AN ABSTRACT OF THE THESIS OF

Stefanie Collar for the degree of Master of Science in Wildlife Science presented on December 12, 2013.

Title: Site Fidelity and Colony Dynamics of Caspian Terns Nesting at East Sand Island, Columbia River Estuary, Oregon, USA.

Abstract approved:

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Daniel D. Roby

Fidelity to breeding sites in colonial birds is an adaptive trait thought to have evolved to enhance reproductive success by reducing search time for breeding habitat, allowing earlier nest initiation, facilitating mate retention, and reducing uncertainty of predator presence and food availability. Studying a seabird that has evolved relatively low colony fidelity, such as the Caspian tern, allowed me to explore the influence of stable nesting habitat on fidelity and nest site selection. The Caspian tern (*Hydroprogne caspia*) breeding colony on East Sand Island (ESI) in the Columbia River estuary is the largest colony of its kind in the world. This colony has experienced a decade of declining nesting success, culminating with the failure of the colony to produce any young in 2011. The objective of my study was to understand the dynamics of this Caspian tern super-colony by investigating the actions of breeding individuals over two seasons, as well as the behavior of the colony as a whole from 2001-2011. I was interested in (1) the degree of nest site fidelity exhibited by breeding terns in successive years and its relationship to

reproductive success, and (2) how the interaction of top-down and bottom-up forces influenced average nesting success across the entire colony, and caused the observed trends in nesting success at the East Sand Island colony from 2001 to 2011. My study investigated the potential influence of bottom-up and top-down drivers for the declining productivity at this once thriving colony of Caspian terns.

I used sophisticated surveying equipment to test for nest site fidelity and group adherence between two consecutive breeding seasons for 80 Caspian terns marked with field readable leg bands. Available bare sand nesting habitat at this colony site declined by 33% between the two years, displacing some focal individuals from their previously held nest territories. Terns whose former nest site was no longer in suitable habitat had twice the inter-annual distance between nest sites when compared with terns whose former nest site was still in suitable habitat. There was a negative association between inter-annual distance between nests and the number of neighbors retained from the previous year. Displaced terns retained few, if any, neighbors, indicating that group adherence by nesting terns was largely a result of individual philopatry to nesting areas within the colony, rather than adherence to neighboring nesting pairs. There was a tendency for displaced terns to nest in closer proximity to the edge of the colony, and to have nesting attempts that ended earlier compared to non-displaced terns. After all nesting attempts failed during year 2 of the study, terns displaced from year 1 nest sites paradoxically exhibited higher fidelity to the colony site after colony failure in year 2 than terns that retained their year 1 nesting area. Failure of the previous nesting attempt and the

novelty of the nest site and its neighbors, factors that should have resulted in low philopatry, were apparently out-weighed by the scarcity of suitable alternative nesting habitat for Caspian terns within the region.

I also investigated the potential influence of bottom-up and top-down drivers for the declining productivity at this once thriving colony of Caspian terns. Since 2001 the decline in reproductive success of Caspian terns at ESI has been associated with a significant increase in average river discharge during May and June. I also found a significant increase in kleptoparasitism rates of terns by glaucous-winged/western gulls (*Larus glaucescens* x *L. occidentalis*) since 2001, and a significant negative relationship between average annual rates of gull kleptoparasitism and Caspian tern nesting success at ESI. There was also a significant increase in disturbance rates by bald eagles (*Haliaeetus leucocephalus*) during June for terns nesting at the ESI colony, and eagle disturbance rates were positively associated with May river discharge. The abundance of forage fish for terns in the estuary was inversely related to river discharge, which also apparently influenced the reliance of tern nest predators on the tern colony as a food source, resulting in increased disturbance to and decreased reproductive success at the tern colony. Although correlational, our results support the hypothesis that the decline in Caspian tern nesting success at this large estuarine colony was primarily driven by bottom-up factors, both as they directly affect tern productivity through the food supply, and indirectly as they affect the alternative food supply of potential predators of Caspian tern nest contents.

Site Fidelity and Colony Dynamics of Caspian Terns Nesting at East Sand Island,
Columbia River Estuary, Oregon, USA

by
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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.

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Stefanie Collar, Author

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CHAPTER 1. GENERAL INTRODUCTION

Stefanie Collar

Caspian terns (*Hydroprogne caspia*) are a nearly cosmopolitan species and the largest member of the tern subfamily (*Sterninae*). The Caspian tern is a relative newcomer to the Pacific coast of North America as a breeding species, displaced from colony sites in the western interior U.S. by dwindling suitable habitat and anthropogenic change (Cuthbert and Wires 1999). In the years since the species first colonized coastal habitats, Caspian terns have encountered increasing constraints on the availability of suitable habitat in which to nest (Collis et al. 2002). The Caspian tern is a facultative colonial nester, preferring sandy, unvegetated, predator-free islands for breeding. Typically, the colonies of Caspian terns range in size from several nests to several hundred (Cuthbert and Wires 1999). Currently, the largest known Caspian tern colony in the world, at more than 7,000 breeding pairs, is located at East Sand Island, which is in the Oregon portion of the Columbia River estuary, eight kilometers upstream of the mouth of the river.

East Sand Island (ESI) is a semi-natural island where dredged material has been deposited on the eastern tip of the island, most recently in 1983. The Caspian tern colony on ESI is located on this dredged material disposal site. ESI has been the site of a perennial Caspian tern colony since 1999. Prior to 1999, Caspian terns nested or attempted to nest on ESI during 1984-1986, immediately after the dredged material was deposited on the island. No records exist of Caspian terns nesting on ESI, or anywhere else in the Columbia River estuary, prior to 1984. The breeding colony that formed on ESI in 1999 has persisted since then because of regular management of nesting habitat for Caspian terns by the U.S. Army Corps of

Engineers (USACE), which owns the island. ESI has supported as many as ~ 10,000 breeding pairs of Caspian terns in a season, which represents about 70% of all the breeding pairs in the Pacific Coast population of the species (Suryan et al. 2004, Lyons 2010).

The breeding colony of Caspian terns on ESI was relocated from Rice Island, a 100-ha dredge spoil island located at river km 34 (Simenstad et al. 1990), during 1999-2001 as an initial management action to reduce the numbers of juvenile salmonids consumed annually by Caspian terns nesting in the Columbia River estuary. Shifting the colony from Rice Island to East Sand Island was considered successful both because of the reduction in salmonid predation - the proportion of juvenile salmonids in the diet declined from 74% in 1998 to 33% in 2001 - and the high reproductive success recorded at the colony immediately following its relocation (Collis et al. 2002, Roby et al. 2002). Although the East Sand Island colony has remained roughly the same size since 2001, productivity rates have gradually waned, with a precipitous drop in nesting success during the 2010 and 2011 breeding seasons.

In accordance with the Final Environmental Impact Statement prepared by the USACE and the U.S. Fish and Wildlife Service (USFWS) in 2005, the number of Caspian tern breeding pairs on ESI is to be reduced to approximately a third of the prior number in order to further reduce predation rates on juvenile salmonids in the Columbia River estuary. The number of breeding Caspian terns at ESI would be limited through a 70% - 80% reduction in available nesting habitat. Once the habitat

reduction action has been completed, the area of nesting habitat will have been reduced from 2 ha (5 acres) to 0.4 - 0.6 ha (1 – 1.5 acres). This would be accomplished through a 'push-pull' management approach. Non-destructive management of the ESI colony would include the erection of dissuasion fences on part of the ESI colony site, physically limiting the area available for tern nesting. Concurrent with the reduction in nesting habitat on ESI, alternative nesting habitat would be built elsewhere in the historical breeding range of the Caspian tern in western North America. The USACE has, to date, built nine islands as alternative Caspian tern nesting habitat, either in interior Oregon or northeastern California. All but one of these islands was colonized by nesting Caspian terns during the first breeding season after construction was completed, with varying degrees of subsequent reproductive success on each island.

East Sand Island is unique in that it has been managed to be consistently available and suitable for nesting by Caspian terns for 15 years. Caspian terns can be considered a 'fugitive species' whose nesting behavior has evolved in environments where suitable breeding habitat is often ephemeral and predators are quick to target persistent colonies, requiring individuals to readily move from one island colony site to another (Cuthbert 1985). Artificial persistent habitat may select for breeding adults that are closely associated with specific areas of a colony and exhibit an uncharacteristic degree of site fidelity (McNicholl 1975). Suzuki (2012) found unexpectedly high natal colony and breeding colony fidelity to ESI by Caspian terns, but it is unclear whether this is mostly a consequence of the persistence of nesting

habitat at this colony site or the lack of suitable alternative colony sites. The appearance of Caspian tern colonies on rooftops and parking lots in the industrial areas of major port cities has become an increasingly common occurrence since 2009 (S.C. pers. obs.), as less 'natural' nesting habitat has become available. Although alternative nesting habitat has been created for Caspian terns in parts of interior Oregon and north-eastern California, these islands are often not predator free, and may not always have a reliable prey base, which are necessary for colony success and fidelity to newly established nesting habitat (Collis et al. 2002).

The Caspian tern colony on ESI is located near the mouth of the Columbia River, where the prey base is both abundant and diverse. The Columbia River estuary is a veritable smorgasbord for piscivorous predators, but as humans figure prominently in the predator assemblage, avian predators can be perceived as competitors for a limited and valuable natural resource. The hydro-power system on the Columbia River, consisting of multiple dams and their slackwater impoundments on the mainstem Columbia and Snake Rivers, constitutes a major obstacle for anadromous salmonids. Dams have a direct impact on out-migrating salmonid smolts through their effects on fish condition, but also through their regulation of river discharge. Hydrosystem-limited river discharge during the historical spring freshet increases the time and energy costs of smolt out-migration, thereby increasing their susceptibility to avian predation.

High river discharge, on the other hand, influences prey availability for piscivores by both decreasing residence time of salmonid smolts out-migrating from

the estuary and inhibiting marine fish from entering the predominately freshwater estuary (Weitkamp et al. 2012). Weitkamp et al. (2012) also found that high flows lead to stratification of estuary waters, creating a predominately freshwater lens on the surface and effectively changing the assemblage of forage fish available for terns. Productivity of nesting Caspian terns is, in turn, affected by availability of forage fish. Many seabird studies investigating reproductive output in relation to prey availability have found correlations between low food availability and poor breeding success (Roberts 1993, Harris 1997, Hall 2004, Bertram 2009, Szostek 2012). Food shortages are felt throughout the estuary ecosystem, including apex predators, causing a cascade of changes in trophic interactions.

Caspian tern nests on East Sand Island are subject to predation pressure from a host of avian predators, including common ravens (*Corvus corax*), American crows (*Corvus brachyrhynchos*), bald eagles (*Haliaeetus leucocephalus*), and brown pelicans (*Pelecanus occidentalis*). East Sand Island is also home to breeding colonies for two taxa of gulls, western/glaucous-winged gulls (*Larus occidentalis* X *L. glaucescens*) and ring-billed gulls (*L. delawarensis*), both of which target nesting terns as a food source to differing degrees. Bald eagle populations have been artificially low for decades because of human persecution, and the impact of persistent and toxic organochlorine pesticides in the environment and in their prey (Watson et al. 2002, Vennesland and Butler 2004, White et al. 2006). In the decades since the ban of DDT in 1972, a dramatic recovery of eagle populations in the Pacific Northwest has occurred. The return of this top predator has been associated

with acute declines in seabird nesting success at some colonies (Isaacs and Anthony 2011, Hipfner et al. 2012).

Bald eagles are able to exploit a variety of prey using diverse foraging techniques, and their diet includes piscine, avian, and mammalian prey. The relative proportions of these prey types in the diet varies depending on the eagle's age, territory habitat, and time of year (Watson et al. 1991). Aside from direct predation on seabirds at their breeding colonies, eagles can have indirect negative effects on seabird nesting success by causing disturbances that allow smaller nest predators, such as gulls and corvids, to prey upon nest contents (Verbeek 1982, Parrish et al. 2001, Vennesland and Butler 2004, White et al. 2006). It is not through the loss of depredated breeding adults, but through the disturbance and subsequent loss of nest contents, that eagles have their greatest impact on seabird colonies (Verbeek 1982, Parrish et al. 2001, Vennesland and Butler 2004, White et al. 2006).

Although colonialism may be an adaptation to improve reproductive success - offering social stimulus, protection from predators, and breeding information - well-established, persistent colonies can have drawbacks, such as overcrowding, resource depletion, increased conspicuousness and disease transmission (Southern and Southern 1979, Tims et al. 2004, Votier et al. 2009, Descamps et al. 2011). If birds are inclined to remain at familiar colonies despite these conditions, their reproductive success and overall fitness may decline as well. At the level of the colony, site fidelity may reduce search time for appropriate breeding habitat and allow for earlier initiation of egg-laying and incubation (Cuthbert 1988). At the level

of the nest site, site fidelity may help facilitate mate retention (Fairweather and

Coulson 1995) and, at large colonies, pair bonds might be more quickly reestablished

if both members of the pair are faithful to a nest site within the colony area. Caspian

terns are generally thought of as a species with low site fidelity because of the

ephemeral nature of their preferred nesting habitat (Cuthbert 1988).

There are few data, however, on the degree of nest site fidelity for ground-

nesting colonial seabirds because it is difficult to obtain these data without causing a

major disturbance to the colony. This has led to a great deal of variation in the

literature as to what is considered a 'high' degree of site fidelity, and a standard

measure of nest site fidelity is lacking for seabirds. Feare and Lesperance (2002)

considered sooty terns (*Onychoprion fuscatus*) nesting within 25 m of the previous

year's nest to be highly site faithful. Several species of gulls (*Larus* spp.) and

common terns (*Sterna hirundo*) are considered to have high site fidelity because they

often return to previously used sub-colonies, sometimes to within 6 meters of

previous nests (Blokpoel and Courtney 1980). Kittiwakes (*Rissa tridactyla*) are a

commonly cited example of a colonial seabird species with high nest site fidelity;

those individuals nesting on ledges on cliffs or buildings have discrete and readily

distinguishable sites for nest building that can be re-used perennially (Coulson

1995).

Nest site requirements can influence the level of nest site fidelity. For

example, kittiwakes nesting on persistent structures such as ledges on rock cliffs or

window ledges on buildings, exhibit strong fidelity to specific nest sites, which has

been shown to enhance reproductive success and mate retention (Fairweather and Coulson 1995, Boulinier et al. 2008). Species that use ephemeral colony sites (e.g., many Larid species) are conventionally believed to have low nest site fidelity out of necessity. Larids may vary widely, however, in their response to changes in colony availability and stability (McNicholl 1975, Southern and Southern 1982, Cuthbert 1988).

Factors influencing an individual's decision to return to or frequent a breeding site include: age (Southern and Southern 1982), natal philopatry, prey availability (Eppley et al. 1986), success of previous reproductive attempts (Cuthbert and Wires 1999), site stability (McNicholl 1975), the outcome of neighboring nest attempts (Boulinier et al. 2008), and group adherence (McNicholl 1975). Group adherence is the tendency of colonial nesting birds to establish nest sites within "familiar social surroundings" that are not limited to a familiar geographic location. This may benefit individuals that are displaced from former breeding territories by lowering the level of novelty encountered at a newly established breeding territory. Several species of terns have been documented to have familiar and persistent neighborhood groups within nesting colonies, some that persist even as old colonies are abandoned and new colonies are formed (Feare and Lesperance 2002).

Understanding the aforementioned behavioral traits is essential when creating and executing successful conservation plans for colonial seabirds. Many seabird species are the focus of translocation and restoration projects in which it is imperative to incorporate a species' natural inclinations, such as by using social

attraction to draw in colonial nesting species, techniques that target non-breeding and prospecting birds that may be more willing to recruit to non-natal colonies, or displacing a group of nesting conspecifics altogether who are likely to move collectively to a new colony. In this thesis I hope to increase the understanding of the social interactions that occur during the breeding season and how these influence an individual's choices and selection of breeding sites. Chapter 2 examines the inter-annual site fidelity exhibited by individual Caspian terns at the ESI colony, at both the nest and colony level. Chapter 3 looks at the interactions of top-down and bottom-up factors that may limit nesting success at the Caspian tern colony on ESI, and how these factors have influenced reproductive output at this colony over the last decade. The results of this study will advance our understanding of individual behaviors in the context of large breeding colonies. This study also informs our understanding of the interactions between top-down and bottom-up controls on food-web linkages within estuary ecosystems.

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CHAPTER 2. NEST SITE FIDELITY AND GROUP ADHERENCE AT THE

WORLD'S LARGEST CASPIAN TERN (*HYDROPROGNE CASPIA*) COLONY

Stefanie Collar, Daniel D. Roby, and Donald E. Lyons

ABSTRACT

Fidelity to breeding sites in colonial birds is an adaptive trait thought to have evolved to enhance reproductive success by reducing search time for breeding habitat, allowing earlier nest initiation, facilitating mate retention, and reducing uncertainty of predator presence and food availability. Colonial nesting can have drawbacks, however, such as overcrowding, resource depletion, attraction of predators, and enhanced disease transmission. I studied a facultative colonial nester, the Caspian tern (*Hydroprogne caspia*), to explore the benefits and drawbacks of colonial nesting. I used sophisticated survey equipment to study nest site fidelity and group adherence between two consecutive breeding seasons for 80 Caspian terns marked with field readable leg bands at a large breeding colony. Available bare sand nesting habitat at this colony site declined steeply between the two years, displacing some focal individuals from their previously held nest territories. Terns whose former nest site was no longer in suitable habitat had twice the inter-annual distance between nests when compared with terns whose former nest site was still in suitable habitat. There was a negative association between inter-annual distance between nests and the number of neighbors retained from the previous year. Displaced terns retained few, if any, neighbors, indicating that group adherence by nesting terns was largely a result of individual philopatry to nesting areas within the colony, rather than adherence to neighboring nesting pairs. After all nesting attempts failed during year 2 of the study, terns displaced from year 1 nest sites paradoxically exhibited higher immediate tenacity to the colony site than terns that retained their year 1

nesting area. Failure of the previous nesting attempt and the novelty of the nest site and its neighbors, factors that should have resulted in low philopatry, were out-weighed by the scarcity of suitable alternative nesting habitat for Caspian terns within the region.

INTRODUCTION

Colony site fidelity, the proclivity to return to natal or previously-used colonies to breed, has been demonstrated in many species of colonial waterbirds (Southern 1977, Southern and Southern 1979, Fairweather et al. 1995, Tims et al. 2004). This trait can range from the general, such as returning to nest within a chain of islands or on the same water body (Cuthbert 1985, Tims et al. 2004), to the specific, such as returning to the same nest cup (Southern and Southern 1982, Stenhouse et al. 2005). Site fidelity is thought to be an adaptive trait that evolved to enhance reproductive success. At the colony level, it may reduce search time for appropriate nesting habitat and promote earlier nest initiation and onset of incubation (Cuthbert 1988). At the level of the nest site, site fidelity may help facilitate mate retention (Fairweather and Coulson 1995) and, at larger breeding colonies, pair bonds might be more quickly re-established if both members of the pair returned to the same nest site within the colony.

Factors potentially influencing an individual's decision to return to or frequent a particular nest site include age (Southern and Southern 1982), natal philopatry, prey availability (Eppley et al. 1986), outcome of previous reproductive

attempts (Cuthbert and Wires 1999), site stability (McNicholl 1975), reproductive success at neighboring nests (Boulinier 2008), and group adherence (McNicholl 1975). Group adherence is the tendency of colonial nesting birds to establish sites within familiar social surroundings, not just fidelity to a specific geographic location. This may benefit individuals that are displaced from previous nest sites by lowering the novelty encountered at newly colonized or re-colonized sites.

Adult colonial breeders frequently return to nest at colonies where they have previously experienced nesting success. For many species, however, young individuals may not return to their natal colony to breed for the first time. Potential reasons for this lack of natal philopatry include (1) the inability to establish and defend a nest territory at a crowded colony (Haymes and Blokpoel 1978, Stenhouse et al. 2005), (2) the discovery as a sub-adult of an alternative colony site with higher prospects for successful breeding (Southern 1977), or (3) recruitment to a newly forming colony (Tims et al. 2004).

The tendency toward nest site fidelity is related to nest site requirements and the availability of sites that meet those requirements. For example, black-legged kittiwakes (*Rissa tridactyla*) nesting on persistent structures, such as ledges on rock cliffs or window ledges on shoreside buildings, demonstrate strong fidelity to specific nest sites, which has been shown to enhance reproductive success and mate retention (Fairweather and Coulson 1995, Boulinier et al. 2008). Species that use ephemeral colony sites (e.g., many species of Laridae) are expected to exhibit lower nest site fidelity out of necessity; however, individual responses to change in colony

site availability and stability may vary widely (McNicholl 1975, Southern and Southern 1982, Cuthbert 1988).

The breeding colony of Caspian terns (*Hydroprogne caspia*) on East Sand Island (ESI) near the mouth of the Columbia River is currently the largest in the world for the species (Cuthbert and Wires 1999), and has supported approximately 65% of the entire Pacific Coast breeding population since the year 2000 (Suryan et al. 2004, Lyons 2010). Caspian terns are facultative colonial nesters, usually breeding in small colonies containing several dozen to several hundred breeding pairs, but sometimes are found nesting as solitary pairs or in very small groups (Cuthbert and Wires 1999). Although colonial breeding is accepted as an adaptation to improve reproductive success - offering security from predators, social facilitation, and breeding information - well-established colonies can also have drawbacks, such as overcrowding, resource depletion, attraction of nest predators, and enhanced disease transmission (Southern and Southern 1979, Tims et al. 2004, Votier 2009, Descamps 2011). Why, then, would individuals choose to remain faithful to a breeding colony when not obligated to? Species that have not evolved strong may help provide insight into the evolution of colony fidelity because they are capable of displaying a broad range of responses to changes in the availability and quality of nesting habitat. A management plan designed to reduce the availability of nesting habitat at the Caspian tern colony on ESI presented an opportunity to study nest site and colony site fidelity in a facultatively colonial species at an exceptionally large and persistent breeding colony.

