AN ABSTRACT OF THE THESIS OF

Allison Patterson for the degree of Master of Science in Wildlife Science presented on November 13, 2012
Title: Breeding and Foraging Ecology of Caspian Terns Nesting on Artificial Islands in the Upper Klamath Basin, California

Abstract approved:

Daniel D. Roby

Availability of suitable nesting habitat that is free of nest predators and provides access to adequate prey resources within commuting distance is a major factor limiting seabird populations. Caspian terns (*Hydroprogne caspia*) in western North America have shifted their breeding habitat from naturally occurring habitats in interior wetlands, lakes, and rivers to primarily human-created habitats in coastal bays and estuaries. This shift has brought Caspian terns into conflict with fisheries of conservation concern, in particular anadromous salmonids. Prior to the 2010 breeding season, three artificial islands were built in the Klamath Basin National Wildlife Refuge (NWR) Complex as alternative nesting habitat for Caspian terns currently nesting at the world's largest colony for the species, near the mouth of the Columbia River, Oregon.

I investigated the efficacy of habitat creation (island building) and social attraction (decoys and recorded vocalizations) for establishing new breeding colonies in the Upper Klamath Basin, California. In 2010, approximately 258 pairs of Caspian terns attempted to nest on the new islands and raised an average of 0.65 fledglings/breeding pair; in 2011, 222 pairs attempted to nest and raised an average of 0.11 fledglings/breeding pair. Competition with California and ring-billed gulls (*Larus californicus* and *L. delawarensis*) for nesting space, gull predation on Caspian tern eggs and chicks, low water levels, and depredation by great horned owls (*Bubo virginianus*) were the primary factors limiting colony development and productivity, especially in 2011. The immediate response by Caspian terns to habitat creation and social attraction in the Upper Klamath Basin demonstrates that these can be effective restoration techniques to establish new breeding colonies where nesting habitat is a major limiting factor; however, continued management of other limiting factors (e.g., control of on-colony predators and competitors) will likely be necessary to promote the development of established, self-sustaining breeding colonies on these artificial islands.

Efforts to conserve and restore seabird colonies can be compromised by low prey availability within foraging distance of the breeding colony. I used GPS telemetry to study the fine-scale foraging behavior of Caspian terns nesting at two newly established colonies and cluster analysis to discriminate behavioral states based on movement characteristics. Terns breeding at the Sheepy Lake colony spent less time at the colony (52% of the day) than terns breeding at the Tule Lake colony (74%).

Caspian terns breeding at Sheepy Lake foraged more extensively than terns breeding at Tule Lake; the foraging trips of Sheepy Lake terns lasted longer (median = 186 min) and were longer-distance (27 km) compared to those of Tule Lake terns (55 min and 6 km, respectively). Between-colony differences in foraging behavior corresponded to 5% lower average body mass of breeding adults and significantly lower size-adjusted body mass of chicks at the Sheepy Lake colony compared to the Tule Lake colony. Proximity to high-quality foraging areas influenced the foraging behavior and parental care of breeding Caspian terns, which in turn had effects on nesting success. The successful use of GPS telemetry to study the fine-scale foraging behavior of Caspian terns represents a significant advance in our ability to investigate the foraging ecology of this species and other moderate-sized seabirds.

Breeding and Foraging Ecology of Caspian Terns Nesting on Artificial Islands in the Upper Klamath Basin, California

by
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APPROVED:

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

Allison Patterson, Author

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CONTRIBUTION OF AUTHORS

Dr. Daniel D. Roby acquired funding, assisted with study design and interpretation of results, and provided editorial comments for all chapters. Dr. Donald E. Lyons provided training in field methods, and assisted with study design, data analysis, and interpretation of Chapters 2 and 3. Ken Collis acquired funding and assisted with logistics for Chapter 2.

TABLE OF CONTENTS

Page

TABLE OF CONTENTS (Continued)

Page

TABLE OF CONTENTS (Continued)

Page

LIST OF FIGURES

LIST OF FIGURES (Continued)

Figure Page

LIST OF TABLES

Breeding and Foraging Ecology of Caspian Terns Nesting on Artificial Islands in the Upper Klamath Basin, California

CHAPTER 1: GENERAL INTRODUCTION

Allison Patterson

Caspian terns (*Hydroprogne caspia*) in western North America have, over the last century, shifted their breeding habitat from solely interior wetlands, lakes, and rivers to primarily coastal bays and estuaries (Gill and Mewaldt 1983, Wires and Cuthbert 2000, Suryan et al. 2004). By 2000, nesting by the Western North America population of Caspian terns had become more concentrated, and most of the adults in the population nested at a single colony, on East Sand Island in the Columbia River estuary (Suryan et al. 2004). Concurrent with the shift from the interior to the coast, there has been a shift from nesting in natural habitats to nesting at anthropogenic sites, such as dredge spoil islands and salt pond levees (Gill and Mewaldt 1983, Suryan et al. 2004); this shift has brought Caspian terns into increasing conflict with fisheries, in particular where Caspian tern colonies co-occur with runs of anadromous salmon and steelhead (salmonids; *Oncorhynchus* spp.) that are of conservation concern (Roby et al. 2002, Roby et al. 2003).

