East Sand Island, and at other Caspian Tern breeding colonies.

Banding of Caspian Tern chicks at ESI with alphanumeric bands has only been conducted since the 2006 breeding season. Because Caspian Terns exhibit delayed onset of breeding, there were not as many terns nesting at the ESI colony during my study that were banded as chicks as there were terns banded as adults. Thus, I could not determine the exact age or extent of previous breeding experience at ESI of the majority of individual terns in my study.

Continued banding and colony monitoring would make analyses like the ones in my study stronger.

While my study found some surprising results, including the number of re-nesting attempts by individual Caspian Terns during a single breeding season, both the 2015 and 2016 breeding seasons were successful at producing substantial numbers of young terns at the Caspian Tern colony on ESI. It would be informative to continue my study to include breeding seasons when the annual average reproductive success of the ESI Caspian Tern colony was higher and lower than in 2015 and 2016. This would allow us to better understand the factors that drive the reproductive success of individual terns at the ESI colony.

Certain results from each data chapter of this thesis are seemingly contradictory. An increase in the average density of tern nests on the ESI colony over the 17-year study period was associated with a significant decline in reproductive success during that period. At the level of the individual, however, an increase in density of neighboring nests was associated with higher odds of reproductive success. These results seem particularly contradictory because the study years for Chapter 3 (2015 and 2016) coincided with the two years when average nesting density was the highest ever recorded at ESI (1.32 nests/m^2 and 1.36 nest/m^2, respectively). Also, average annual reproductive success for the colony in 2015 and 2016 was relatively high (0.59 young fledged/breeding pair and 0.49 young fledged/breeding pair, respectively) compared to that of the previous five years, and annual reproductive success in 2015 was the highest since 2009. The relationship between Neighborhood Nest Density and Reproductive Success described in Chapter 3 would benefit from additional study in years when annual reproductive success was lower overall, in order to determine whether this relationship still holds. These two results can be reconciled by acknowledging the differences in conditions on the Caspian Tern colony throughout 2001-2017. Density increased throughout this period, while reproductive success declined. Eagle disturbance and gull predation, however, also increased throughout the study period. The increase in predation risk benefits those individuals nesting at higher densities, while earlier in the study period there was likely no benefit to nesting in dense areas. If the study in Chapter 3 had been conducted early in the study period, we may not have found a relationship, or even a negative relationship, between reproductive success and neighborhood nest density.

To understand the factors influencing variation in reproductive success of Caspian Terns at ESI, it is vital to investigate at both the colony-wide and individual-level scales to get the full picture. The Caspian Tern colony at East Sand Island is extremely important to the Pacific Flyway population of Caspian Terns. Suzuki *et al.* (2018) found that maintaining a colony of Caspian Terns at ESI consisting of at least 1,000 breeding pairs is key to the long-term persistence of the species' population in the Pacific Flyway. Conversely, the hypothetical elimination of the tern colony at ESI resulted in a projected long-term decline in the Caspian Tern population in the Flyway. Thus, understanding the drivers of reproductive success at the ESI colony, at both the colony and individual levels, is imperative for maintaining past levels of fledgling success and the long-term resilience of the Pacific Flyway population of Caspian Terns in the face of environmental change.

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