Seabird colonies are often quite large and found on isolated islands and sea-stacks, allowing these colonies to persist for decades or longer. Caspian terns are nearly a cosmopolitan species, occurring on all continents except Antarctica, that takes advantage of a wide range of potential nesting habitat; but the preferred breeding habitat is loose sand with little vegetation on islands free of mammalian predators. The ephemeral nature of this preferred habitat means that Caspian tern colonies often relocate between, or even within, nesting seasons (Cuthbert 1985). Caspian terns display natal philopatry, but they sometimes choose to breed at novel colonies that were visited in years prior to the breeding attempt. If persistent, predator-free nesting habitat is available, however, site fidelity might be selected for and could, over time, become more prevalent in a population (McNicholl 1975). If the tendency toward shift among nesting colony philopatry is selected for in the case of Caspian terns nesting at ESI, then individuals may react to the sudden loss of nesting habitat at the colony with behavior that is either consistent with the species' tendency to move frequently amongst ephemeral colony sites, or behavior more typical of colonial species that use persistent colony sites.

Understanding a species' response to changes in the quality and availability of nesting habitat is essential for conservation, restoration, and management. Conservation of a number of coastal colonial seabird species is largely dependent on restoring or creating suitable nesting habitat along densely-settled coastlines that are subject to intensive anthropogenic habitat change. The ESI colony of Caspian terns includes breeding adults with a wide range of ages, breeding experience, and history

of breeding success that fledged from various natal colonies throughout western North America. Observing individual and colony-wide responses to changing habitat conditions allowed us to make inferences about the benefits and drawbacks of colony philopatry, site fidelity, and group adherence. At my study site, the planned, gradual reduction of suitable nesting habitat allowed for the comparison of behavior between Caspian terns facing loss of their nest site due to habitat change, and those whose nest sites were located in persistent nesting habitat.

The objective of this study was to investigate the extent of nest site fidelity among Caspian terns nesting at the colony on East Sand Island in the Columbia River estuary, a colony of unprecedented size (ca. 9,500 breeding pairs) for this facultatively colonial species. If Caspian terns demonstrated nest site fidelity within a colony of this size, I wanted to understand the relationship between nest site fidelity and reproductive success. I was also interested in whether breeding pairs that experienced the loss of their nest site due to habitat change would exhibit group adherence and attempt to nest among former neighboring nesting pairs. I predicted that Caspian terns would exhibit nest site fidelity when their nest site remained in suitable nesting habitat, and that nest site fidelity would be associated with higher reproductive success. I also predicted that Caspian terns whose nest site was lost due to habitat change would have lower nesting success due to the costs of establishing a new nest territory. Finally, I predicted that nest site fidelity would be dictated by previous reproductive success, and the success of neighboring breeding pairs. Many colonial waterbirds form cohesive nesting groups in successive years, and I predicted

that this group cohesion would be detectable amongst Caspian terns nesting at East

Sand Island, and exhibited most strongly by groups of displaced terns forced to

relocate to new areas of the breeding colony.

METHODS

Study Area

East Sand Island (ESI) (46°15'45"N, 123°57'45"W) is in the Columbia River

estuary near the mouth of the Columbia River (river kilometer 8), and has been the

site of a perennial Caspian tern breeding colony since 1999. This colony was

intentionally restored by providing nesting habitat, deploying social attraction

(decoys and audio playback of vocalizations), and controlling predatory gulls on-

colony. Annual maintenance of early seral stage habitat at the colony site has

ensured that suitable nesting habitat for Caspian terns persisted on ESI. ESI is owned

and managed by the U.S. Army Corps of Engineers (USACE), which manages the

habitat on a small portion of the island as suitable habitat for nesting Caspian terns.

In accordance with the Final Environmental Impact Statement and Records of

Decision prepared by the USACE and the U.S. Fish and Wildlife Service (USFWS)

in 2005 and 2006, management reduced the number of breeding pairs of Caspian

terns nesting on ESI to approximately one third of peak colony size (ca. 10,000

breeding pairs) in order to reduce predation on juvenile salmonids listed as

threatened or endangered under the U.S. Endangered Species Act (ESA) (USFWS

2005).

Focal Individual Observations

As Caspian terns initiated courtship displays on the ESI breeding colony in 2010, I identified individual breeding adults that were previously marked with colored, field-readable alpha-numeric leg bands and mapped their nest locations using a Leica TPS 1200+ rangefinder (n = 193 marked individuals). Observations were made with the aid of binoculars and spotting scopes from three different observation blinds located at the edge of the colony. Leg band number, nest location, and nest initiation date (when the first egg in the clutch was laid) were recorded for any breeding pair of Caspian terns that included at least one banded individual (i.e., a focal nest). Each focal nest was checked at least once every three days throughout the breeding season. I collected data on initial lay date, clutch size, initial hatch date, and number of chicks surviving to at least 20 days post-hatch for each focal nest. Chicks were assumed to have fledged if they survived until 20 days post-hatch; increased chick mobility and abandonment of the nest site makes identification of individual chicks problematic after 20 days (Antolos et al. 2006). In 2011, the nests of 80 of the 193 banded individuals whose nest sites were mapped in 2010 were located, mapped, and monitored on the ESI colony using the aforementioned protocol.

Banding

Terns were individually marked with two colored, rolled plastic leg bands (indicating year and location banded) and a numbered metal USGS leg band on the

right leg; a field-readable plastic leg band, engraved with a unique alpha-numeric code, was placed on the left leg. A total of 485 adult Caspian terns and 2,656 fledglings were marked on ESI with alpha-numeric bands between 2005 and 2009, and an additional 181 adult terns were marked with alpha-numeric bands in 2010 for this study. Pre-fledging, Caspian tern chicks were rounded up on the colony and banded. Adult Caspian terns were captured on the ESI colony for banding during late incubation in 2010 using monofilament noose-mats placed around nests containing eggs. In 2010, the first year of this study, I mapped the location of nests of focal individuals before and after capture and banding. Marking terns with field-readable leg bands provided a unique identifier for each individual bird, which could then be recognized and identified on the colony from the observation blinds. Of the 80 focal marked breeders included in this analysis, two had mates that were also banded; only one member of each of these pairs was monitored as a focal individual.

After the banding effort I located as many of the newly banded individuals as possible, and added those with active nests to the sample of focal nests with adults that had been banded in prior years. Hatch date was used to back-calculate laying date for focal nests added to the sample after the onset of incubation using an average incubation period of 26 days (Cuthbert 1999). No banding of adult terns occurred on the ESI colony during the 2011 breeding season.

Reduction in Tern Nesting Habitat

The number of breeding Caspian terns using the colony at ESI was reduced through a reduction in available nesting habitat to less than one third of the former area. The tern nesting habitat eliminated from ESI was replaced by artificial islands constructed by the USACE within the historical breeding range of Caspian terns in western North America. Once the planned habitat reduction on ESI was completed, the area of suitable nesting habitat was reduced from 2 ha (5 acres) to 0.4 - 0.6 ha (1 – 1.5 acres).   The proximate goal of restricting the available habitat for tern nesting was to require displaced individuals to relocate to one of the constructed alternative colony sites. The ultimate goal of this colony redistribution was to both reduce avian predation on ESA-listed juvenile salmonids and to limit the effects of any catastrophic event at the ESI colony on the population of Caspian terns in western North America.

Caspian terns prefer to nest in open, sandy areas with good visibility and will avoid nesting where there is not a clear view to the horizon (DDR, pers. obs.). As such, they can be dissuaded from nesting at specific sites using visual barriers. This technique was used successfully to re-locate the breeding colony of Caspian terns from a dredged material disposal island in the upper Columbia River estuary, upriver of ESI, to the current breeding colony site on ESI (Roby et al. 2002). In accordance with the Final Environmental Impact Statement prepared by the USACE and the USFWS in 2005, visual barriers to deter tern nesting were erected on the ESI breeding colony prior to the tern breeding season in 2011, eliminating 0.4 ha (1 acre)

of formerly-available, suitable nesting habitat along the south, west, and east edges

of the colony, habitat that had been available in 2010. Fences of landscape fabric

were erected in parallel rows at 5-m intervals, using metal t-posts and fencing wire,

to preclude Caspian terns from nesting in areas of bare sand substrate outside the 0.8-

ha area of designated nesting habitat. To further ensure that terns did not nest

between rows of landscape fabric, nylon rope was strung between rows from the t-

posts and 1-m lengths of caution tape were attached to the rope at 1.5-m intervals.

Areas of the colony where nesting dissuasion had been erected could be seen clearly

from the observation blinds and were monitored closely for use by nest predators and

to ensure that no terns nested between rows of landscape fabric.

Nest Coordinate Mapping

Following Antolos et al. (2006), GPS coordinates (latitude/longitude) were

assigned to each focal nest using a Leica TPS1200+ total station. The total station

was used to measure the distance and direction to each focal nest from a known point

in each observation blind. The rangefinder emits a narrow (8 mm x 20 mm at 50 m)

red laser beam that bounces off the target and uses the signal relay time to calculate

distance. The Leica TPS1200+ can be used on non-reflective targets and corrects for

elevation differences between the instrument and the target. The total station also

emits a visible red laser beam so that targets can be verified and is accurate to $\pm$ 2

mm with non-reflective targets. Inter-annual distance between the nest scrape of

each focal individual was determined using the Pythagorean Theorem and the nest

site coordinates for each focal pair in each breeding season.

The nest site locations recorded with the Leica TPS1200+ total station were

post-processed using Leica Geo Office software, allowing nest site coordinates (x, y)

to be managed in ArcGIS10 and overlaid on geo-referenced aerial photography of

the ESI tern colony for both study years (Figure 1). Detailed methodology for aerial

photography of the tern colony is described by Collis et al. (2002). For analysis

purposes, focal individuals were assigned one of two groups after field data

collection was concluded. Focal individuals whose nest site in 2010 was eliminated

due to the reduction in area of nesting habitat in 2011 were considered

"DISPLACED". Focal individuals whose nest site in 2010 was available in 2011

were considered "NON-DISPLACED". The resulting ArcGIS maps provided a

spatial representation of reproductive parameters for known focal individuals over

two breeding seasons, and were used to determine inter-annual site fidelity, neighbor

identity and retention, and proximity to colony edge. Distances between nest sites of

focal individuals in the two study years were compared between these two groups to

test for an effect of displacement on the distance between nest sites of focal

individuals in the two years. Distance of a nest site from the edge of the colony was

measured using ArcGIS10 to define the colony edge in each study year. Nests of

focal individuals that were within 10 m of the colony edge were considered edge

nests. All nest sites of focal individuals within the 10-m wide colony edge were

recorded for each year and compared between years.

Behavior of Breeding Adults After Nest Failure

A number of nests of focal individuals that were monitored in each year of the study failed before young from the nests were 20 days post-hatch, the criterion for nest success. The presence of banded adult terns on the ESI colony was monitored regardless of the fate of a banded individual's nesting attempt; detailed records were kept of ESI colony attendance for all focal individuals, as well as observations of focal birds found at other breeding colonies or roosting sites along the Pacific coast or at inland colonies. These observations were used to establish two distinct categories of behavioral response by focal birds whose nesting attempts at the ESI colony failed in 2011: (1) continue to attend the ESI colony ("STAY"), (2) intermittently visit the ESI colony or abandon the ESI colony entirely for the remainder of the nesting season ("LEAVE").

Group Adherence to Nesting Areas

To determine the number and identity of neighbors retained over the two study years, ArcGIS10 was used to describe buffers of 10 m around each nest of a focal individual, referred to as the 'nest neighborhood'. The identity of focal individuals that were nesting within these buffers was recorded for each focal individual in each year and then compared. The same technique was applied to six simulations of 80 randomly generated x, y coordinates within the 2011 colony area, simulating randomly placed nest sites within the nesting habitat available during

2011. The random points were generated using ArcGIS, and the nesting density for each year was incorporated into the random points generator. The results for the observed and the six simulated 'nest neighborhoods' were compared in order to test whether groupings were random or, alternatively, supported the hypothesis of group cohesion within the larger colony.

Statistical Analyses

Unequal variance in the inter-annual distance between nesting locations for each group (DISPLACED or NON-DISPLACED) was determined using Levene's test for equal variance. The data were log-transformed to correct for unequal variances, and all other tests were performed on log-transformed data. Reported confidence intervals for log-transformed data are back-transformed. The log-transformed data on inter-annual nest distance met assumptions of normality, and the difference between the medians of each group was tested using the exact Mann-Whitney U test. I used Welch's 2-sample t-tests to explore the relationships between inter-annual distance between nest sites of a focal individual (m) and the explanatory variables of group, nest initiation date, nest completion date (the date when the young reached fledging age or the nest failed), duration of nesting attempt (days) and fledging success (number of young fledged/nest of focal individuals in 2010). I used Wilcoxon Signed Rank tests and Spearman's rank correlation tests for paired variables (e.g., nest initiation date in 2010 and nest initiation date in 2011). Because of small sample sizes, I used Fisher's exact probability tests to explore relationships

between groups, fledging success, behavioral response post-nest failure, nest duration, and number of banded neighbors retained.

I used logistic regression to assess the effects of group, distance from colony edge, inter-annual distance moved, duration of nesting attempt, and nest failure date on the discrete response variable "behavioral response to nest failure" (STAY or LEAVE). The STAY response group included individuals that regularly attended the colony following the total-colony failure, while LEAVE consisted of individuals that, post-colony failure, visited the colony infrequently or not at all. Models were created for all possible permutations of the chosen explanatory variables, and then compared using AICc score. Model averaging was performed for all models within 2 AICc points of the best fit model. All statistical analyses were conducted using program R, packages *Mass*, *Hmisc*, *lawstat*, *exactRankTests*, *visreg* and *bbmle* (R Development Core Team 2011).

RESULTS

Nesting Success

The Caspian tern colony on ESI experienced low fledging success in the first year of the study, 2010, with an average of only 0.07 fledglings raised per breeding pair, an order of magnitude less than the average of about 0.76 fledglings per pair during 2000-2009. In 2010, 18% of focal individuals successfully fledged at least one chick (n = 14), while the nesting attempts of the other focal individuals (n = 66) were not successful. In 2011 the entire ESI Caspian tern colony failed to produce

any fledglings. Fledging success in 2010 was not a good predictor of the behavioral response of STAY vs. LEAVE after nest failure in 2011 (p = 0.77).

Nest Initiation Date and Nest Duration

There was no correlation between date of nest initiation in 2010 and date of nest initiation in 2011 (R^2 = 0.02, p = 0.27, Spearman's rank correlation, p = 0.38). Although more DISPLACED individuals (n = 12) initiated nests late in the nesting period (nest initiation between 13 May to 24 May 2011) than did NON-DISPLACED individuals (n = 7), there was no significant difference in year 2 initiation date between the two groups (p = 0.18, 95% CI: -4.94 - 0.95). There was also no difference in year 2 nest initiation date between the two response groups (STAY vs. LEAVE; p = 0.96).

In year 2 of this study, there was a lag of approximately two weeks between the time when the majority of terns arrived at the colony and nest initiation. Additionally, nest failures in year 2 occurred mostly during a few days when disturbances to the colony by bald eagles (*Haliaeetus leucocephalus*) were particularly intense. For this reason I used nest duration, the number of days a nest was considered 'active', as an index to each focal individual's reproductive investment in year 2. There was a significant difference in the duration of the nesting attempt between the two groups (p = 0.04, 95% CI: -7.59 - -0.11); the median duration of the nesting attempt was 15.7 days for DISPLACED individuals (n = 29) and 19.5 days for NON-DISPLACED individuals (n = 51). A significant negative

relationship also existed for inter-annual distance between nest sites nest duration

(days) (R^2 = 0.1213, p < 0.001; Figure 2). Although the mean nest duration was

slightly longer for focal birds that exhibited the STAY response (19.0 days)

compared to those exhibiting the LEAVE response (17.2 days), the difference was

not significant (p = 0.31).

Nest duration was significantly different depending on how far from the

colony edge a nest was located. Nests within 5 m of the colony edge lasted

significantly fewer days (mean duration = 12.4 days) than nests located between 5 m

and 10 m from the colony edge (mean duration = 21.4 days; p = 0.01, 95% CI: -

15.74 - -2.34). There were suggestive differences in nest duration between

individuals nesting within 5 m of the colony edge and nests located more than 10 m

from the colony edge (mean duration = 17.9 days; p = 0.08, 95% CI: -11.92 - 0.81),

and also between nests 5 - 10 m from the colony edge and nests located more than 10

m from the colony edge (p = 0.08, 95% CI: -0.50 - 7.47).

Distance from Colony Edge

In 2010, nine focal individuals from the DISPLACED group (31% of

DISPLACED individuals) and nine focal individuals from the NON-DISPLACED

group (18% of the NON-DISPLACED individuals) nested within 10 m of the colony

edge. In 2011, 15 focal individuals from the DISPLACED group (52%) and 10 focal

individuals from the NON-DISPLACED group (20%) nested within 10 m of the

edge of the colony. In 2010 there was no statistical difference between the two

groups in proportion of nests located within 10 m of the colony edge (p = 0.18);

however, there was a statistical difference in 2011 (p = 0.005), such that a greater

proportion of individuals in the DISPLACED group nested at the edge of the colony

compared to individuals in the NON-DISPLACED group. This suggests that

breeding individuals that lost their nest site in year 2 of the study were more likely to

nest in a new site close to the edge of the colony compared to breeding individuals

that retained their nest site in year 2. There was a slight, non-significant difference

in mean distance from the colony edge for nests of individuals in the STAY response

group (12.8 m) compared to the LEAVE response group (16.2 m; p = 0.09).

Inter-annual Distance Between Nest Sites

The median between-year distance in a focal individual's nest sites was 12.5

m (range = 1.19 – 87.97 m, n = 51) for individuals that could nest at the same site

used in year 1 (NON-DISPLACED group), and 22.07 m (range = 2.83 – 118.73 m, n

= 29) for individuals that lost their nest site from the previous year (DISPLACED

group; Figure 1). The median of the DISPLACED group was significantly greater

than that of the NON-DISPLACED group (p < 0.001, 95% CI: 1.66 - 3.56 times

greater). Among the focal nests in the NON-DISPLACED group, 41% were less

than 10 m from the previous year's nest site, while only 3% of the nests in the

DISPLACED group were within 10 m of the previous year's nest.

Nest success in year 1 of the study (2010) was not a good predictor of the

distance to the nest site used in year 2 (p = 0.98). There was a significant positive

correlation between the inter-annual distance between nest sites and the date of nest initiation in year 2 ($R^2 = 0.067$, $p = 0.02$), suggesting that nest initiation date was influenced by the distance from the previous year's nest site. This relationship, however, explains very little of the variation in date of nest initiation. Median distance moved by early nesters was significantly greater than that of individuals nesting in the middle of the egg-laying period ($p < 0.01$, 95% CI: 1.51 - 3.63 times greater). There was no significant difference in the median inter-annual distance moved between early versus late nesters ($p = 0.16$, 95% CI: 0.90 - 2.63), or between middle versus late nesters ($p = 0.13$, 95% CI: 0.88 - 3.03). There was a suggestive difference in mean distance moved between individuals in the STAY response group (18.6 m) and those in LEAVE response group (12.5 m; $p = 0.06$, 95% CI: 0.45 - 1.01).

Response After Nest Failure

Coincident with the peak of incubation in 2011, the ESI Caspian tern colony was subjected to daily disturbances by lone adult bald eagles over a 2-week period, resulting in intense predation on tern eggs and chicks by glaucous-winged/western gulls (*Larus glaucescens* X *L. occidentalis*) and the failure of all nesting attempts on the ESI tern colony during the last half of May. Those eagle disturbances with the greatest impact on the tern colony occurred at dawn and dusk over nine consecutive days, and resulted in the periodic abandonment of the colony by breeding adult terns. Colony abandonment, ranging from 10's of minutes to several hours, left tern nests

unguarded and provided an opportunity for gulls to consume the undefended contents of Caspian tern nests. On June 1, the last active Caspian tern nest on the ESI colony was destroyed by gulls.

Focal adult terns that stayed at the ESI colony in 2011 following the failure of their nesting attempt were re-sighted on the colony repeatedly and consistently following the failure of the colony on June 1. Of the 80 focal birds monitored in 2011, 50% (n = 40) remained at the ESI colony and repeatedly attempted to re-nest despite the failure of their initial nesting attempt (the STAY response to colony failure).

The remaining focal adult terns (n = 40) left the ESI colony after the failure of their first nesting attempt in 2011, and either were not seen again on ESI during the 2011 breeding season or were re-sighted on the colony intermittently (approximately every 9-14 days) following colony failure (LEAVE response to colony failure). Of these 40 birds, 7 (18%) were observed at other Caspian tern breeding colonies or roosting locations outside of the Columbia River estuary during the 2011 nesting season, following failure of the ESI colony. One focal tern was discovered at another breeding colony on an island in Padilla Bay, near Anacortes, Washington less than 2 weeks after the failure of its nest on ESI. This tern had re-nested and was incubating eggs, but the Padilla Bay colony ultimately failed to produce any young terns and all nesting attempts at this colony were also unsuccessful in 2011. Other focal terns that were not subsequently seen at the ESI

colony may have recruited to other breeding colonies after leaving ESI and initiated second nesting attempts, but were not re-sighted during their re-nesting attempt.