East Sand Island, located near the mouth of the Columbia River, supported what was likely the largest Caspian tern breeding colony in the world during the first decade of the 21st Century (Wires and Cuthbert 2000, Roby et al. 2002). Caspian terns nesting at this colony are estimated to consume annually between 4 million and 7 million juvenile salmonids out-migrating to the Pacific Ocean from throughout the Columbia River basin (USFWS 2005). A federal management plan entitled “Caspian Tern Management to Reduce Predation of Juvenile Salmonids in the Columbia River Estuary” (hereafter the Caspian Tern Management Plan; USFWS 2005) was developed by the U.S. Fish and Wildlife Service (USFWS) and the U.S. Army Corps

of Engineers (USACE), in consultation with other federal, state, and tribal natural resource management agencies.

As part of this plan, the USACE seeks to provide 3.2 ha (8 acres) of new alternative nesting habitat for Caspian terns in Oregon and California, while reducing the amount of Caspian tern nesting habitat on East Sand Island from 2.0 ha (5 acres) to 0.4 ha (1 acre; USFWS 2005). This reduction in nesting habitat is expected to reduce the number of Caspian terns nesting at East Sand Island from approximately 9,000 - 10,000 pairs to approximately 2,500 – 3,200 pairs (USFWS 2005), thereby substantially reducing predation rates on juvenile salmonids. Redistributing breeding Caspian terns from one large colony in the Columbia River estuary to several smaller colonies over a broad geographic area could also help reduce the risk to the Western North America Caspian tern population from catastrophic local events (Cuthbert and Wires 1999, Roby et al. 2002).

By the start of the 2010 breeding season the USACE had prepared a total of 2.95 ha (7.3 acres) of new nesting habitat on eight islands constructed in interior Oregon and California. Due to drought conditions, only 1.54 ha (3.8 acres) of alternative nesting habitat, on five new islands, was available to breeding Caspian terns in 2010 (Roby et al. 2011). By 2011, a total of 2.75 ha (6.8 acres) of alternative nesting habitat, on seven new islands, was available (Roby et al. 2012). This allowed the USACE to reduce the amount of nesting habitat available for Caspian terns on East Sand Island to 1.25 ha (3.1 acres) in 2010 and 0.81 ha (2.0 acres) in 2011. Consequently, the lowest number of breeding Caspian terns (ca. 7,000 breeding pairs)

were recorded at East Sand Island since 1999 (ca. 1,400 breeding pairs; Roby et al. 2011, Roby et al. 2012). Further habitat reduction will likely be necessary to further reduce the size of the East Sand Island tern colony and bring it down to the proposed colony size. Therefore, the USACE will probably build more islands as alternative nesting habitat to compensate for further reductions in the area of Caspian tern nesting habitat on East Sand Island (USFWS 2005).

As part of the Caspian Tern Management Plan, the USACE constructed three artificial islands in the Klamath Basin National Wildlife Refuge Complex prior to the 2010 breeding season, one in Tule Lake National Wildlife Refuge (NWR) and two in Lower Klamath NWR (USFWS 2009). These sites were chosen because the Upper Klamath Basin historically supported large numbers of breeding colonial waterbirds, including Caspian terns (Finley 1907, Finley and Bohlman 1907, Finley 1915). Small numbers of Caspian terns still breed in some years at Clear Lake NWR (Gill and Mewaldt 1983, Shuford and Craig 2002), and hundreds of non-breeding Caspian terns use the Upper Klamath Basin during the breeding season (Shuford et al. 2004). Because of this history of nesting and continuing use, resource managers believed that the number of Caspian terns breeding in the Upper Klamath Basin was limited by the availability of suitable nesting habitat. Most of the natural wetland habitat in Tule Lake and Lower Klamath Lake was lost due to agricultural development during the early 20th Century (NRC 2004), and the wetlands that remain within the Klamath Basin NWRs do not provide suitable nesting substrate for Caspian terns (USFWS 2009). In low-water years, most or all of the islands in Clear Lake that serve as nesting

habitat for Caspian terns become land-bridged, accessible to mammalian predators, and therefore unsuitable for breeding colonial waterbirds (Moreno-Matiella and Anderson 2005). Constructing artificial nesting islands for Caspian terns in the Klamath Basin NWRs could help to meet the requirements of the Caspian Tern Management Plan while restoring the breeding population of Caspian terns to the Upper Klamath Basin (USFWS 2009).