The behavioral response of focal terns to colony-wide nesting failure in 2011 (STAY or LEAVE) was not associated with the reproductive success of the individual at the ESI colony during the 2010 breeding season ($p = 0.77$). The response by focal terns to colony-wide nesting failure in 2011 was, however, significantly associated with whether the individual had access to the nest site it used in 2010 ($p = 0.005$). Contrary to expectation, individuals in the DISPLACED group were more likely to remain on the ESI colony after the failure of their first nesting attempt in 2011 (n = 21, 72%), compared to individuals in the NON-DISPLACED group (n = 19, 37%).

Group Adherence

Focal Neighbors in Year 1

Group adherence was evaluated by investigating the proximity of nest sites for focal individuals nesting on the ESI colony in both study years, and comparing this with the results of completely random nest placement simulations. In 2010, 96% of the nests of focal terns (n = 77) had at least one focal "neighbor," defined as a focal adult with an active nest within 10 m. In 2011, 81% of the nests of focal terns had at least one focal neighbor (n = 65). Only two focal individuals did not nest within 10 m of another focal individual in either breeding season. I ran six simulations of 80 randomly-located nest sites on the colony area in year 1, with an

average of 91% of simulated focal nests within 10 m of at least one other focal nest

(n = 73, range = 71 - 75). The six simulations of random nest placement for year 2

indicated that an average of 93% of simulated nests were located within 10 m of at

least one other focal nest (n = 75, range = 73 - 76). The random placement

simulations took into account the actual nesting densities in 2010 and 2011, which

were 0.70 nests/m^2 and 0.85 nests/m^2, respectively.

Retained Focal Neighbors in Year 2

      If the nests of the same focal terns were located within the 10-m radius 'nest

neighborhoods' of a focal tern in both years, that focal tern was considered to have

retained some of its neighbors. In six random-placement simulations, the median

number of simulated nest sites that were within 10 m of at least one other simulated

nest in year 1 was 72.5 nests (range = 71 - 75), and 12% of those simulated nests

retained a banded neighbor (median = 9.5 nests, range = 4 – 14, SD = 3.44, 95% CI:

5.72 - 12.95). Of the 77 nests of focal terns that were within 10 m of at least one

other focal nest in 2010, 60% of those focal terns (n = 46) retained at least one focal

neighbor in 2011. Based on the confidence intervals from the simulations, the

observed and simulated results are significantly different. Almost half of the focal

individuals on ESI retained between 1 - 5 focal neighbors in year 2 (n = 35), while

the median number of simulated nests retaining 1 - 2 neighbors was 9.5. No more

than 2 neighbors were retained in any simulation (Table 1). The differences in

distributions between observed and simulated neighborhoods suggest that the

location on the colony of the nests of focal terns during year 2 of the study was not random with respect to their banded nesting neighbors the previous year.

There was a significant negative relationship between how far a focal individual's nest moved between years and the percent of neighbors the individual retained from the previous year ($R^2 = 0.82$, $p = 0.01$; Figure 3). Focal individuals that moved their nest site more than 28 m from 2010 to 2011 retained no marked neighbors from their 2010 nest site at their 2011 nest site. Thus, there was a clear negative relationship between the distance a focal bird's nest moved between years and the number of focal neighbors that the focal bird retained in year 2.

Neighbor Retention and Group

Of the 46 focal terns whose nests in 2011 retained at least one focal neighbor from 2010, 72% (n = 33) were NON-DISPLACED focal terns, whereas 28% (n = 13) were DISPLACED. Therefore, 65% of NON-DISPLACED focal terns retained at least one focal neighbor, whereas only 45% of DISPLACED focal terns retained at least one focal neighbor. Of these 13 DISPLACED focal terns that retained a neighbor in 2011, all retained between 1 and 5 neighbors. Of the 33 NON-DISPLACED focal terns that retained a neighbor in 2011, 67% (n = 22) retained 1-5 focal neighbors and 33% (n = 11) retained six or more neighbors. The difference in number of neighbors retained by group was significant (Fisher's exact test, $p = 0.02$, 95% CI: 1.20 - Inf). Of the 34 focal individuals that did not retain any neighbors, 47% (n = 16) were DISPLACED focal terns and 53% (n = 18) were NON-DISPLACED focal terns. Therefore, 55% of DISPLACED focal terns retained no

focal neighbors, whereas only 35% of NON-DISPLACED focal terns retained no

neighbors. There was no significant difference between retaining no neighbors and

retaining at least one neighbor, by group type (DISPLACED or NON-DISPLACED;

Fisher's exact test, p = 0.10, 95% CI: 0.81 – 6.35).

Neighbor Retention and Response after Nest Failure

 Of the 34 focal individuals that did not retain any focal neighbors, the

response to nest failure of 17 focal individuals (50%) was to STAY and the response

of the other 17 was to LEAVE. There was no difference in response to nest failure

between individuals retaining no neighbors and individuals retaining 1-5 neighbors

(p = 0.47), and there was only a suggestion of a difference between focal individuals

retaining no neighbors and focal individuals retaining six or more neighbors (p =

0.09).

 Of the 35 focal individuals that retained 1-5 banded neighbors in 2011, 21

(60%) remained at the ESI colony after their nesting attempt failed (STAY), and

40% (n = 14) left the ESI colony (LEAVE). Focal terns that retained six or more

banded neighbors in 2011 (n = 11) were significantly more likely to LEAVE (n = 9,

82%) than to STAY (n = 2, 18%; p = 0.04) after nest failure.

Logistic Regression

 I used AICc model selection to investigate which explanatory variables were

most closely associated with the likelihood that a focal individual would remain at

the ESI colony following nest failure (STAY), as opposed to leaving the colony to

search for other nesting opportunities (LEAVE). The best fit model included the variables group (DISPLACED vs. NON-DISPLACED), duration of nest attempt, and distance from the colony edge (Table 2). DISPLACED focal individuals were more likely to STAY than NON-DISPLACED individuals; focal individuals whose nesting attempt lasted longer were more likely to STAY than those whose nesting attempt was brief in duration; and focal individuals whose nests were further from the colony edge were more likely to STAY than those whose nests were closer to the edge.

The two competitive models in the model set (within two AICc points of the best candidate model) included between them all explanatory variables used in the logistic regression analysis, so model averaging was used to determine the relative importance of each explanatory variable. The average relative importance values for group, duration of nest attempt, and distance from colony edge were each 1.0, date of nest failure was 0.39, and inter-annual distance between nests was 0.17 (Figure 4A-E).

After accounting for all other explanatory variables, being a NON-DISPLACED individual resulted in a 93% reduction in the odds of staying at the colony following nest failure ($\beta = 0.07$, 95% CI: 0.01 - 0.40) compared to DISPLACED individuals (Figure 4A). For every additional day a nest was active, the odds of an individual staying at the colony after nest failure increased by 9% ($\beta = 1.09$, 95% CI: 1.01 - 1.18; Figure 4B). For every 1 meter increase in distance from the colony edge, the odds of an individual staying at the colony following nest failure

increased by 13% (β = 1.13, 95% CI: 1.05 - 1.23; Figure 4C). Every day later that a

nest failed resulted in a 4% reduction in likelihood that the individual would stay at

the colony (β = 0.96, 95% CI: 0.77-1.05; Figure 4D), and for every meter increase in

distance between an individual's year 1 nest and its year 2 nest there was a 1%

reduction in likelihood that the individual would stay at the colony following nest

failure (β = 0.99, 95% CI: 0.96-1.02; Figure 4E).

DISCUSSION

Results of my study suggest that the reduction in available nesting habitat for

Caspian terns at the East Sand Island colony between 2010 and 2011 influenced the

nesting behavior of Caspian terns that lost access to their 2010 nest site in 2011.

Terns displaced from their 2010 nest site by the reduction in nesting habitat in 2011

nested further, on average, from their 2010 nest site than those terns whose nest site

in 2010 remained in suitable habitat during 2011. There was a tendency for displaced

terns to nest in closer proximity to the edge of the colony, nest among fewer

neighboring terns, and to have nesting attempts that ended earlier than did non-

displaced terns. These differences, taken together, suggest that those terns that lost

access to the nest site used in 2010 were competitively disadvantaged with regards to

nest site establishment at this colony in 2011. As such, displaced terns that failed in

their nesting attempt at a new nest site on the colony might be expected to more

readily abandon the East Sand Island colony and emigrate to other colony sites than

non-displaced terns that failed in their nesting attempt. The opposite was observed,

however, with displaced terns remaining at the ESI colony at higher rates than non-displaced terns after nest failure. Additionally, non-displaced terns were more likely to be found prospecting at colony sites other than ESI after their nesting attempt failed, compared to displaced terns.

Site Fidelity

A standard metric for the degree of nest site fidelity shown by ground-nesting colonial birds has not yet been developed, in part because it is difficult to obtain data on inter-annual differences in nest site location of individuals without causing considerable disturbance to the colony and, consequently, high rates of nest failure. This has led to much variation in what is considered a "high degree" of nest site fidelity. Snow geese (*Chen caerulescens*) are considered to have high nest site fidelity if nesting within 100 - 500 m of their previous nest site (Ganter and Cooke 1998). Stenhouse and Robertson (2005) described Sabine's gulls (*Xema sabini*) as highly faithful to their nest site when breeding within 100 m of previously used nest cups, while Feare and Lesperance (2002) considered sooty terns (*Onychoprion fuscatus*) nesting within 25 m of the previous year's nest site as highly site faithful. Several species of gull (*Larus* spp.) and common terns (*Sterna hirundo*) are considered to have high site fidelity because they often return to previously used sub-colonies, sometimes to within 6 m of previous nest sites (Blokpoel and Courtney 1980). Kittiwakes are a colonial seabird species with very high nest site fidelity;

individuals nesting on cliff or window ledges use discrete and readily distinguishable sites for nest building that can be repeatedly re-used (Coulson 1995).

Caspian terns are generally considered as species with low nest site fidelity because of the ephemeral nature of their preferred nesting habitat (Cuthbert 1988), but Caspian terns nesting on ESI displayed an unexpectedly high degree of nest site fidelity. Cuthbert's (1988) studies of Caspian tern nest site fidelity in the Great Lakes region focused on inter- and intra-seasonal movements among multiple small colonies within a group of islands; fidelity to a specific colony in subsequent years was reliably predicted by reproductive success at that colony in the current year. Caspian terns nesting on ESI tended to return to the colony in subsequent breeding seasons, regardless of the success of the previous year's nesting attempt. Further, the banded terns in my study were faithful not only to the ESI colony as a whole, but to specific areas of the expanse of bare sand nesting habitat that is occupied by the colony.

In many colonial nesting birds it is assumed that older, more experienced individuals tend to locate their nests more in the core of the colony as a result of social dominance, earlier arrival at the colony, or occupation of vacated territories, leaving subordinate individuals to occupy nest sites at the periphery of the colony (Brunton 1997, Ganter and Cooke 1998). My results support the hypothesis that Caspian terns nesting at the ESI colony are faithful to particular locales on the colony when the nesting habitat at their former nest site remains suitable, rather than being faithful to the ESI colony site in general, and vying for centrally-located (core)

nest sites. This may indicate that Caspian terns nesting at the ESI colony are using the contiguous colony area as if it were multiple sub-colonies, despite the absence of physical features separating these sub-colonies. There is evidence from other published studies of site fidelity in colonial seabirds at the sub-colony level, but in most examples these sub-colonies are located in discrete areas of a colony or in separate habitat patches (Parejo et al. 2006). At a super-colony, such as the Caspian tern colony on ESI, it may enhance the fitness of breeding individuals to repeatedly nest in the same 'sub-colony' area to reduce agonistic interactions with neighbors and facilitate mate retention.

Response after Nest Failure

The Caspian tern colony on ESI succumbed to intense disturbance and nest predation at the peak of the 2011 breeding season, causing all active nesting attempts to fail, and subsequently there were no successful re-nesting attempts during that breeding season. Other colonial nesting bird species have been documented abandoning nesting efforts for the season after nests have failed, but continuing to attend the colony site (Southern and Southern 1982, Coulson 1995, Levermann and Tottrup 2007). Arctic terns (*Sterna paradisaea*) and Sabine's gulls abandoned a breeding colony after late sea-ice breakup and nest predation by arctic foxes (*Vulpes lagopus*) thwarted breeding efforts. Colony abandonment was temporary, however, and all breeding pairs subsequently returned to the colony site, although no

subsequent re-nesting attempts occurred that breeding season (Levermann and Tottrup 2007).

The individual response to colony failure by breeding adults at the ESI colony in 2011 was evident in the differing patterns of colony attendance following nesting failure. As supported by the best fit model, the response to the failure of the initial nesting attempt was strongly influenced by whether or not an individual had access to its nest site from the previous year. Counter-intuitively, it was those individuals that had lost their previously used nest site that showed a higher tendency to remain at the ESI colony after their initial nesting attempt failed.

In an effort to understand this unexpected result, I considered various hypotheses for how breeding birds evaluate potential breeding areas. Factors that could potentially influence a bird's decision on where to nest include food availability, weather, climate change, social signals (e.g., signals that nearby nesting birds are successful), body condition, mate survival/retention, decision-making cues (i.e., switching from private to public information), and predation pressure (Schmidt 2004, Naves et al. 2006, Boulinier 2008). The hypothesized strategy for selecting a breeding territory of 'success-stay/failure-leave' (Shields 1984) predicts that an individual would try to maximize its fitness by not returning to a territory in which its reproductive attempts had been unsuccessful, and has been supported in studies of many bird species, ranging from passerines to seabirds (Schmidt 2004). Adherence to this strategy may be influenced by the timing of nest failure (Naves et al. 2006). At sites where nesting substrate is stable, but other resources are highly variable,

birds might take into account several years of prior breeding success, not just the previous year's success (Naves et al. 2006), especially if evaluation of nesting habitat is unreliable Schmidt (2004). Buckley (1997) posited that a breeding adult may make the 'selfish' choice to remain at a colony, even after a colony has surpassed its optimal size or resources have become limiting, because of increased ease of locating food resources.

If breeding Caspian terns rely on past reproductive success to choose nest sites, then terns returning in 2011 to nest near their unsuccessful 2010 nest site would have experienced at least two successive nesting failures at that nest site. This may have motivated non-displaced individuals to leave ESI and seek an alternative colony site after their initial nesting attempt failed in 2011. Terns that were displaced from their 2010 nest site and forced to select a new nest site at the beginning of the 2011 breeding season, and then failed, could also be considered 2-time losers; first, they lost their preferred nesting area on the colony and then subsequently lost their active nest at the new nest site. As such, one might expect these individuals to be more likely to leave the colony to search for a nest site at a different colony. Displaced terns, however, had already faced the challenge of prospecting for and defending a new nest site at the beginning of the nesting season, and the subsequent failure of their nesting attempt was their first failure at the newly occupied territory. Under these circumstances, breeding individuals may elect to spend the remainder of the season becoming familiar with this new nest site and area of the breeding colony, and continue exploiting familiar foraging areas, rather than attempting to establish a

new territory at a new colony site with unfamiliar foraging habitat. Levermann and Tottrup (2007) found that both arctic terns and Sabine's gulls at their study site continued pair bonding activities and territory guarding for weeks after nesting attempts had ceased, activities that were considered to be in preparation for breeding the following year.

The best fit model also suggested that the number of days a nest was active in 2011 and proximity to colony edge influenced an individual's decision to stay at the colony after nest failure. Regardless of whether focal individuals were displaced from their 2010 nest site or not, the likelihood of remaining at the ESI colony for the remainder of the breeding season tended to be greater for those individuals that failed further along in the nesting cycle and, therefore, might be expected to have a higher investment in their clutch and/or nest territory when failure occurred. Individuals that nested between six and 10 m from the edge of the colony had the longest mean nest duration, which was positively related to staying at the colony after nest failure, but both responses, STAY and LEAVE, were represented throughout the colony, regardless of distance to colony edge. Birds that abandoned the colony after failure of their initial nesting attempt came from both groups, but had in common a relatively short duration to their nesting attempt. Perhaps exceeding a threshold of time and energy invested in a particular nest site played a role in determining an individual's response to nesting failure in 2011.

Cuthbert (1988) also found that Caspian terns nesting in the Great Lakes region showed flexible within-season behavioral responses to nest failure. Terns in

her study overwhelmingly left the colony at which they had been nesting following nest failure and were not seen again, or were found nesting at an alternative colony site nearby. Cuthbert (1988) found that terns used their reproductive success in the previous year to inform their decision on whether or not to switch colonies following nest failure. In contrast, our study found that even with widespread nest failure in year 1, individuals returned to breed at ESI in year 2, and most remained after failure of initial nesting attempt in year 2.

It is possible that the response of most focal individuals to remain faithful to the ESI colony after failure of their nesting attempt may say less about the quality of the nesting habitat at ESI, or the fidelity of these individuals to the ESI colony site, then it does about the availability of suitable alternative nesting habitat elsewhere in the Pacific Northwest region. Breeding Caspian terns are a relative newcomer to the Pacific coast of North America, displaced from much of the species' former nesting habitat in the Great Basin by anthropogenic change that reduced nesting and foraging habitat (Suryan et al. 2004). In the years since coastal colonies were first reported, however, Caspian terns have again faced declines in nesting habitat and increasingly use anthropogenic sites, such as man-made islands, rooftops, parking lots, and even barges (Collis et al 2002; Suryan et al. 2004; SC, pers. obs.). The colony site on East Sand Island is unique in that it has been managed to be consistently available and suitable for nesting for 15 years. All focal terns were known to have attempted to nest at the ESI colony for a minimum of two consecutive nesting seasons, so perhaps the persistence of the colony site was more important for an individual's decision on

where to breed in a given year than its previous breeding success at that colony site. Artificially maintained nesting habitat may allow birds to become more faithful to specific areas of a colony and to show an unusual degree of nest site fidelity (McNicholl 1975). Consequently, persistent availability of nesting habitat at ESI and the scarcity of suitable nesting habitat elsewhere may be the most important factor currently influencing nest site fidelity and tenacity by Caspian terns at ESI.

Group Adherence

On East Sand Island, Caspian terns must orient themselves on a large patch of bare-sand nesting habitat with shifting boundaries, where vegetation and micro-topography vary seasonally and annually, where landmarks both on and surrounding the colony site shift and change, and where competition for space can be intense, with a breeding population of more than 6,000 other nesting pairs. Several other species of terns have been documented to maintain persistent neighborhood groups within their nesting colonies, with some neighborhood groups persisting even as breeding birds move among colonies (Feare and Lesperance 2002). At ESI, I found strong evidence of nest site fidelity by Caspian terns toward specific areas of the colony, and a consequent pattern of association by neighboring nesting individuals between years; however, I found no evidence of preferentially nesting near the same individuals among years, regardless of whether the individual nested in the same area across years.

Our data support the hypothesis that terns nesting on ESI are exhibiting nest site fidelity at the level of discrete areas within the larger colony. There was a clear association between the number of neighbors retained by a focal tern and the inter-annual distance between nests of that tern. Consequently, the observed retention of neighbors across years reflects an individual's fidelity to a specific area of the colony, rather than a preference for nesting in a group of 'known' neighbors. If group adherence was at work, one would expect birds that lost their 2010 nest sites due to habitat change to move as a group to new areas of the colony. Instead, our results indicated that banded terns that were displaced from their 2010 nest site established their nest further from their previous nest site and retained fewer neighbors, compared to banded terns that were not displaced. McNicholl (1975) suggested that in areas of stable nesting habitat one would expect to find strong fidelity to a colony site, but fewer examples of group adherence because group adherence is most advantageous to species that must frequently pioneer new colony sites because of shifting and fluctuating habitat suitability. The latter situation accurately describes the status of breeding habitat in much of the range of Caspian terns, but not at ESI.

CONCLUSION

In this study I found that Caspian terns nesting at East Sand Island showed a degree of nest site fidelity that is not usually attributed to species that nest in ephemeral habitats and can move among a network of colony sites in successive years. Individuals at the ESI Caspian tern colony behaved as if the large, contiguous

area of nesting habitat was made up of many smaller sub-colonies, to which they were philopatric. This philopatry led to nesting in close proximity to known individuals across years. I found that some individual terns remained faithful to this colony despite successive nesting failures, and that previous breeding success seemed to be less important in nest site selection for Caspian terns nesting at the ESI colony than has been found in other studies of the species. The highest colony site tenacity was seen in terns displaced from previously used sub-colonies, that nested farther from the colony edge, and whose nesting attempt lasted longer. Nest site selection at the ESI colony seems to depend most on the continued availability of suitable nesting habitat on ESI, despite increased nest predation rates and reduced area of nesting habitat. This may be due to a regional limitation in suitable colony sites for Caspian terns that reinforces nest site fidelity.

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Table 2.1. Comparison of the number of focal Caspian tern nests that retained banded neighbors within a 10-meter radius 'neighborhood' from Year 1 (2010) to Year 2 (2011) at the East Sand Island breeding colony, compared to random nest placement simulations. Observed values on East Sand Island in 2011 include the percent of the total sample (n = 80) and the number of focal individuals represented in each category. Results for the random placement simulations are an average of six simulations; simulations were run in ArcGIS.

Neighbors Retained in Year 2	Observed at East Sand Island colony	Random Placement simulations (n = 6)
0	42%, n = 34	88%, n = 70.5
1 - 5	44%, n = 35	12%, n = 9.5
6 - 9	11%, n = 9	0
10+	3%, n = 2	0

Table 2.2. The top three candidate models for logistic regression analysis explaining variation in response of Caspian terns (STAY or LEAVE) after failure of their initial nesting attempt at the East Sand Island colony in 2011. The models were ranked using Akaike Information Criteria for small sample sizes (AICc) and compared using the ΔAICc value, which is the difference between an individual model's AICc score and the lowest (most probable) AICc score of all the candidate models in the model set, i.e., the best candidate model.

Rank	Model	AICc	ΔAICc	W_i
1	group + distance to colony edge + duration of nest attempt	94.19	0.00	0.44
2	group + distance to colony edge + duration of nest attempt + date of nest failure	94.42	0.23	0.39
3	group + distance to colony edge + duration of nest attempt + inter-annual distance between nests	96.03	1.84	0.17
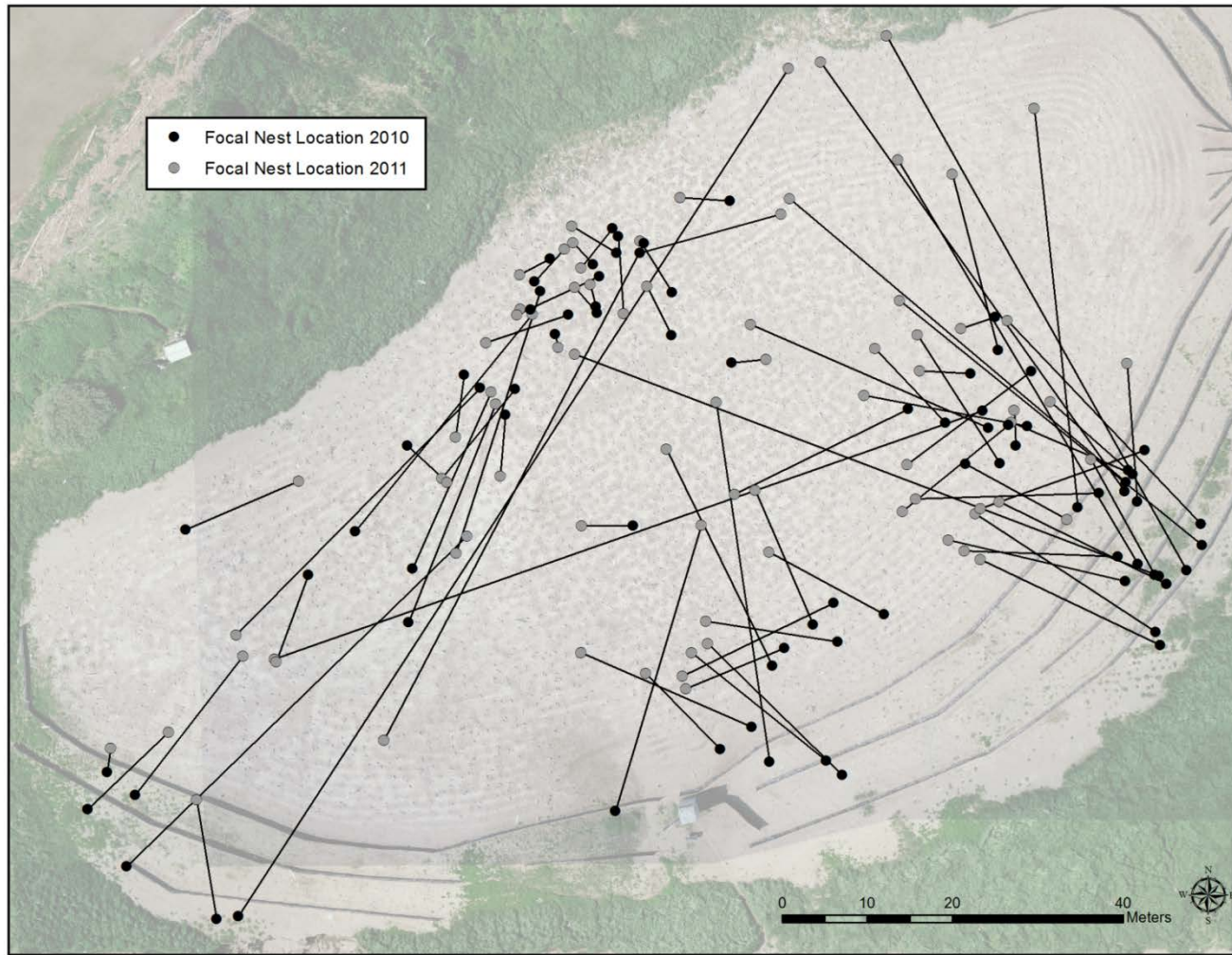
Figure 2.1. Aerial photography of the East Sand Island Caspian tern colony in 2011 showing the inter-annual differences in nest placement for each focal individual in the study (n = 80). The nest site of each focal individual in Year 1 (2010: closed black circle) and Year 2 (2011: shaded gray circle) are connected by a solid black line. Concentric black lines to the south and east of the main colony area are landscape fabric fences erected before the 2011 nesting season that precluded terns from nesting in these portions of the former colony area. Year 1 nest sites outside of the 2011 inner landscape fabric fence represent focal individuals unable to re-use their Year 1 nest site in Year 2 (DISPLACED group).
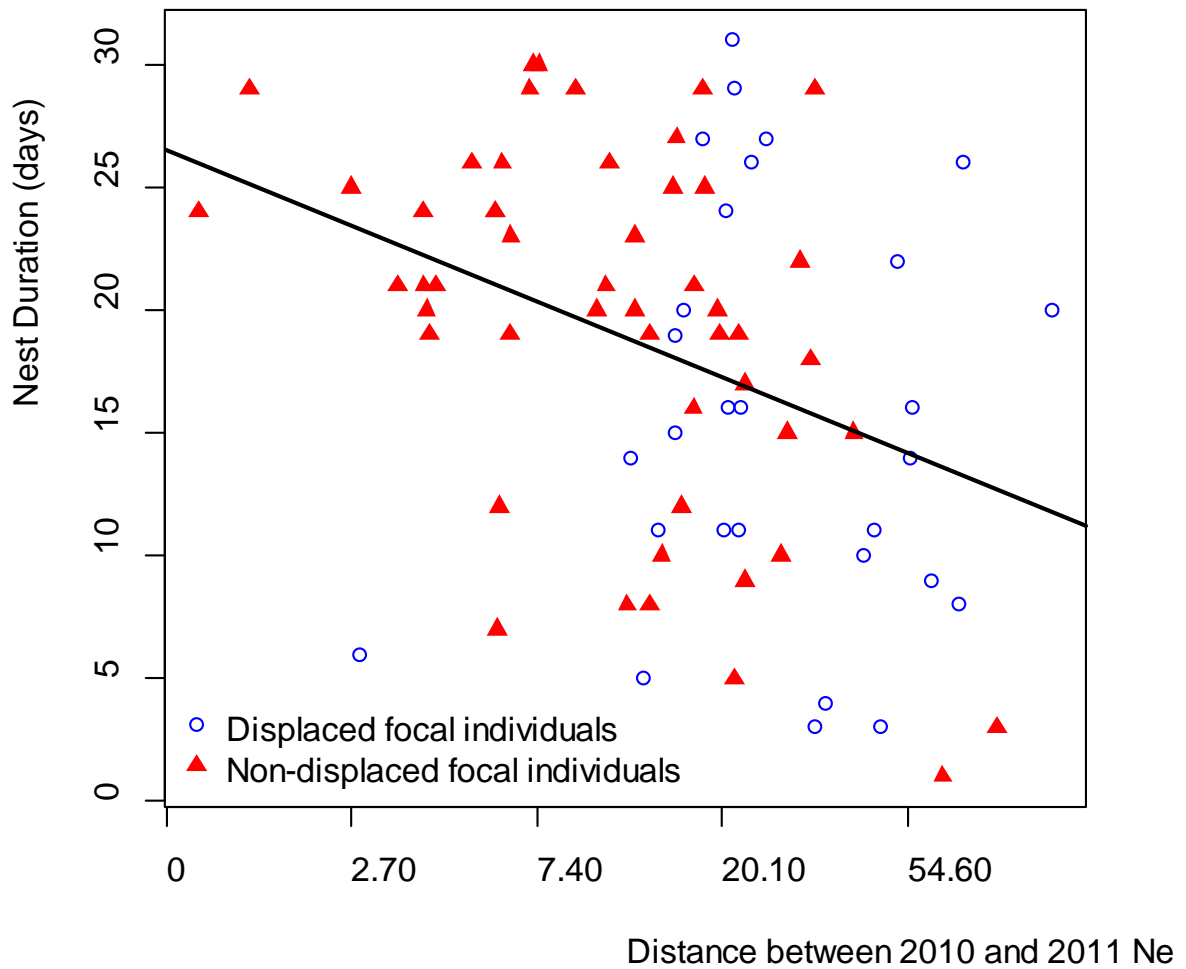
Figure 2.2. Nest duration dates for marked Caspian terns nesting on East Sand Island in 2011 as a function of the inter-annual distance between nests in 2010 and 2011 for each marked individual. Each marked individual was classified by whether its Year 1 nest location was available in Year 2 (Non-Displaced), or not (Displaced). The correlation was significant ($p < 0.001$).
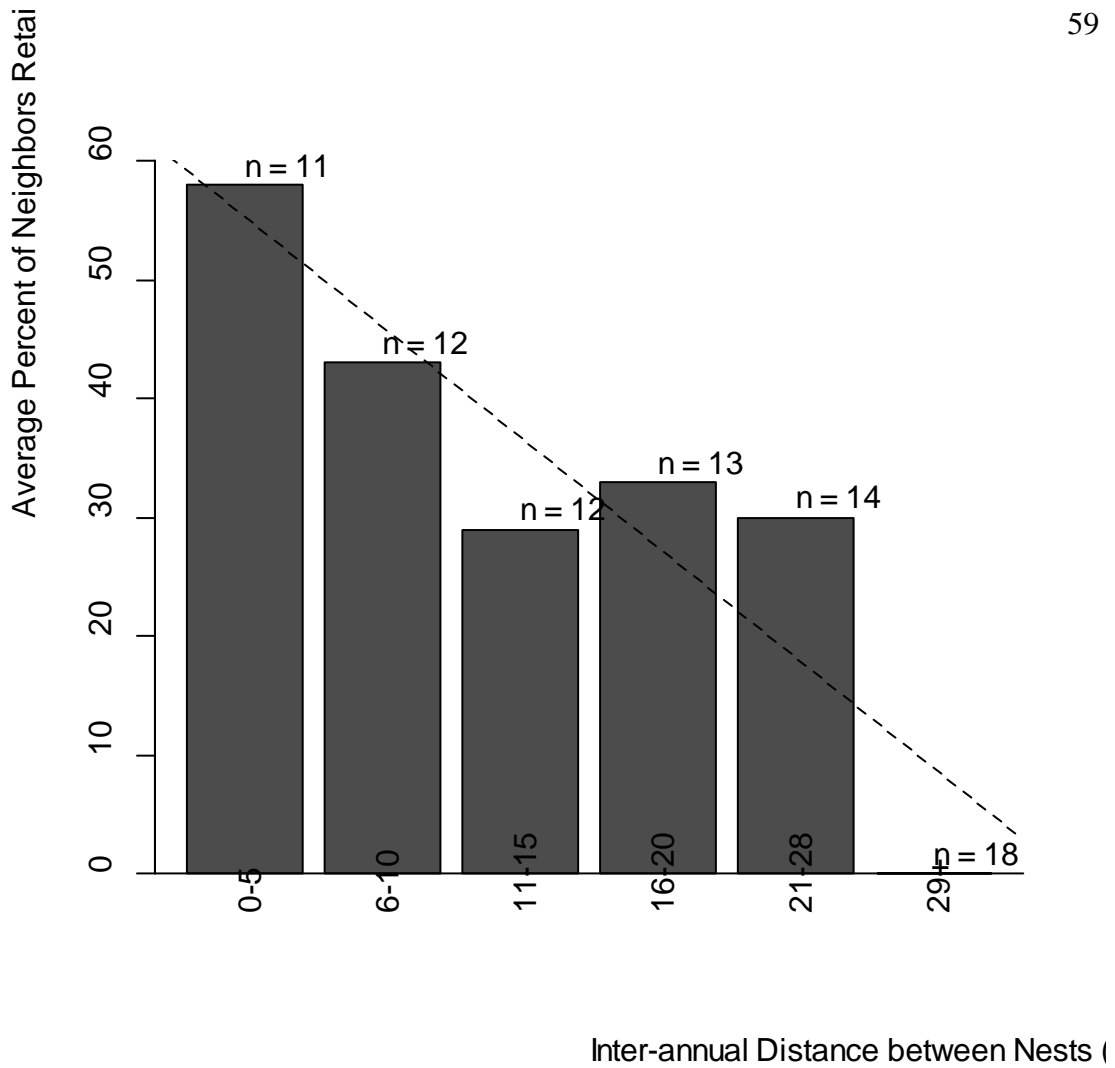
Figure 2.3. The average percent of neighbors retained in Year 2 within a 10-m radius 'neighborhood' regressed against the inter-annual distance between nests of marked Caspian terns at the East Sand Island colony. The number of marked terns represented in each distance category is identified above each bar. The negative relationship between the proportion of neighbors retained and the inter-annual distance between nest locations was significant ($p = 0.01$).
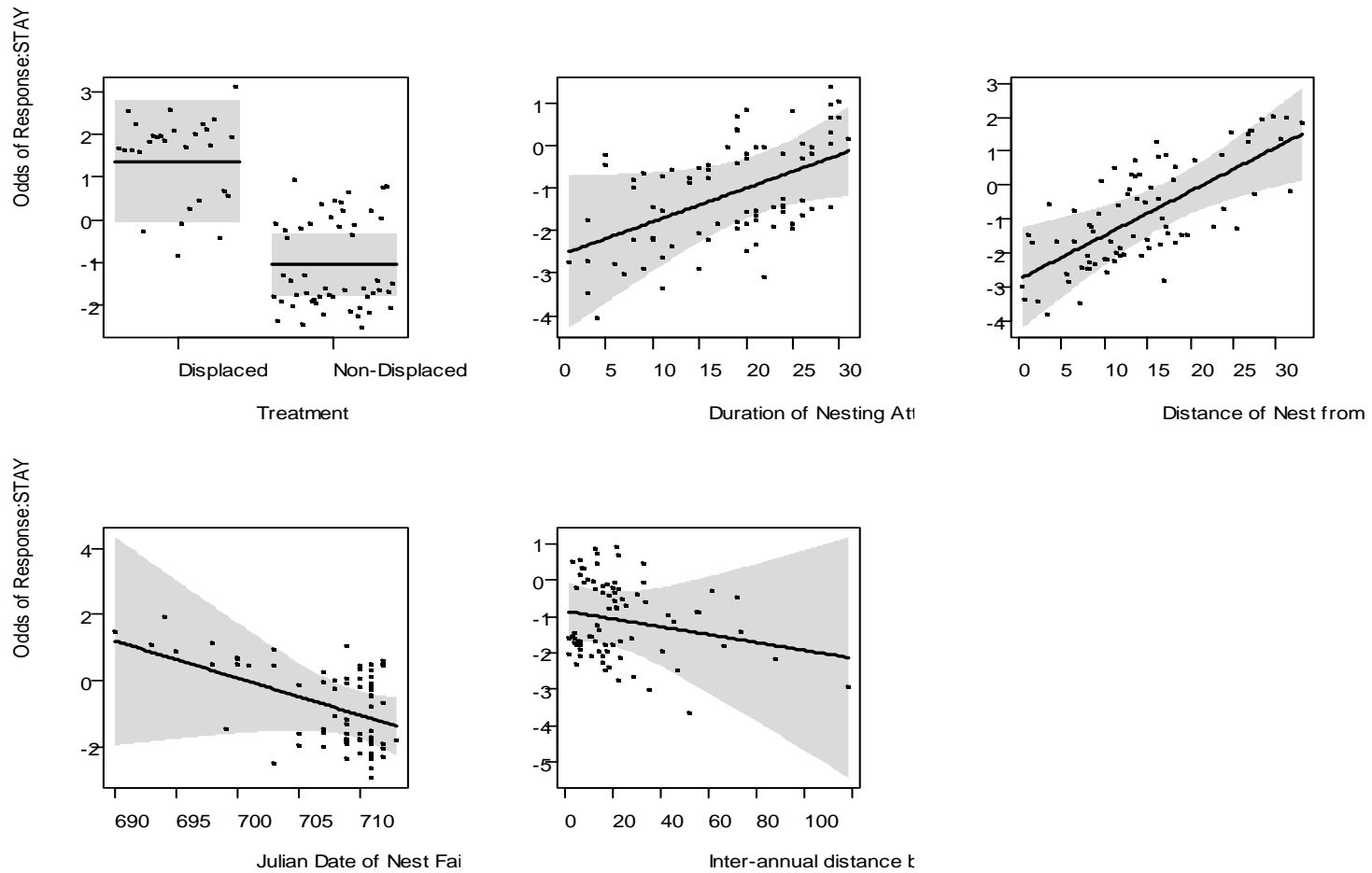
Figure 2.4. Graphical representation of the logistic regression model coefficients included in model averaging of factors explaining the odds of breeding Caspian terns staying on the East Sand Island colony following nest failure in 2011. Each graph depicts the relationship between an explanatory variable (x axis) and the odds of being associated with the logistic response STAY (y axis), after accounting for all other explanatory variables. Prediction line (solid black line), 95% confidence band (gray shading), and partial residuals are shown for each explanatory variable. The average relative importance values for group (A), duration of nest attempt (B), and distance from colony edge (C) were each 1.0, date of nest failure (D) was 0.39, and inter-annual distance between nests (E) was 0.17.

CHAPTER 3. TOP-DOWN AND BOTTOM-UP INFLUENCES ON NESTING

SUCCESS AT THE WORLD'S LARGEST COLONY OF CASPIAN TERNS

(*HYDROPROGNE CASPIA*)

Stefanie Collar, Daniel D. Roby, and Donald E. Lyons

ABSTRACT

The Caspian tern (*Hydroprogne caspia*) breeding colony on East Sand Island
(ESI) in the Columbia River estuary, the largest colony of its kind in the world,
experienced a decade of declining nesting success, culminating with the failure of the
colony to produce any young in 2011. Our study investigated the potential influence
of bottom-up and top-down drivers for the declining productivity at this once
thriving colony of Caspian terns. Since 2001 the decline in reproductive success of
Caspian terns at ESI has been associated with a significant increase in average river
discharge during May and June. I also found a significant increase in
kleptoparasitism rates of terns by glaucous-winged/western gulls (*Larus glaucescens*
x *L. occidentalis*) since 2001, and a significant negative relationship between average
annual rates of gull kleptoparasitism and Caspian tern nesting success at ESI. There
was also a significant increase in disturbance rates by bald eagles (*Haliaeetus
leucocephalus*) during June for terns nesting at the ESI colony, and eagle disturbance
rates were positively associated with May river discharge. The abundance of forage
fish for terns in the estuary was inversely related to river discharge, which also
apparently affected the reliance of tern nest predators on the tern colony as a food
source, resulting in increased disturbance and decreased reproductive success at the
tern colony. Although correlational, our results support the hypothesis that the
decline in Caspian tern nesting success at this large estuarine colony was primarily
driven by bottom-up factors, both as they directly affected tern productivity through

the food supply, and indirectly as they affected the alternative food supply of

potential predators on the contents of tern nests.

INTRODUCTION

In the decades since the start of the top-down versus bottom-up debate in community ecology, focus has shifted to a more nuanced view: That the unique interactions between predators and producers shape individual ecological communities (Hunt and McKinnell 2006, Suryan et al. 2006, Grippenberg and Roslin 2007). Nesting success at seabird breeding colonies requires distinct interactions between prey availability, suitable nesting habitat, avoidance of predators, and favorable weather. For this reason, seabird nesting colonies tend to reflect the complex interplay of top-down and bottom-up constraints, rather than supporting one cause over the other (Suryan et al. 2006). Monitoring seabird colonies offers a chance to better understand this interplay. Seabirds often breed in environments that can strongly limit productivity even in the best of years (Roberts and Hatch 1993, Hall and Kress 2004), and breeding adults must balance the needs of their current offspring with their own survival (Finney et al. 1999, Satterthwaite et al. 2012). Munch et al. (2005) posited that bottom-up forcing should be most obvious in its regulation of adult recruitment to the breeding population, and that top-down regulation would be reflected in high egg and chick mortality. Treating bottom-up and top-down factors as competing alternative hypotheses to explain nesting success at seabird colonies may not be appropriate given the complexity of the interactions at a large breeding colony.

The ample and accessible prey resources required for seabird breeding colonies to be successful can also be crucial resources for potential predators of the

nest contents or even the breeding adults at the seabird colony. For example, some gull species (*Larus* spp.) that nest among or near colonial seabirds can be voracious egg and chick predators, and many raptors will opportunistically take adult colonial seabirds or their eggs and chicks, especially if alternative food sources or prey are scarce (Isaacs and Anthony 2011, Harvey et al. 2012). It is in complicated systems such as these that one can potentially see the 'chutes and ladders' of a dynamic food web proposed by Hunter and Price (1992). Rather than the simplistic view of two prospective hypotheses in conflict, Hunter and Price (1992) emphasized the importance of food web connections that are not restricted by trophic level or direction. Acknowledging the inherent dynamism of seabird colony ecology allows for a more complete understanding of trophic interactions. In the present study, I sought to understand the ways in which top-down and bottom-up forces interacted in our system and influenced the reproductive success of Caspian terns (*Hydroprogne caspia*) at our study colony.

Since the year 2000, the largest Caspian tern breeding colony in the world has been located on East Sand Island in the Columbia River estuary (Lyons 2010). East Sand Island (ESI) is located 8 km up-river from the mouth of the Columbia River on the Pacific coast of North America. The island has undergone considerable anthropogenic change, and the habitat near the eastern end of the island has been modified and managed to support nesting by Caspian terns since 1999 (Roby et al. 2002). The breeding colony of Caspian terns on ESI had been relocated from Rice Island, a 98-ha (235-acre) dredged material disposal island located at river km 34

(Simenstad et al. 1990). Colony relocation occurred during 1999-2001 as part of management actions designed to reduce the numbers of juvenile salmonids consumed annually by Caspian terns nesting in the Columbia River estuary (Roby et al. 2002).

The relocation of the Caspian tern colony from Rice Island to ESI was considered successful both because of the reduction in mortality of salmonids due to tern predation - the proportion of juvenile salmonids in the tern diet declined from 74% in 1998 to 33% in 2001 - and because of the high reproductive success of Caspian terns at the ESI colony after its relocation (Collis et al. 2002, Roby et al. 2002). Although the size of the ESI colony remained approximately stable during the decade that ended in 2009, nesting success gradually declined during this period. Management initiatives to reduce the number of Caspian tern breeding pairs at the ESI colony by reducing the availability of nesting habitat were initiated in 2008 (USFWS 2005), raising the possibility that management to reduce the size of the ESI colony might also be negatively affecting nesting success.

A potential explanation for declining nesting success at the Caspian tern colony on ESI is top-down factors, such as increasing predation pressure on breeding adults and their eggs and chicks. In addition to the large Caspian tern colony, East Sand Island is home to large breeding colonies of two taxa of gulls, glaucous-winged/western gulls (*Larus glaucescens* x *L. occidentalis*) and ring-billed gulls (*L. delawarensis*). Both of these gull species are known to use tern colonies, including tern eggs and chicks, as a food source to varying degrees. During the first two

breeding seasons (1999-2000) when managers sought to shift nesting Caspian terns from Rice Island to East Sand Island, limited lethal control of glaucous-winged/western gulls was implemented to enhance nesting success of early tern immigrants to the ESI colony (Roby et al. 2002). No efforts to limit gull predation on Caspian tern eggs and chicks were implemented during 2001-2011. Bald eagles (*Haliaeetus leucocephalus*) are common in the Columbia River estuary and frequently use colonial seabirds as a food source (Isaacs and Anthony 2011). There are other avian predators that frequent the island and are known to depredate the contents of Caspian tern nests, including peregrine falcons (*Falco peregrinus*), common ravens (*Corvus corax*), American crows (*C. brachyrhynchos*), and brown pelicans (*Pelecanus occidentalis*).

An alternative explanation for declining nesting success at the large Caspian tern colony on ESI are bottom-up factors that influence food availability to nesting adults. The prey base for the ESI colony, located near the mouth of the Columbia River, is influenced by both river discharge and tidal fluctuations (Weitkamp et al. 2012). Because of its proximity to the Pacific Ocean, ESI can be affected by severe storms that can destroy nests, kill chicks, and limit the foraging ability and foraging success of breeding adults (Aebischer 1993, Finney et al. 1999, Lyons and Roby 2011). Estuaries are dynamic ecosystems of great complexity - biologically, hydrologically, and meteorologically (Weitkamp et al. 2012), and this means that bottom-up factors could influence the success of disparate organisms throughout the food web, effectively turning bottom-up limitations on tern nesting success into top-

down controls. Consequently, it is imperative to consider the interactions between bottom-up and top-down forcing as constraints for seabird nesting success.

Our study investigated the potential drivers for the declining productivity at this once thriving colony of Caspian terns, attempting to identify causal factors behind the decline in reproductive success during the decade since the colony became established. I used historical data collected at the ESI Caspian tern colony during 2001-2009, as well as data collected especially for this study during 2010-2011, to investigate the relationships between various prospective explanatory variables and average nesting success in each year of the study period. Our primary objective was to identify trends in both colony attributes and environmental factors, and to understand how these elements might be linked. I explored decadal trends evident in these relationships and attempted to understand which factors limited productivity, especially during the 2010 and 2011 breeding seasons, factors that could be responsible for the decline in nesting success during the previous decade.

METHODS

Study Area

East Sand Island (ESI) (46°15'45"N, 123°57'45"W) in the Columbia River estuary near the mouth of the Columbia River has been the site of a perennial Caspian tern breeding colony since 1999. This colony was intentionally restored using nesting habitat restoration, social attraction (decoys and audio playback of vocalizations), and limited control of predatory glaucous-winged/western gulls.

Annual maintenance of early seral stage nesting habitat at the colony site has ensured that suitable nesting habitat for Caspian terns has persisted on ESI.

ESI is owned by the U.S. Army Corps of Engineers (USACE), which manages the habitat on a small portion of the island so as to be suitable for nesting Caspian terns. In accordance with the Final Environmental Impact Statement and Records of Decision prepared by the USACE and the U.S. Fish and Wildlife Service (USFWS) in 2005 and 2006, habitat management would reduce the number of breeding pairs of Caspian terns nesting on ESI to approximately one third of the maximum colony size (ca. 10,000 breeding pairs) in order to reduce predation on juvenile salmonids listed as threatened or endangered under the U.S. Endangered Species Act (ESA).

The number of breeding Caspian terns using the colony at ESI would be limited through a reduction in available nesting habitat to less than one third of the former area. The habitat eliminated from ESI would be replaced by constructing artificial islands built by the USACE within the historical breeding range of Caspian terns in western North America. When the habitat reduction plan on ESI is completed, the area of suitable nesting habitat would be reduced from 2 ha (5 acres) to 0.4 - 0.6 ha (1 – 1.5 acres). Reduction of Caspian tern nesting habitat on ESI would initially be accomplished through the erection of visual barriers (landscape fabric fences) on part of the existing colony area.

The proximate goal of restricting available tern nesting habitat using these methods was to induce displaced individuals to relocate to one of the new alternative

colony sites. The ultimate goal of this redistribution of the Caspian tern breeding

population was to both reduce avian predation on juvenile salmonids listed as

threatened or endangered under the U.S. ESA and to limit the effects on the

population of Caspian terns in western North America of any local catastrophic event

at the ESI colony.

Data Collection

Average annual reproductive success of Caspian terns nesting at the ESI

colony was estimated through a combination of counts from aerial photography and

simultaneous counts from the ground of the number of adults and chicks on sample

plots within the colony. First, the number of Caspian tern breeding pairs was

estimated late in the incubation period by counting the total number of terns on-

colony in the aerial photography, and adjusting this count using the ratio of

incubating to non-incubating terns in 36-m^2 sample plots (n = 12) within the tern

colony. Then, just prior to the peak of fledging, all on-colony Caspian terns were

again counted in aerial photography, and the total number of fledglings was

estimated by adjusting this count using the ratio of fledglings to adults in sample

plots within the colony. The estimated total number of fledglings produced was then

divided by the estimated number of breeding pairs to estimate colony productivity

(the average number of young fledged per breeding pair). For more details on the

aerial photo census methods used in this study, see Collis et al. (2002).

To better understand how the nesting success of Caspian terns at the colony on ESI was influenced by environmental factors, I created simple linear regressions using average nest success per breeding season (average number of young fledged/breeding pair) as the response variable. I investigated a wide range of potential explanatory variables that may have influenced the reproductive success of the tern colony in a given year. These potential explanatory variables fell into three categories: (1) climate, (2) food supply, or (3) predators. Whenever possible, values for each explanatory variable were obtained during each year of the study (2001-2011).

Climate

Pacific Decadal Oscillation

Monthly index values (January-April) for the Pacific Decadal Oscillation (PDO) during 2001-2011 were obtained from the University of Washington Joint Institute for the Study of Atmosphere and Ocean (http://jisao.washington.edu/pdo). Winter and spring months have previously been shown to be correlated with salmonid consumption by Caspian terns nesting at ESI (Lyons 2010), so I chose to include spring months leading up to nest initiation to look for an effect of climate on productivity. These values were then summed for each year and converted to a yearly First Difference Correlation by subtracting the PDO value for a given year from the PDO value for the preceding year. This derived variable represents the magnitude of change in PDO from one year to the next, and was used in this analysis

to test for an effect of shifting between warmer and cooler regimes on tern productivity.

River discharge

Data on river discharge for the Columbia River were downloaded from the U.S. Geological Survey website (http:/waterdata.usgs.gov) for river km 86 (site number 14246900), which is downstream of the confluence of all major tributaries to the Columbia River. Average monthly river discharges (thousands of cubic feet per second; *kcfs*) were compiled for the months of April, May, and June during 2001-2011, which includes the period of Caspian tern nest initiation, incubation, and early chick-rearing at our study site.

Rainfall

Rainfall data collected at the Astoria Regional Airport, Oregon, USA (Station USW00094224, 46.157° N, 123.882° W) were downloaded from the NOAA National Climatic Data Center website (http://www.ncdc.noaa.gov). Monthly totals for precipitation, as well as daily totals for precipitation during nest initiation, incubation, and early chick-rearing, April-June, in 2001-2011 were used in the analysis. All precipitation totals were converted to centimeters. Precipitation data were compiled into 48-h totals to capture the effect of stochastic, prolonged storm events that caused flooding on the breeding colony, submerging many nest scrapes.

Food Supply

  Diet composition

Caspian terns are piscivorous birds that carry whole fish back to the breeding colony in their bills to feed mates and chicks. Throughout each breeding season, twice daily observations were made of Caspian terns returning to the breeding colony with bill-load fish. Fifty bill-load fish were visually identified during each session, and the sessions took place at high and low tides each day to control for potential effects of tide stage and time of day on tern diet composition.

The average taxonomic composition of Caspian tern diets was calculated for each breeding season using standardized methods (Collis et al. 2002). The species composition of fish in Caspian tern bill-loads (% of identifiable bill-loads) was determined visually at the colony during each two-week period of the breeding season, and then the overall composition of the diet during each breeding season was based on the average of these two-week percentages. The annual taxonomic composition of the Caspian tern diet for each year during 2001-2011 was used in the analysis (www.birdresearchnw.org).

Predators

  Eagle disturbance

Any disturbance that resulted in at least 10% of the adult terns on the breeding colony taking flight during a scheduled bill-load identification observation period was recorded by the observer and entered into a database. Each record included the time of the disturbance, the percent of adults on-colony that were

flushed, the cause of the disturbance (if discernible), and the number of seconds elapsed from the start of the disturbance until 50% of flushed terns re-landed on the colony. The cause of each disturbance was assigned to one of the following six categories: (1) avian predator, (2) human (pedestrian), (3) watercraft, (4) aircraft, (5) other, or (6) unknown.

I used data for disturbances to the tern colony by bald eagles that were collected during 2004-2011 to re-construct monthly rates of eagle disturbance. To estimate eagle disturbance rates for each month, the number of disturbances by eagles recorded during a month was divided by the number of hours of bill-load observations recorded in that month. Eagle disturbances were further subdivided by the magnitude of the disturbance: Large disturbances were those that caused 50% or more of the adults on-colony to flush, while small disturbances caused less than 50% of the adults on-colony to flush. Disturbances were also categorized by time period: Morning disturbances occurred between 05:00 and 13:00 PDT, while afternoon disturbances occurred between 13:00 and 19:00 PDT. Eagle disturbances were separated into these two periods of the day because observations indicated there were differences between morning and afternoon in the behavioral reactions of Caspian terns to eagles. A median duration of eagle disturbances (from start until 50% of the flushed terns had re-landed) was also calculated for each month of each nesting season.

Gull predation rates

At the ESI Caspian tern colony, observers spent three hours per week in each of three observation blinds recording events when gulls were observed to depredate Caspian tern eggs or chicks within a pre-designated group of 50 active tern nests. Rates of gull predation on Caspian tern nest contents were determined by dividing the total number of gull predation events recorded in a month by the number of hours spent recording gull predation events during that month. Observations from each blind were pooled to estimate each monthly rate. Data on gull predation rates were collected during 2007-2011.

Kleptoparasitism by gulls

As described above, twice daily observation periods were conducted throughout the Caspian tern nesting season to obtain information on tern diet composition. Each bill-load observation was assigned one of several final fates: (1) eaten by the individual transporting the bill-load, (2) fed to another adult tern, (3) fed to a tern chick, (4) stolen by a conspecific, or (5) kleptoparasitized by a gull. The gull kleptoparasitism rate was calculated by dividing all kleptoparasitized fish by the total number of fish with assigned final fates. The kleptoparasitism rates used in the analysis were the total rates for each breeding season during 2001-2011.

Data Analysis

The 8 potential explanatory variables described above were included in the analysis to determine which variables explained inter-annual variation in colony

productivity. For each of these explanatory variables, I looked for the presence of a correlation with tern productivity prior to the 2010 and 2011 breeding seasons. In cases where a significant correlation existed between an explanatory variable and the response variable of productivity during 2001-2009, I used the relationship to predict values of productivity for 2010 and 2011, and compared the predicted and actual values for 2010 and for 2011. A small difference between observed and predicted values provided support for the hypothesis of a causal relationship between explanatory and response variables. If there was no significant relationship between explanatory and response variables during 2001-2009, I investigated whether a potential threshold effect for that particular explanatory variable may have occurred during 2001-2011.

I created multiple linear regression models corresponding to *a priori* biologically relevant hypotheses. I used Akaike's Information Criterion corrected for small sample sizes (AICc) to identify the most parsimonious model supported by the data. Because of high correlation between some explanatory variables, and the small sample size for the response variable (n = 11), all interactions could not be included in prospective models. Potential correlations between explanatory variables were identified using the Pearson's correlation function in R, and variables with correlations significant at the $\alpha = 0.05$ level were not included together in the potential model selection sets. ΔAICc values were calculated for all potential models, and the top 5 models are presented here for comparison. All analyses were

performed using the R statistical packages *bblme*, *Hmisc*, and *Mass* (R Development

Core Team 2011).

RESULTS

Reproductive Success

From 2001 to 2011 the reproductive success of Caspian terns at the East Sand

Island colony declined significantly (R^2 = 0.82, df = 9, p < 0.0002; Figure 1).

Reproductive success declined from a high of 1.39 chicks fledged/breeding pair in

2001 to 0 chicks fledged/breeding pair in 2011. Nesting success in 2011 was the

worst ever recorded for Caspian terns nesting in the Columbia River estuary, with a

total nest failure throughout the colony and no fledglings produced.

Climate

Pacific Decadal Oscillation

There were no significant relationships between the PDO index during

January-April and subsequent colony productivity for the years 2001 to 2009 (R^2 =

0.17, df = 7, p = 0.27) or for the years 2001 to 2011 (R^2 = 0.01, df = 9, p = 0.82).

River discharge

Average discharge of the Columbia River (kcfs) during May increased

significantly (R^2 = 0.56, df = 9, p = 0.008) from 2001 to 2011. There was a

significant negative relationship (R^2 = 0.50, df = 7, p = 0.032) between river

discharge in May and the productivity of the ESI Caspian tern colony for the years

2001 to 2009. The predicted value for average colony productivity in 2010 based on

May river discharge was 0.97 fledglings/breeding pair, while the observed value was 0.05 fledglings/breeding pair. Similarly, the predicted value for colony productivity in 2011 was 0.41 fledglings/breeding pair, while there were no fledglings produced during the 2011 breeding season. When 2010 and 2011 were added to the regression, however, the relationship was still significant (R^2 = 0.43, df = 9, p = 0.028).

Average discharge of the Columbia River in June also increased significantly during 2001-2011 (R^2 = 0.56, df = 9, p = 0.008). The correlation between June river discharge and productivity of the Caspian tern colony was not significant for the years 2001 to 2009 (R^2 = 0.17, df = 7, p = 0.269); however, the correlation was significant for the years 2001 to 2011 (R^2 = 0.49, df = 9, p = 0.016; Figure 2). Average river discharge in both May and June of 2011 was over 100 kcfs, the highest river discharge for those two months during the 11-year study period.

Rainfall

There were no significant correlations between the amount of precipitation during a breeding season (April-July) and average annual productivity for the Caspian tern colony on ESI. In June 2010 the Columbia River estuary received a total of 9.86 cm of rain, while in June of 2011 there was only a total of 4.24 cm of rain. The maximum rainfall in a 48-hour period during June 2010 was 5.46 cm, and during June 2011 was 1.32 cm. In 2011, the total rainfall in June, as well as the June maximum rainfall in a 48-hour period, fit within the range of values for years during 2001-2009, whereas in 2010 the total rainfall in June and the June maximum rainfall

in a 48-hour period far exceeded those of any other year during 2001-2011. Both in terms of total rainfall in June and maximum rainfall in a 48-hour period, June of 2010 was an extreme month.

Food Supply

Diet composition

There was little inter-annual variation in the taxonomic composition of the diet of Caspian terns nesting on ESI during 2001-2011, except for the steady decline in the proportion of clupeids (shad [*Alosa sapidissima*], herring [*Clupea pallasi*], and sardines [*Sardinops sagax*]) in the diet, and a corresponding increase in the proportion of salmonids (*Oncorhynchus* spp.) in the diet. The inverse relationship between consumption of salmonids and clupeids was highly significant ($R^2 = 0.57$, df $= 9$, p $= 0.007$; Figure 3), and did not exist between any other two families of prey in the Caspian tern diet. In 2010 and 2011, clupeids made up 9% and 6% of tern diets, respectively, whereas the average percent clupeids in the tern diet during 2001-2009 was 17%. The decline in average proportion of clupeids in the diet as a function of year was highly significant ($R^2 = 0.60$, df $= 9$, p $= 0.005$; Figure 4). There was a highly significant positive correlation ($R^2 = 0.54$, df $= 9$, p $= 0.009$) between average annual productivity of Caspian terns at ESI and percent clupeids in the diet during 2001-2011.

Predators

Eagle disturbance

The rate of bald eagle disturbance to the Caspian tern colony on ESI

(disturbances/hour of colony observation) exhibited a general seasonal trend across

years, with the disturbance rate tending to be high in May and declining as the

breeding season progressed. Eagle disturbance rates at the tern colony during May

increased from 2001 to 2008, but decreased from 2008 to 2011 (Figure 5). The

frequency of eagle disturbances to the tern colony in June, however, increased

significantly from 2001 to 2011 ($R^2 = 0.53$, df = 6, p = 0.041). In 2010, the rate of

eagle disturbance was 0.55/h in May and 0.21/h in June, whereas in 2011 the rate of

eagle disturbance was 0.31/h in May and 0.51/h in June, a higher eagle disturbance

rate in June than had previously been recorded.

The incidence of major eagle disturbance events (defined as disturbances that

flushed 50% or more of the adult Caspian terns on the colony) increased from 2001

to 2011. In May 2010, 26% of all eagle disturbance events were major (causing at

least half of the adult terns on-colony to flush), while in June 2010 this value was

58%. In comparison, during May 2011, 67% of all eagle disturbance events were

major, and in June 2011 this value increased to 80%.

There were no significant correlations between the rate of eagle disturbance

to the tern colony and average productivity of the tern colony. There was, however,

the suggestion of a negative correlation between the rate of major eagle disturbances

to the tern colony during June and tern colony productivity ($R^2 = 0.47$, df = 6, p = 0.06).

In May 2010 there were 13 eagle disturbance events at the tern colony that were recorded between 05:00 and 13:00 PDT ("morning") and 14 eagle disturbance events that were recorded between 13:00 and 19:00 PDT ("afternoon"); in May 2011, 7 eagle disturbance events were recorded in the morning and 17 were recorded in the afternoon. In June 2010 there were 5 eagle disturbance events at the tern colony that were recorded in the morning and 7 eagle disturbance events recorded in the afternoon, while in June 2011 there were 8 eagle disturbance events recorded in the morning and 19 eagle disturbances recorded in the afternoon. These disturbance events were only those recorded during fish-watch observations, and consequently represent an index to eagle disturbance rates, not a measure. There was also a highly significant positive relationship between river discharge in May and eagle disturbance rate in June during 2004-2011 ($R^2 = 0.90$, df = 6, p = 0.0003; Figure 6).

The median duration of each eagle disturbance event at the tern colony was similar in May and June of each year. The median duration of eagle disturbance events changed little from 2003 to 2009, with an average duration of 37 sec in May and 35 sec in June. The median duration of eagle disturbance events in 2010 was somewhat below average in May, with a median duration of 29 sec, but median duration was 35 sec in June. The median duration of eagle disturbance events in 2011, however, far exceeded the longer term average, with a median duration of 68 sec in May and 90 sec in June. In 2011, crepuscular disturbances of the Caspian tern

colony by bald eagles resulted in temporary total colony abandonment by all adult terns, and during these crepuscular disturbance events the undefended nest contents were depredated by gulls at a high rate (Figure 7).

Gull predation on tern nest contents

The rate of predation by glaucous-winged/western gulls on the contents of Caspian tern nests at the ESI colony was generally higher in May than in June. The median gull predation rate during 2007-2009 was 0.29 events/hr in May and 0.19 events/hr in June. During the 2010 nesting season this pattern changed dramatically, with the gull predation rate averaging 0.22 events/hr in May and 0.79 events/hr in June; the latter rate was far in excess of the longer-term average. During the 2011 nesting season, the gull predation rate averaged 0.51 events/hr in May, considerably higher than the longer-term average for May. There were no data collected on gull predation rates during June 2011 because all Caspian tern nests on the ESI colony had failed by the first week of June.

Kleptoparasitism by gulls

There was a significant negative correlation between the observed average rate of gull kleptoparasitism and average annual productivity at the ESI Caspian tern colony ($R^2 = 0.38$, df = 9, p = 0 .04). There was a significant increase in rates of gull kleptoparasitism from 2001 to 2011 ($R^2 = 0.51$, df = 9, p = 0.01; Figure 8). The average gull kleptoparasitism rate during 2001-2009 was 0.05 fish kleptoparasitized/bill-load fish monitored. In 2010 the kleptoparasitism rate, averaged over the entire nesting season, was 0.078 fish kleptoparasitized/bill-load

fish, while in 2011 the kleptoparasitism rate was 0.076 fish kleptoparasitized/bill-

load fish.

Model Selection

After exploring the relationship of each explanatory variable with the

response variable "average annual nest success" independently, and assessing the

correlations among all explanatory variables (Table 1), I created a set of *a priori*

additive models to compare the predictive power of models containing a single

explanatory variable to models containing multiple explanatory variables (Table 2).

Because of the highly significant positive correlation between river discharge in May

and June (Table 1), a single variable combining the average flow rate during May

and June was used in model selection. When ranked using ΔAICc scores, the model

that best fit the data contained only the explanatory variable 'river discharge during

May and June', and had a model weight of 0.52 (R^2 = 0.51, p = 0.013; Table 2).

None of the other candidate models was competitive with this top model (ΔAICc <

2.0; Table 2).

DISCUSSION

I found that the declining reproductive success experienced by Caspian terns

nesting at the ESI colony during 2001-2011 was associated with several top-down

and bottom-up factors, plus their interactions. But a consistent and key explanatory

variable for the variation in reproductive success was the increasing discharge in the

Columbia River during the study period. There was an inverse correlation between

average river discharge during the nesting season and average annual reproductive success at the ESI colony, and the model that included just the explanatory variable of average river discharge during May and June was the model best supported by the data. Also, the high positive correlation between river discharge in May and June and rates of eagle disturbance events in June illustrates the link between the effects of bottom-up and top-down factors on nesting success at the ESI Caspian tern colony.

Freshwater input to the Columbia River estuary can have a direct effect on the recruitment, residence time, and location in the estuary of marine forage fishes (Jassby et al. 1995, Loneragan and Bunn 1999, Purtlebaugh and Allen 2010). It is likely that increased river discharge altered fish assemblages and reduced the abundance of marine forage fish (Loneragan and Bunn 1999), leading to food stress in Caspian terns nesting at ESI. Reduced availability of marine fish prey was apparently responsible for the decline in clupeids in the tern diet and the increase in out-migrating salmonids in the diet. Lower availability of marine forage fish may also be responsible for prey switching in gulls and bald eagles, leading to increased top-down pressure on the tern colony. Suryan et al. (2006) found that the influence of top-down or bottom-up forces on seabird colonies in Prince William Sound, Alaska oscillated depending on physical processes governing phytoplankton bloom. Similarly, at the ESI Caspian tern colony, the primary physical process that influenced bottom-up and top-down effects on tern reproductive success appeared to be river discharge.

Bottom-up Regulation

During both the 2010 and 2011 nesting seasons, Columbia River discharge was high throughout the season; recorded discharge at Bonneville Dam in 2011 were the highest in the previous decade (http://www.cbr.washington.edu/dart/dart.htm). Lyons (2010) found that in years with relatively high river discharge, Caspian terns at the ESI colony had correspondingly high predation rates on salmonid smolts, and this study supports that association. As river discharge increased between 2007 and 2011, salmonids as a proportion of the diet also increased, while the proportion of clupeids in the diet decreased. This is in contrast to the finding that steelhead smolt survival in the mid-Columbia River increased with increasing river discharge (Antolos et al. 2005, Hostetter et al. 2012). Increased flow likely shortens the period of out-migration, as well as estuary residence time, for some out-migrating salmonid smolts (Hostetter et al. 2012, Weitkamp et al. 2012).

High freshwater inputs to an estuary can alter a fish's preferred habitat within the estuary, thereby altering its likelihood of encountering predators (Jassbyet al. 1995, Loneragan and Bunn 1999). Weitkamp et al. (2012) suggested that, during high flow events in the Columbia River estuary, juvenile salmonids may move laterally into the shallows. Increased turbidity during high flows on the mid-Columbia River were associated with higher susceptibility of steelhead smolts to Caspian tern predation (Hostetter et al. 2012). Both of these factors could make steelhead smolts more vulnerable to plunge-diving predators, such as Caspian terns, when river discharge is high. Weitkamp et al. (2012) also found that high river

discharge led to greater stratification in the Columbia River estuary, creating a predominately fresh-water lens on the surface. This could effectively change the assemblage of forage fish available to Caspian terns, which capture prey near the surface.

Jassby et al. (1995) described freshwater input as the principal physical factor determining the characteristics of an estuary, but it is not clear how changes in river discharge, stratification, and nutrient input affect biotic interactions within the estuary. Estuarine species react differently to increased freshwater inputs (Kimmerer 2002, Purtlebaugh and Allen 2010). Differences in salinity preference between clupeids and out-migrating salmonid smolts are likely responsible for Caspian terns foraging more heavily on salmonids in years of high river discharge. Also, marine forage fish may be inhibited from entering or recruiting into the estuary during high river discharge, and this could make them a less reliable food resource for the terns (Lyons 2010, Purtlebaugh and Allen 2010, Weitkamp et al. 2012). Alternatively, Caspian terns may alter their preferred foraging areas during high discharge events or years, resulting in higher encounter rates with salmonids compared to clupeids.

The average annual proportion of salmonids in the diet of Caspian terns nesting at ESI increased during the study period. The low overall abundance of forage fish in the estuary during 2008-2011, however, may have played a role in the declining reproductive success at the ESI colony (Weitkamp et al. 2012; Figure 9). The 2011 breeding season saw the lowest indexes to forage fish abundance and available biomass (excluding sticklebacks [*Gasterosteus aculeatus*]) of all the years

when data were available. Low forage fish availability was possibly due to

unprecedented high freshwater inputs to the Columbia River estuary during the 2011

nesting season (Weitkamp et al. 2012). Seabird studies that have examined prey

availability in relation to reproductive output have demonstrated the link between

years of low food availability and poor breeding success (Harris and Wanless 1997,

Hall and Kress 2004, Votier et al. 2009, Satterthwaite et al. 2012). Productivity is

affected both directly and indirectly by poor foraging conditions. Food availability

can directly affect adult or chick survival through its effects on nutrition. In addition,

chronically low food availability can lead to longer-distance adult foraging trips,

longer foraging trip duration, lower adult nest attendance, and, ultimately, nest

abandonment (Anderson et al. 2005). Lower adult nest attendance can also result in

periods when neither parent is present at the nest, leaving eggs and chicks

unprotected and vulnerable to predation at the nest (Coulson and Thomas 1985,

Roberts and Hatch 1993, Finney et al. 1999, White et al. 2006).

Top-Down Constraints

Bald eagle disturbance events during May and June of 2011 played a

prominent role in the subsequent failure of all Caspian tern nesting attempts at the

ESI colony during the 2011 breeding season. Bald eagle populations were at

artificially low levels for decades because of persecution and high levels of persistant

organochlorine pesticides in the environment and in eagle prey (Watson et al. 2002,

Vennesland and Butler 2004, White et al. 2006). Since the banning of DDT in the

U.S. in 1972, bald eagle populations in the Pacific Northwest have experienced a

dramatic recovery with numbers of occupied territories expanding throughout

Oregon and Washington, and both east and west of the Cascade Range (Watson et al.

2002, White et al. 2006). There was an astonishing 738% increase in occupied

territories along the lower Columbia River between 1978 and 2007 (Isaacs and

Anthony 2011). The return of this top predator has had a dramatic effect on many

seabird colonies, where the presence of bald eagles often initiates major changes in

nesting success and interspecific interactions (Isaacs and Anthony 2011, Hipfner et

al. 2012).

Aside from direct predation on the breeding adults at a seabird colony, bald

eagles can have major indirect effects by causing disturbances that allow smaller

predators, such as gulls and corvids, to more readily prey on nest contents (Verbeek

1982, Parrish et al. 2001, Vennesland and Butler 2004, White et al. 2006). ESI is

home to a sizable breeding colony of glaucous-winged/western gulls (ca. 6,000

breeding pairs), some of which specialize in kleptoparasitism of Caspian terns and

predation on Caspian tern nest contents. These gulls can be highly aggressive and

may use their size advantage to displace terns from their nest scrapes and consume

both eggs and chicks (SC, pers. obs.). The advent of high rates of bald eagle

disturbance at the ESI Caspian tern colony in 2011 offered the gulls many additional

opportunities for depredation of tern nest contents. This same association between

increased bald eagle presence and higher nest depredation rates on colonial seabirds

has been documented at other breeding colonies, and in some cases has been linked

with subsequent colony failure (Verbeek 1982, Parrish et al. 2001, Vennesland and Butler 2004).

Bald eagles are not new to East Sand Island, and likely were common there before Caspian terns began to nest on the island (Watson et al. 1991). Nevertheless, the prolonged period of targeted predation on nesting Caspian terns that occurred on East Sand Island in 2011 was unprecedented for this colony. It was not through the loss of depredated adult terns, but through the disturbance and subsequent loss of nest contents to secondary nest predators, that bald eagles most negatively affected the ESI Caspian tern colony (Verbeek 1982, Parrish 2001, Vennesland and Butler 2004, White et al. 2006). The frequency, magnitude, timing, and duration of colony disturbance events are important limiting factors for colony productivity because of the facilitation of nest predation events that were widespread in their impact on colony productivity. In 2011, only a handful of adult Caspian terns were actually taken by bald eagles, but over 7,000 active Caspian tern nests failed because of gulls that opportunistically depredated unattended nests during eagle disturbances.

In addition to increased nest depredation rates, the increase in kleptoparasitism rates by gulls likely contributed to the gradual decline in reproductive success of Caspian terns at ESI. Although kleptoparasitism is widespread among animal taxa (Morand-Feron et al. 2007), it is a behavior most often employed opportunistically, or at times when food availability is low (Flower et al. 2013). At ESI, however, some gulls have come to rely heavily on kleptoparasitism as a food source. The increased rate of kletoparasitism seen at ESI

since 2001 is likely the result of specific individuals relying more and more on kleptoparasitizing bill-load fish from terns. Recent studies suggest that animals will kleptoparasitize over other foraging behaviors when kleptoparasitism opens up otherwise unattainable foraging niches (Flower et al. 2013). Caspian terns are able to more efficiently capture fish prey compared to gulls; if, as our study suggests, high river discharge has reduced the availability of forage fish to avian predators in the Columbia River estuary, it would be adaptive for gulls to put more energy into stealing high-value prey from terns.

In 2012, the same pattern of eagle disturbance and subsequent nest depredation and kleptoparasitism by gulls began to develop on the Caspian tern colony at ESI as in 2011. But complete failure of the tern colony was averted in 2012 through limited lethal removal of gulls from the tern colony (n = 50) under permit (A. Peck-Richardson, OSU, pers. comm.). This supports the hypothesis that a segment of the ESI gull population had become highly reliant on tern kleptoparasitism as a source of food.

CONCLUSIONS

Our results, although correlative, suggest that interactions between bottom-up and top-down regulating factors, driven largely by variable freshwater input to the estuary, limits Caspian tern breeding success at the large breeding colony on East Sand Island. We found that river discharge was highly negatively correlated to nesting success at this colony. Freshwater inputs during the tern breeding season

have increased as productivity of the tern colony has declined. Recent higher than average river discharge has likely led to declines in the abundance and diversity of marine forage fishes in the estuary, which in turn can limit food availability to many estuary consumers. The change in prey availability has likely contributed to the increase in bald eagle disturbance at the Caspian tern colony, and the corresponding increase in depredation rates on tern nests by gulls, due to the synergistic impact of eagle disturbance and gull predation on tern nesting success.

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Table 3.1. Pearson's correlation matrix showing the correlations between all explanatory variables used in the analysis of potential factors explaining variation in average nesting success of Caspian terns at the East Sand Island colony. The top number is the Pearson's correlation coefficient, the bottom number is the P-value, representing the significance of the correlation for each pair of explanatory variables. Bolded values represent those correlations significant at the $\alpha = 0.05$ level

	Productivity	June River Discharge	Kleptoparasitism Rate	May Disturbance Rate	Max. Rain in 48 hrs	June Disturbance Rate
June River Discharge	**-0.7**	---	---	---	---	---
	0.02	---	---	---	---	---
Kleptoparasitism Rate	**-0.62**	**0.7**	---	---	---	---
	0.04	**0.02**	---	---	---	---
May Disturbance Rate	-0.12	0.36	**0.74**	---	---	---
	0.78	0.38	**0.04**	---	---	---
Max. Rain in 48 hrs	-0.22	0.33	0.08	0.28	---	---
	0.51	0.32	0.82	0.50	---	---
June Disturbance Rate	-0.39	**0.81**	0.69	0.55	-0.15	---
	0.34	**0.01**	0.06	0.16	0.73	---
May River Discharge	**-0.66**	**0.83**	**0.68**	0.31	-0.17	**0.95**
	0.03	**0.002**	**0.02**	0.46	0.62	**0.0003**

Table 3.2. The top five linear models selected from the set of models based on *a priori* hypotheses of the factors affecting productivity of the Caspian tern colony on East Sand Island in the Columbia River estuary. No models included in the model set included explanatory variables that were significantly correlated ($\alpha = 0.05$) with each other. Models are ranked in ascending order based on ΔAICc score. The ΔAICc score is calculated by subtracting each model's AICc score from the lowest AICc score, i.e., the model best supported by the available data.

Rank	Model[a]	AICc	ΔAICc	W_i
1	*Avg. River Discharge in May and June	11.1	0.0	0.52
2	Avg. River Discharge in May and June + Avg. Annual Kleptoparasitism Rate	13.6	2.5	0.15
3	Avg. Annual Kleptoparasitism Rate	13.7	2.6	0.14
4	Avg. River Discharge in May and June + Maximum Rainfall in 48 hrs	13.7	2.6	0.14
5	Avg. Annual Kleptoparasitism Rate + Maximum Rainfall in 48 hrs	16.1	5.0	0.04

* denotes the model best supported by the data and the only competitive candidate model among the model set

[a] Variables included in model selection: 1) average river discharge in May and June,
    2) average annual kleptoparasitism rate, 3) maximum rainfall in 48 hours

Figure 3.1. Anuual productivity (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 year during 2001-2011.
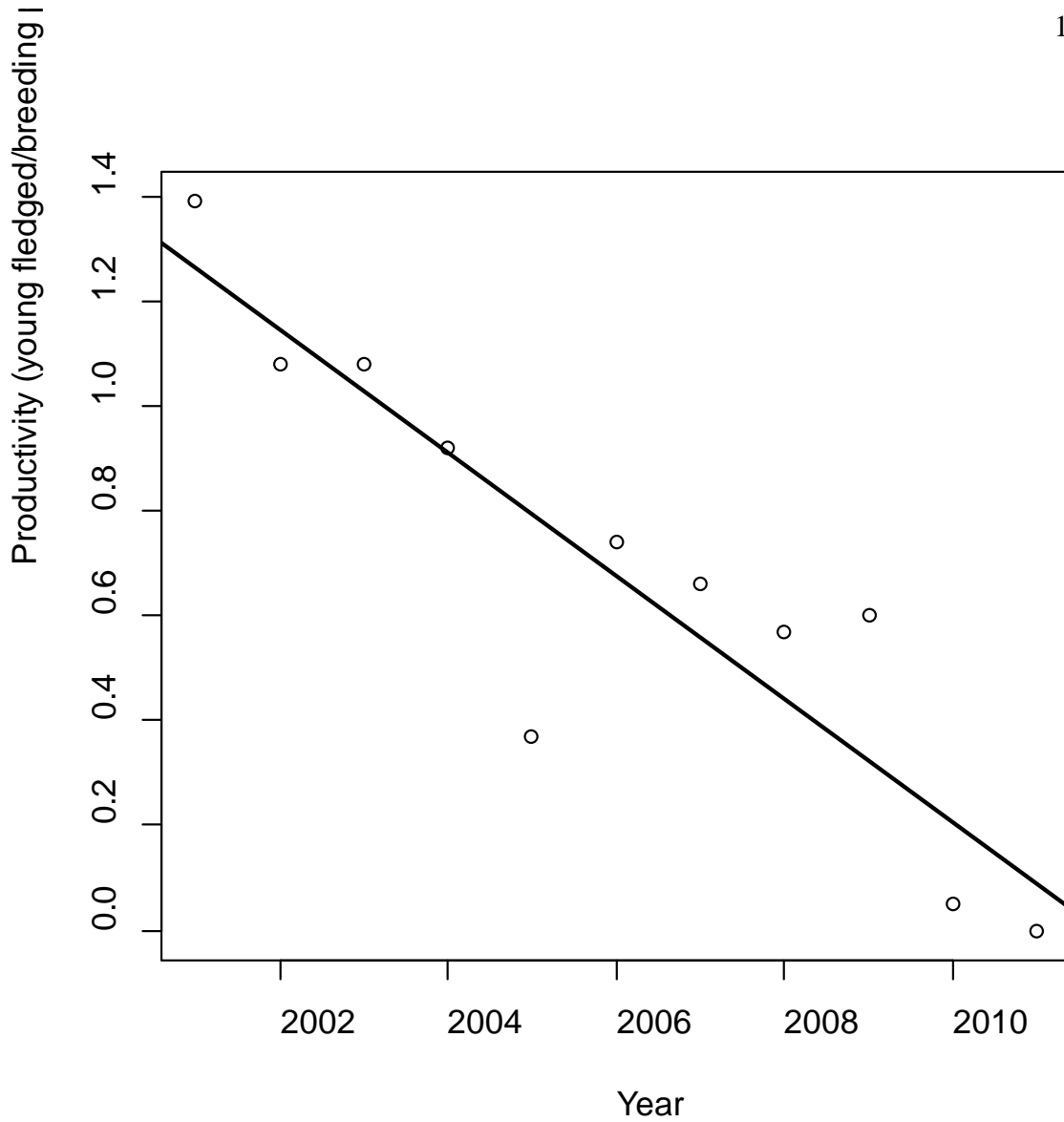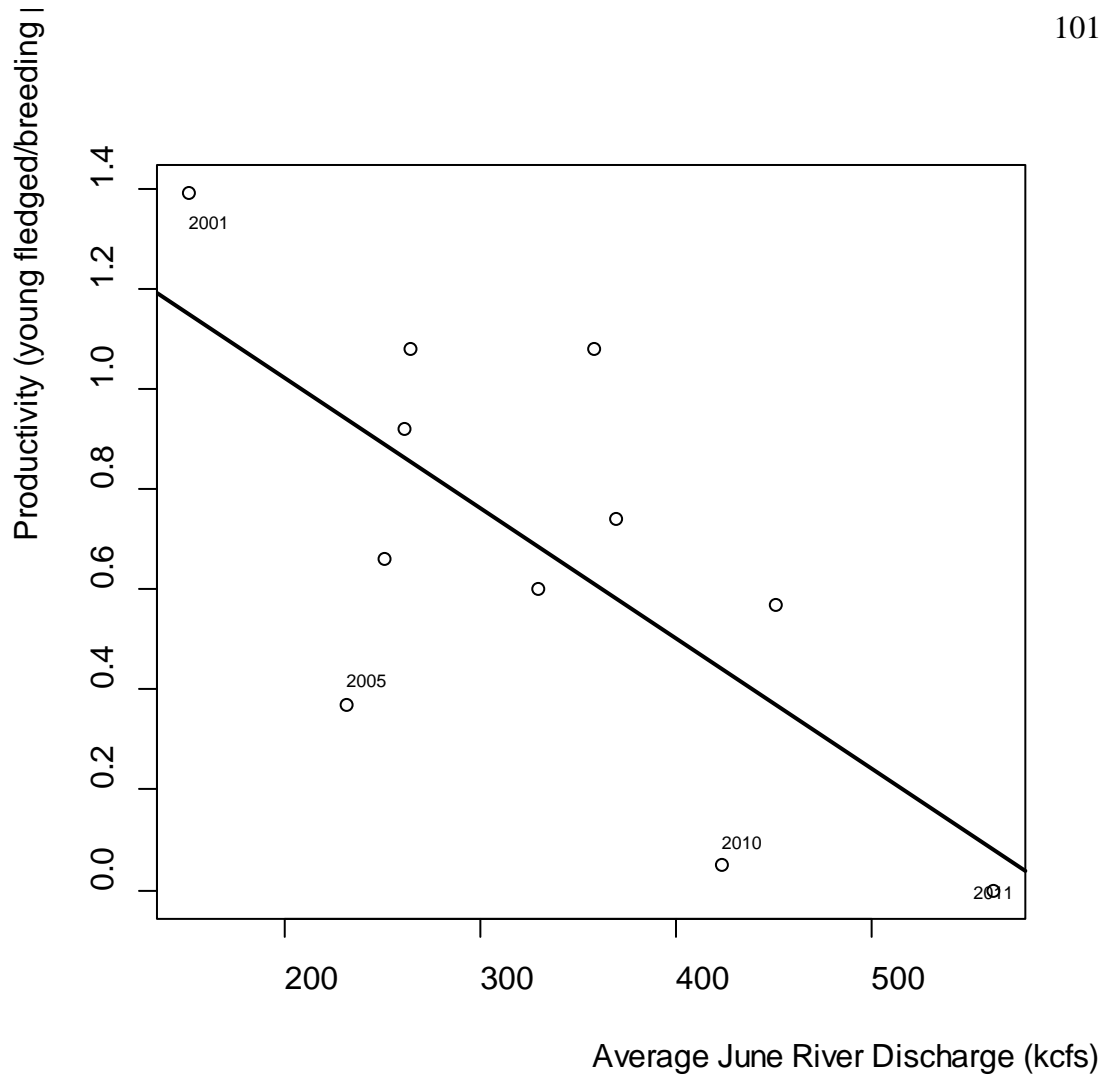
Figure 3.2. Annual productivity (average number of young fledged per breeding pair) of the Caspian tern breeding colony on East Sand Island in the Columbia River estuary as a function of average discharge of the Columbia River (thousands of cubic feet per sec) in June during 2001-2011.
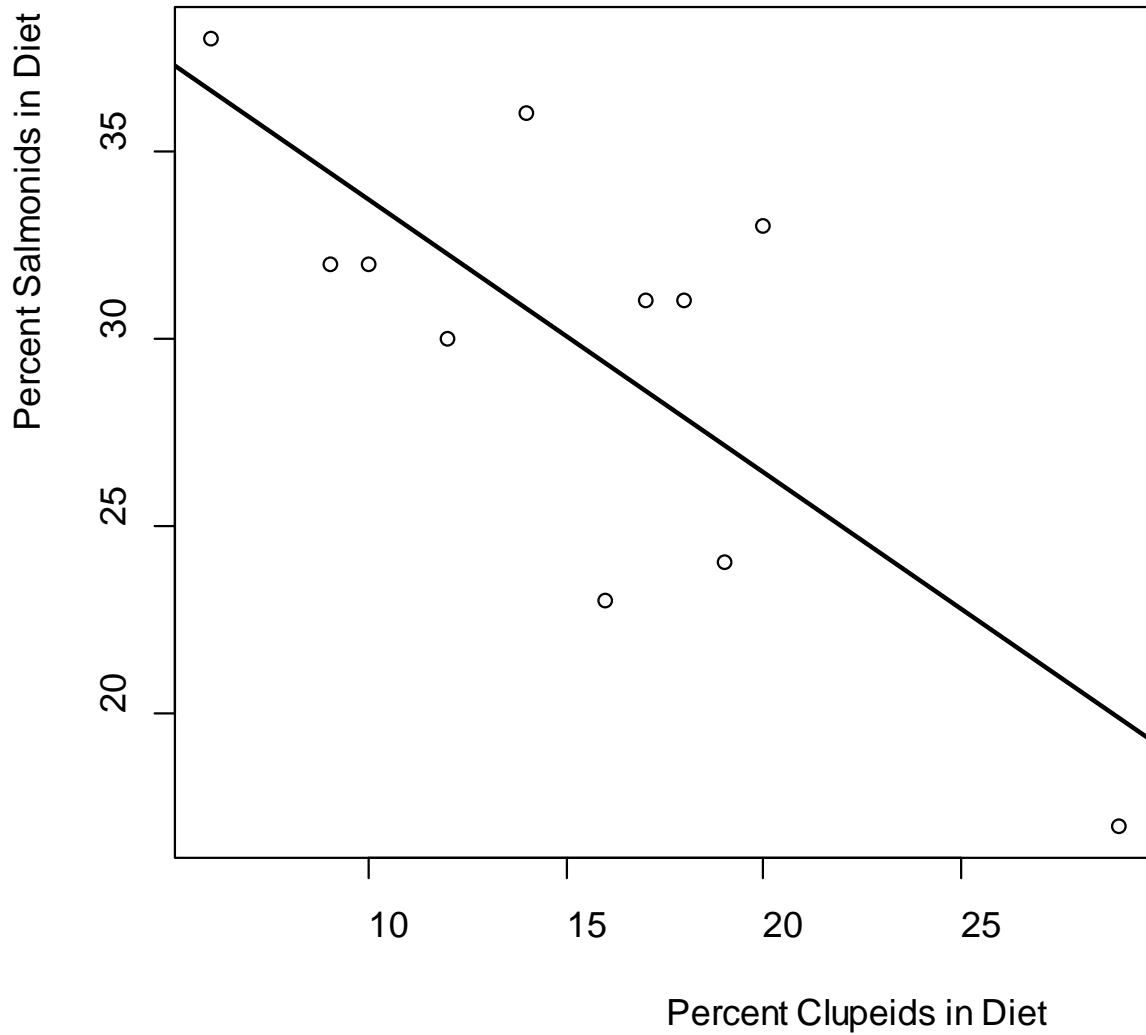
Figure 3.3. Average proportion of salmonids in the diet as a function of the average proportion of clupeids in the diet for Caspian terns nesting at East Sand Island in the Columbia River estuary during 2001-2011.
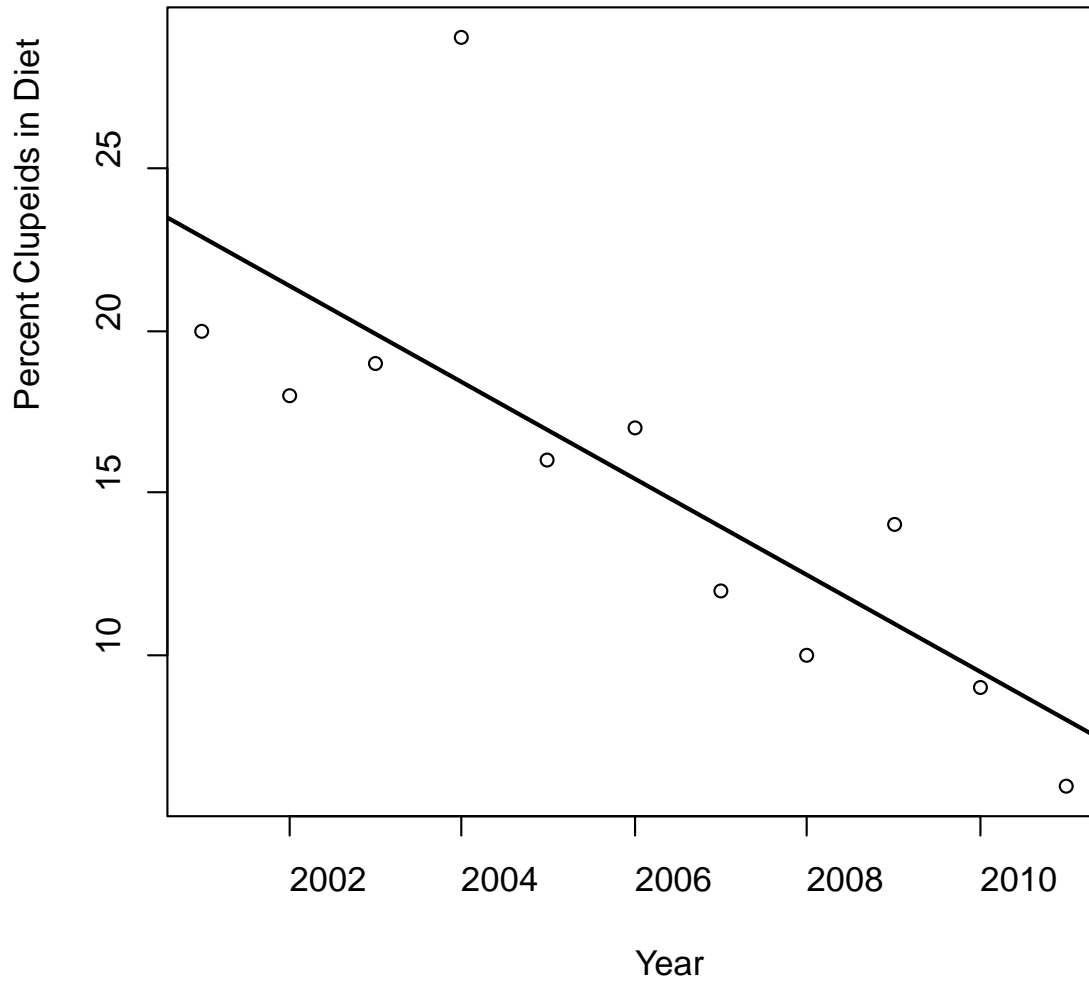
Figure 3.4. Average proportion of clupeids in the diet of Caspian terns nesting at East Sand Island in the Columbia River estuary as a function of year during 2001-2011.
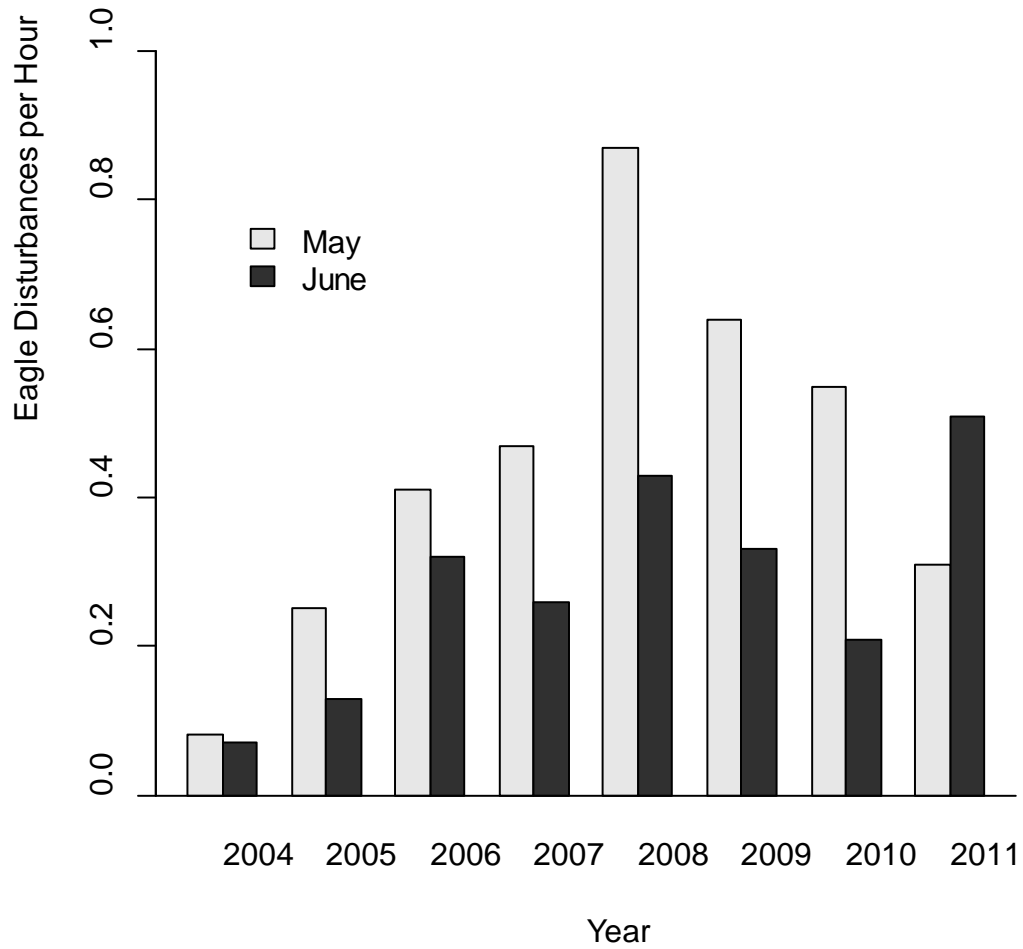
Figure 3.5. Rate of bald eagle disturbance events (average number per hour of observation) at the Caspian tern breeding colony on East Sand Island, Columbia River estuary in May and June during 2001-2011.
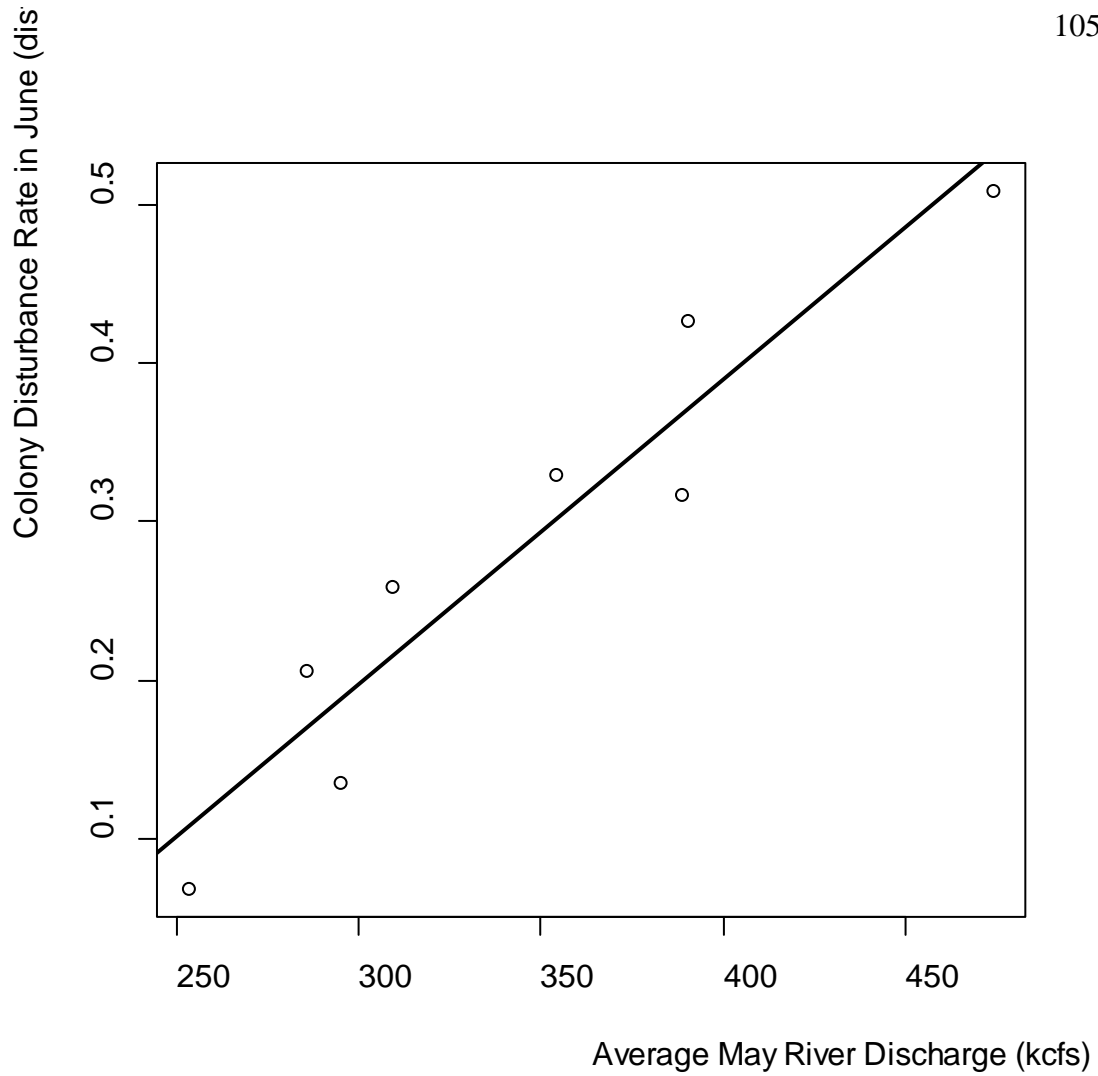
Figure 3.6. The average rate of bald eagle disturbance events at the Caspian tern colony on East Sand Island in the Columbia River estuary during June (disturbances/hour of observation) as a function of average river discharge (kcfs) during May for the period 2004-2011.
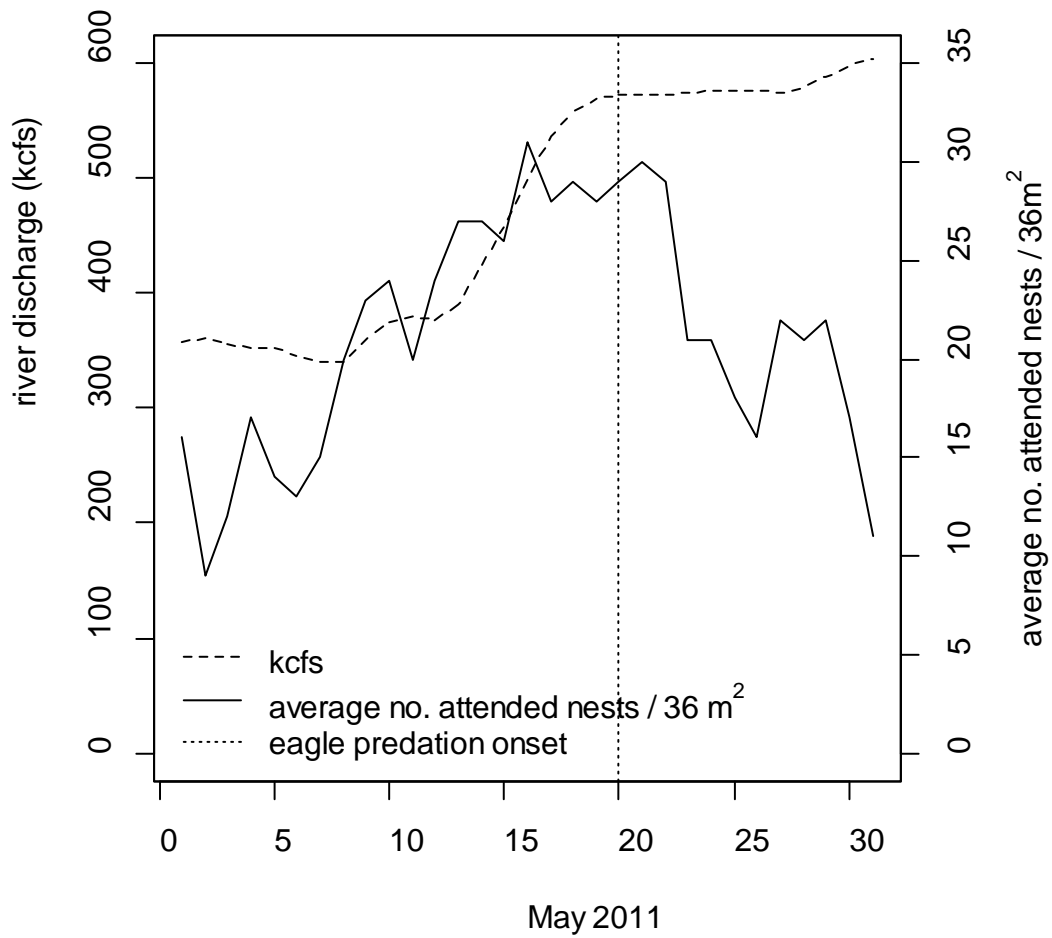
Figure 3.7. Average discharge (kcfs) of the Columbia River and average number of occupied nests in 12 36 m^2 plots on the Caspian tern breeding colony at East Sand Island during May 2011. The dotted vertical line denotes the onset of regular crepuscular eagle disturbances, which ultimately led to the failure of all active Caspian tern nests at this colony by the end of May.
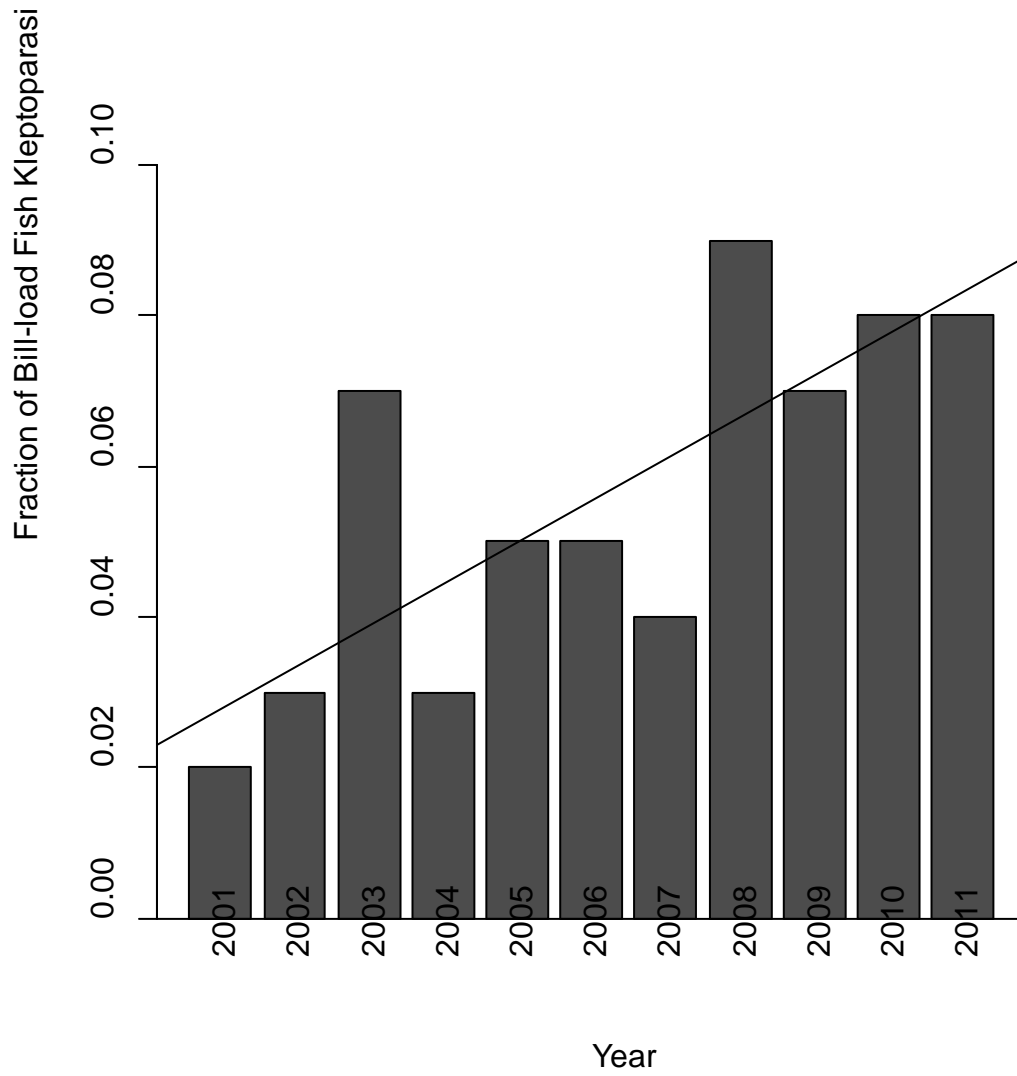
Figure 3.8. Proportion of fish being transported by adult Caspian terns to the breeding colony on East Sand Island in the Columbia River estuary that were kleptoparasitized by glaucous-winged/western gulls as a function of year.
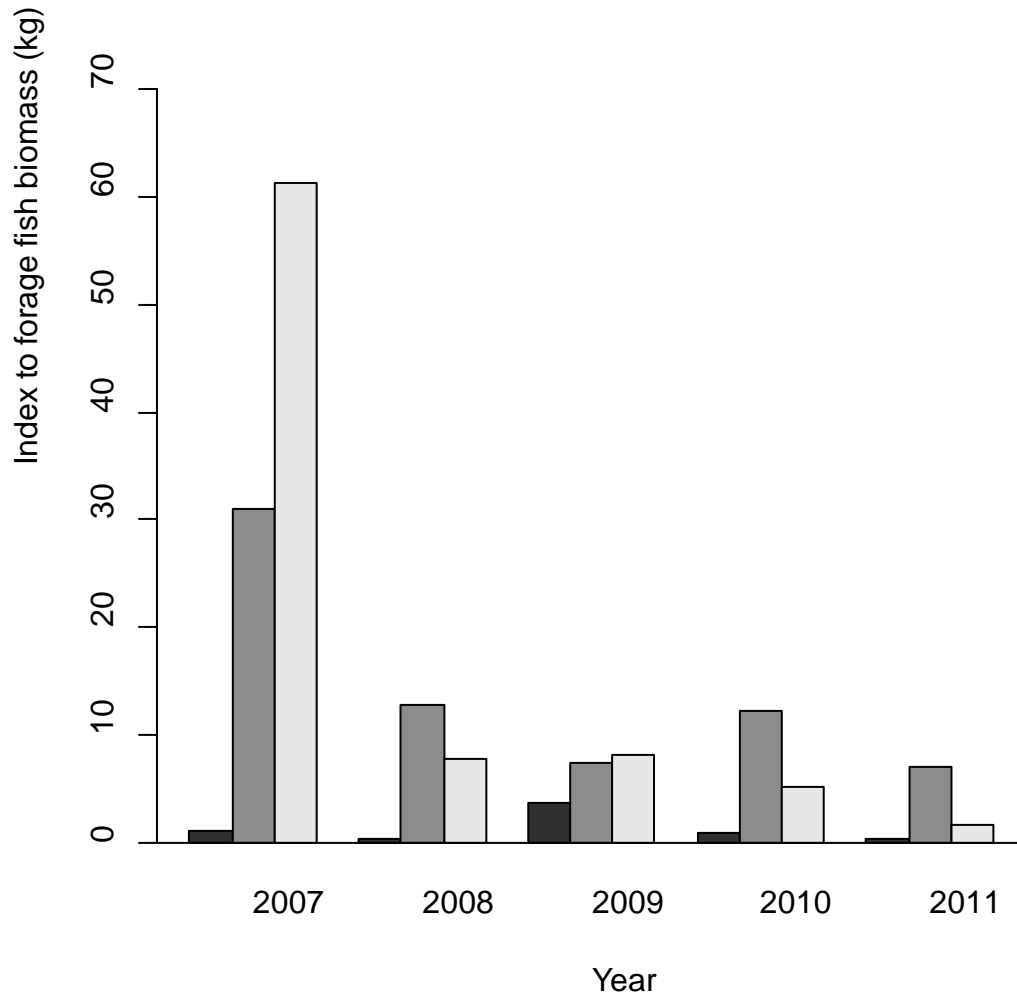
Figure 3.9 . Index to biomass availability of forage fish in the lower Columbia River estuary based on trawl samples collected in April (dark gray), May (intermediate gray), and June (light gray) during 2007-2011. Stickleback (*Gasterosteus aculeatus*) were removed from the data-set before calculating biomass because this prey type, although abundant is rarely consumed by Caspian terns nesting in the Columbia River estuary. *Data from L.A. Weitkamp, with permission.*

CHAPTER 4. SYNOPSIS AND CONCLUSIONS

Stefanie Collar

The objective of my study was to understand the dynamics of the Caspian tern super-colony on East Sand Island (ESI) in the Columbia River estuary, Oregon by investigating the behavior of individual breeders, as well as the behavior of the colony as a whole, over two breeding seasons. I was interested in (1) the degree of nest site fidelity exhibited by breeding terns in successive years and its relationship to reproductive success, and (2) how the interaction of top-down and bottom-up forces influenced average nesting success across the entire colony, and caused the observed trends in nesting success at the East Sand Island colony from 2001 to 2011. The planned management to reduce the area of nesting habitat at this relatively long-lived tern colony provided an excellent opportunity to investigate how Caspian terns in the Columbia River estuary evaluate prospective breeding colonies - at both large and small scales.

My results, although correlative, strongly suggest that interactions between bottom-up and top-down regulating factors, driven largely by inter-annual variation in freshwater input to the estuary, limits Caspian tern breeding success at this colony. I found that nesting success at this large breeding colony was negatively correlated with river discharge. Freshwater inputs to the estuary during the tern breeding season have increased as productivity of the tern colony has declined. Higher than average river discharge likely has led to declines in the abundance and diversity of marine forage fishes in the estuary, which in turn can limit food availability to many estuary consumers. This change in prey availability has likely contributed to an increase in

bald eagle disturbance at the tern colony, and a corresponding increase in depredation rates on tern nests by gulls, due to the synergism between eagle disturbance and gull nest predation rates.

Elevated river discharge may depress the availability of key forage fish prey types for Caspian terns nesting on ESI, as well as for other avian species that depend on the Columbia River estuary during the spring and summer months. Somewhat surprisingly, I found a reciprocal relationship between the proportion of clupeids (sardines, herring, and shad) in Caspian tern diets and the proportion of salmonids (salmon and steelhead) in their diets. Lyons (2010) had previously found that as river discharge increased, so did the proportion of salmonids in tern diets, but it was interesting to reveal that river discharge may be limiting the ability of terns to capture clupeids, causing the terns to shift their focus to the more accessible out-migrating salmonids.

The mechanism responsible for this dietary shift is not known. It is possible that there are behavioral differences between salmonids and clupeids when salinity declines in the lower estuary due to a large influx of freshwater in years of high river discharge. High discharge and the associated strong current may physically alter the river channel, which in turn displaces fish from their normal spatial use of the river and estuary (Jassby et al. 1995). Also, a 'freshwater lens' may develop in estuaries experiencing extremely high river discharge, where the water becomes stratified close to the area of tidal influx, and this could create a physical or chemical barrier to marine fishes with low tolerance for freshwater (Weitkamp 2012). This stratification

could also entice out-migrating salmonids undergoing smoltification to remain near the surface in freshwater, making them more susceptible to predation from surface plunge-divers like Caspian terns. Perhaps smoltification is more stressful in years when river flows are high and fast-moving freshwater transports salmonid smolts quickly to the mixing zone at the mouth of the river, where they are not physiologically prepared to enter seawater and, consequently, may be more vulnerable to tern predation. Hostetter et al. (2012) found that turbid river water was associated with increased tern predation rates on juvenile salmonids in the mid-Columbia River, especially during years of high river flows, perhaps because fish in turbid water are slower to seek cover to avoid predators.

Estuaries are highly productive and species-rich environments that support complex and intricate food webs. When food resources are diminished in estuaries, the consequences are far-reaching, and may manifest in higher-order interactions not at first attributable to food-scarcity. The dataset on the Caspian tern colony at ESI encompasses more than a decade (2000-2013) of detailed records, providing a unique opportunity to investigate some of the ecological links between this large tern colony and the estuarine ecosystem. As the proximate cause of the complete nesting failure at the ESI Caspian tern colony in 2011, the high frequency and intensity of disturbance by bald eagles, concurrent with the peak in tern incubation, seemed the likely cause. It appeared as though bald eagles were at last keying in on the tern colony as a permanent food source, and that future nesting success of Caspian terns on ESI was unlikely. Eagles have consistently targeted nesting cormorants on ESI,

depredating adults, eggs, and fledglings, but the tern colony has rarely been subjected to direct predation pressure from bald eagles.

As eagle numbers have rebounded in the last 40 years, seabird colonies on the western coast of North America have been increasingly targeted as sources of prey (Parrish et al. 2001, Isaacs and Anthony 2011). Murre (*Uria aalge*) colonies from Washington to northern California have been especially hard hit by increased eagle visitation, and studies have documented the resulting loss of productivity and increased frequency of colony abandonment (Parrish et al. 2001). East Sand Island is home to tens of thousands of roosting and nesting seabirds each year, so it seemed inevitable that as bald eagle numbers recovered in the Columbia River estuary, there would be more frequent disruptions to the colony, and the reproductive success of Caspian terns on ESI would remain well below previous levels.

A lack of alternative prey, however, may have contributed to increased eagle disturbance of the tern colony, rather than simply an increase in the frequency of adult terns in eagle diets. Bald eagles can exploit a wide range of prey resources, and in the Columbia River estuary they do a great deal of scavenging and kleptoparasitizing of prey from other predators (Isaacs and Anthony 2011, Harvey et al. 2012). This includes scavenging salmon and sturgeon carcasses, as well as stealing smaller prey from osprey (*Pandion haliaetus*) and terns. High river flows might result in fewer carcasses making their way to shore where eagles can access them. Also, if decreased prey availability causes smaller predators to capture less prey, eagles may find it increasingly difficult to exploit them through

kleptoparasitism, eventually leading to nesting Caspian terns becoming a new and necessary alternative food resource.

It is also possible that the depredation of nesting Caspian terns on the ESI colony in 2011 by bald eagles was the work of a single eagle that had moved into the estuary from another territory where it had learned to successfully exploit seabird colonies. The eagle disturbances to the colony in 2011 occurred at nearly the same time each day: immediately preceding and following sunrise and sunset, respectively. This suggests that the same individual eagle was responsible for repeated instances of tern depredation on the colony. The consistency of the timing of these disturbances suggests that the individual eagle responsible could have been targeting the tern colony as it commuted to and from the island each day. Many eagles in the estuary nest and roost on the mainland close to East Sand Island, but apparently concentrate their foraging efforts around the cormorant colony and remaining on the island for the duration of each day (S.C., pers. obs.) Although groups of eagles were always present on ESI during the day, there was never more than one eagle at a time attempting to capture incubating Caspian terns on the colony.

The eagle disturbance to the ESI Caspian tern colony during 2011 was so effective in causing tern nest failure because of the synergism between predation on adult terns by eagles and nest predation by gulls. Caspian terns are often found breeding in close proximity to gulls and, although in some colonies there are no agonistic interactions between the species, on the ESI colony the nest contents of

terns have long been a reliable food resource for a segment of the gull breeding population (Roby et al. 2002, Antolos et al. 2005). There was a significant negative relationship between the rates of gull kleptoparasitism on the Caspian tern colony at ESI and tern reproductive success. Declining Caspian tern reproductive success was also linked with the increasing rate of eagle disturbance to the tern colony over the past 10 years. This is a trend that could have to do with the longevity of this colony, or with individual nesting gulls becoming more adept at kleptoparasitism and passing this tradition on to their offspring. Gulls are long-lived and breed on ESI annually, so this cultural transmission is certainly possible. It is also possible that the increases in gull kleptoparasitism and nest depredation rates are linked to the ongoing food stress attributable to the sustained high river discharge since the mid-2000s. Gulls, like eagles and terns, may simply be responding to a decline in readily available prey by shifting their focus to an alternate prey type or foraging technique.

The outcome of my analysis clearly suggested that the Caspian tern colony at ESI was under increasing pressure from multiple predators and a declining prey base. I also showed, however, how these stressors were apparently linked to river discharge. It is possible that when river discharge declines in the future, the ecology of the Caspian tern colony in the Columbia River estuary may again resemble the ecology and productivity recorded during the first few years following colony restoration. The two nesting seasons that have elapsed since my study was completed seem to support this hypothesis. The 2013 breeding season saw reduced river discharge, with a corresponding increase in reproductive success and decrease

in eagle disturbance to the Caspian terns at the ESI colony. Tracking Caspian tern

diets, eagle disturbance rates and gull depredation over the next decade, in

association with river discharge, would be an excellent follow-up for testing some of

the hypotheses that were supported in my study.

I, I also investigated how individual breeding birds were using the nesting

habitat on the ESI Caspian tern colony, both within and across breeding seasons, in

addition to investigating the ecology of the ESI Caspian tern colony on a large scale.

In this study I found that Caspian terns nesting at ESI showed a degree of nest site

fidelity that has not usually been attributed to a species that often nests in ephemeral

habitats and moves within a network of prospective breeding colonies between

successive years. Individuals at the ESI Caspian tern colony behaved as if the large,

contiguous area of nesting habitat was made up of many smaller sub-colonies, to

which they were philopatric. This philopatry led to nesting in close proximity to

known individuals across years. Previous breeding success seemed to be less

important in nest placement decisions for Caspian terns nesting at the ESI colony

than has been found in other studies of the species. Nest site selection at the ESI

colony seemed to depend mostly on the continued availability of suitable nesting

habitat on ESI, despite increased nest predation rates and declining area of nesting

habitat. This may be due to a regional limitation in suitable colony sites for Caspian

terns that reinforces nest site fidelity.

Breeding colonies of birds are often assumed to function as a cohesive unit,

but it may be more informative to investigate the behavior of individuals or small

groups within the greater colony (Coulson and Thomas 1985, Cuthbert 1988).

Although there may be synchronous arrival and nest initiation at a colony, this could

be the result of an affinity among many discrete groups of individuals, more so than

fidelity of all birds to a colony. As more research is conducted in the area of animal

personality, it is becoming increasingly evident that organisms make decisions based

on individual traits that may differ from the traits or impulses of conspecifics

(Dingemanse and Reale 2005). When a breeding colony is evaluated not as a super-

organism, but instead as groups of individuals expressing disparate 'personality'

traits, there are new and interesting comparisons that can be made concerning the

behavior and functioning of the colony as a whole.

For example, I found that focal terns in this study exhibited two very

different responses after the colony-wide nest failure at the beginning of June of

2011. I found that these responses were associated with whether or not the

individual tern had been displaced from the nest site used in the previous year. This

effect (DISPLACED vs. NON-DISPLACED) did not explain all of the variation,

however, and this could be because behavioral responses were a product of different

'personality types'; essentially, individuals displaying different responses when

faced with the same problem. Traditionally, it has been thought that breeding birds

rely on cues from conspecifics or past experience to select appropriate breeding

colonies, but it is difficult to always be confident in this assumption (Coulson 1995,

Boulinier et al. 2008). It is possible that this 'win-stay/lose-switch' hypothesis is an

over-generalization, or simply describes one personality type that may predominate

in a particular colony or region. With continued monitoring of individual behaviors, we may better understand the underlying drivers of decision-making and how different personality types may interact within a colony.

It is also assumed that 'public information' is used by breeding individuals to select a suitable nest site (Boulinier et al. 2008). Perhaps Caspian terns depend on East Sand Island as an information center, and this dependency is why the propensity to change colony sites seems to be so uncommon among Caspian terns nesting at ESI. Much of the work on Caspian tern nest site fidelity has been conducted on the Great Lakes population (Cuthbert 1988). Terns in the Great Lakes nest on a series of associated islets, whose availability as nesting habitat changes in each season depending on fluctuating water levels. Among these nesting birds, colony fidelity is necessarily low and group adherence appears high. In contrast, the Pacific Northwest region has fewer colony sites offering suitable nesting habitat and refuge from predators, other than East Sand Island, suitable colony sites are all at considerable distances. Perhaps this isolation results in the slowed transmission of information about alternative colony sites within a nesting season, requiring terns in the area to rely more heavily on a single information center - ESI - than would be the case in habitat with multiple options for ephemeral nesting habitat.

I found that Caspian terns are not only philopatric to the East Sand Island colony in general, but more specifically to certain areas of the colony. This was very surprising given that Caspian terns are considered a species with low nest site-fidelity, readily switching colonies to compensate for the ephemeral nature of their

preferred breeding habitat (Cuthbert 1988). East Sand Island, unlike much of the Caspian tern nesting habitat in the Great Lakes, has been available each year for over a decade, potentially allowing breeding terns to become more attached to the colony than previously observed in the species.

Additionally, the size of the ESI colony, much larger than most Caspian tern breeding colonies, may have necessitated a higher degree of site fidelity in these individuals. With thousands of breeding individuals, as well as over half a hectare of contiguous bare-sand habitat, breeding birds that established their territory close to the same location each year may have gained an advantage. Streamlining the process of re-establishing pair bonds, choosing a territory, and initiating breeding is thought to enhance reproductive success, so perhaps increased site-fidelity began to develop at this colony in the early years of its existence (Cuthbert 1988, Fairweather and Coulson 1995). If so, we would expect site fidelity to be strongest in older individuals who have bred at ESI for many consecutive years. More research should be conducted on known-age breeding individuals at ESI, and whether the number of consecutive breeding seasons at ESI influences fidelity to areas within the colony site.

It is commonly believed that avian breeding colonies are organized from the center out, with experienced individuals arriving first in order to establish central territories, and with the periphery of the colony consisting of inexperienced or subordinate individuals (Antolos et al. 2005). At ESI we did not see evidence of this phenomenon, as even early initiating individuals tended to return to their previously

held territories, whether those areas were located on the edge of the colony or in the center. The focal individuals whose nests were closest together during the two study years, as well as the individuals that retained the highest percentage of marked neighbors, were located on the northern edge of the colony, not in the center. Focal individuals whose original nesting territories in 2010 were lost to the reduction in nesting habitat on the south edge of the colony in 2011 overwhelmingly moved into the same relative position on the colony within the new habitat boundaries. Further study could investigate individual fidelity to 'neighborhoods' on the colony, and whether these 'sub-colony' areas are occupied from the center out. Also, my investigation of group adherence could be conducted at other tern colonies to compare nesting behavior and site fidelity between colonies of different size and duration of persistence.

McNicholl (1975) suggested that group adherence may be difficult to recognize at stable bird colonies and, indeed, I was unable to detect an influence of group adherence on the nest site placement of banded Caspian terns. I also did not detect any evidence of group cohesion among Caspian terns displaced from ESI, based on re-sighting of banded birds at other colonies during the 2011 nesting season. As management continues at East Sand Island, however, there is the opportunity to study this phenomenon more closely. There is evidence that multiple banded Caspian terns from one colony have relocated to a different colony (Suzuki 2012), but until my study there was no detailed record of how closely associated these individuals had been at their former colony.

The results of my study suggest that managers should not expect that dissuading Caspian terns from nesting on a portion of the colony site will result in all, or even the majority of the birds relocating to an alternative colony. Also, my findings suggest that the birds that do leave the managed colony will not necessarily relocate as a group, or over the period of one breeding season. Most importantly, managers should consider that although dissuasion may disrupt breeding activities, there is no guarantee that the displaced terns will leave the area. In my study, terns that left the Columbia River estuary and took up residence elsewhere comprised a small percent of all focal individuals. Most of the focal birds that ceased breeding after the colony failed in 2011 continued to use East Sand Island for the duration of the field season. This means that the desired effect of reducing avian predation on salmonids through colony dissuasion was limited at best.

Cuthbert (1988) also suggests that nesting failures resulting from a disturbance that may threaten adult survival are more likely to result in the adult switching to a different breeding colony the following year, and she gives many examples of this. It is possible that this pattern was not observed at ESI in 2011 because of the dynamic interaction of predators that caused the nesting failure at the ESI tern colony. Although the ultimate cause of tern colony failure in 2011 was bald eagle disturbance, the proximate cause of tern nest failures was gulls depredating nest contents, not life-threatening to adult terns. Burger (1982) suggested that black skimmers (*Rynchops niger*) changed colonies between breeding seasons based on whether or not a source of nest failure was 'predictable'. In her study, skimmers

would abandon a colony site if the previous nesting season had been ruined by mammalian predators, but not if it was the result of flooding or high water. If mammalian predators are able to access a colony one year, Burger (1982) argued, it is likely they will be able to do so in following years, while flooding events typically do not predictably occur in the same area. The eagle predation events at the ESI tern colony were relatively short-lived compared to the continuous nest depredation by gulls. Gulls have been constant nest predators at ESI since the inception of the colony, and so may be a predictable source of egg and chick loss that Caspian terns take for granted when nesting on ESI. This is yet another discrepancy in the behavior of the ESI Caspian terns as compared with other colonial nesting birds that have been studied.

It is possible that in some populations of low-fidelity colonial species, such as terns, human alteration or management of breeding habitats can can select for philopatry. Increased philopatry could have unintended consequences. Even when habitat management is implemented for the good of the target species, colony sites that remain artificially available for many generations could select for individuals less likely to pioneer and colonize new colony sites. In the event that these colonies begin to attract predators or deplete local prey resources, the advantages of the colony could be overshadowed by the colony's new attribute as an ecological trap or population sink.

Alternatively, the process of pioneering new colony sites, or relocating to existing alternative colony sites, may be a gradual one. At a colony as large as ESI it

may be difficult to distinguish small groups of associated individuals, especially if those groups of birds are not all uniquely marked. At large, persistent colonies the trait of group adherence may selected against as a criterion for choosing a breeding location until conditions change drastically enough to cause breeding birds to again rely on pre-existing relationships with neighboring birds to help find a suitable nesting location.

Regardless of the underlying mechanism, the fact that Caspian terns in the Pacific Northwest region of the conterminous U.S. are unexpectedly faithful to the colony site on East Sand Island is noteworthy. Despite perennial human activity on the island, diminishing productivity, declining food resources, increased distiurbance from predators, and decreased suitable habitat on the main, contiguous nesting area, Caspian terns continue to return to East Sand Island. So far, the ESI Caspian tern colony has seen more of an increase in nest density than a decrease in the number of breeding pairs. Although elsewhere in the region artificial nesting habitat has been constructed to compensate for the loss of nesting habitat on East Sand Island, the majority of banded Caspian terns have remained faithful to the Columbia River estuary. This suggests that although conditions may have become less favorable for successful breeding in the estuary, it is still a primary nesting location for Caspian terns, and should be valued and protected as such.

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