Caspian terns nest in habitats that are naturally ephemeral and will readily colonize new breeding sites when conditions become favorable (Collis et al. 2002, Suryan et al. 2004). Social attraction techniques (decoys and recorded vocalizations) have been used to attract terns (*Sterna* spp. and *Hydroprogne*) to nest at restored and artificial nesting locations since the early 1980s (Kress 1983, Roby et al. 2002). If availability of nesting habitat is limiting the numbers of Caspian terns nesting in the Upper Klamath Basin, then with the aid of social attraction techniques the breeding population of Caspian terns should increase quickly following the creation of suitable artificial nesting habitat.

Availability of nesting habitat may not be the only factor limiting breeding by Caspian terns in the Upper Klamath Basin and other inland basins. Nest predation by mammalian or avian predators (Hatch 1970, Stienen et al. 2001, Donehower et al. 2007), competition for nesting habitat with gulls (Stienen and Brenninkmeijer 1999, Garcia et al. 2010), or low availability of forage fish within commuting distance of potential colony sites (Becker et al. 1997, Davoren and Montevecchi 2003) could also limit the size, number, and reproductive success of Caspian tern colonies in the Upper

Klamath Basin. Colonial breeding birds are known to use social information and personal experience about reproductive performance in dispersal decisions (Danchin et al. 1998, Doligez et al. 2003, Tims et al. 2004). Management actions to maximize tern nesting success on artificial islands while incipient breeding colonies become established could be important for attracting and retaining prospecting terns, and ultimately establishing self-sustaining colonies on these islands (Schmidt 2004).

Caspian terns are central-place foragers during the breeding season; their foraging behavior is constrained by the need to return to the nest to incubate eggs and provision young (Orians and Pearson 1979). For central-place foraging species, habitat availability is inversely related to distance from the central location (Matthiopoulos 2003, Wakefield et al. 2009). As the distance from the nest site to suitable foraging habitat increases, breeding birds face greater trade-offs between allocating resources to themselves for survival and maintenance vs. their offspring, and between spending time foraging vs. spending time at the nest to care for and guard offspring. Colonial-nesting terns can be further constrained because suitable nesting habitat may not be available in proximity to readily available prey resources.

Advances in satellite- and GPS-telemetry have created new opportunities to study individual behavior and movements, as well as how animals interact with features of their environment (Schick et al. 2009, Cagnacci et al. 2010). Investigations of the foraging behavior of Caspian terns have been limited to studies using radio-telemetry because of the relatively small average body size of Caspian terns (ca. 650 g) and the difficulty of recapturing individual terns on the breeding colony. In this

study I use micro-GPS transmitters weighing less than 15 g with remote download capabilities to collect fine-scale movement data on breeding Caspian terns over multiple days without having to retrieve the data logger. This represents a significant advancement in our ability to study the basic foraging behavior of moderate-sized seabirds and species that cannot be reliably recaptured. I use cluster analysis to infer behavioral state from movement data (Van Moorter et al. 2010); this allows me to quantify foraging behavior and examine how daily activity rates, foraging effort, and foraging distribution are affected by colony location and breeding status.

Chapter 2 of this thesis addresses the question of whether nesting habitat availability was the primary factor limiting the numbers of Caspian terns breeding in the Upper Klamath Basin. Based on data collected during the first two years following island construction, I evaluate the response of Caspian terns to the creation of artificial nesting habitat and social attraction at three new islands designed to restore the breeding population of Caspian terns in the Upper Klamath Basin. I monitored the development of tern colonies on the three artificial islands, the number of breeding pairs, their reproductive success, and the factors limiting colony size and reproductive success at each site. I compare the total number of breeding pairs at all colonies within the Upper Klamath Basin to data from the previous thirteen years and compare reproductive success at the new colonies to current and long-term productivity at other established Caspian tern colonies in the Pacific Coast region. Additionally, I collected data on predation from and competition with other species at the three artificial islands

in order to identify any other factors that could limit the size, productivity, and persistence of Caspian tern colonies that develop on these islands.

In Chapter 3 I investigate whether prey availability could affect the success of Caspian terns nesting at artificial islands in the Upper Klamath Basin. I used GPS-transmitters to measure foraging behavior of Caspian terns breeding at Sheepy Lake and Tule Lake during late-incubation and early chick-rearing. My study represents the first time that GPS telemetry has been used to continuously track breeding Caspian terns and provide a complete profile of individual foraging trips and daily movements. This approach allowed me to quantify and compare foraging effort by Caspian terns nesting at two newly established colonies that were about 30 km from each other. I also measured adult body mass and chick body condition (size-adjusted body mass) to determine whether differences in foraging behavior between tern colonies were associated with differences in the physical condition of terns.

Key objectives of my study were to (1) determine if nesting habitat availability was the primary factor limiting the numbers of Caspian terns breeding in the Upper Klamath Basin, (2) assess the initial reproductive success of Caspian terns that attempted to nest at the new islands, (3) identify factors that could limit the size and nesting success of Caspian tern colonies that form on the new islands, and (4) assess foraging conditions for Caspian terns breeding at these three artificial islands. The results of this study will provide information to assist in the restoration of Caspian tern breeding colonies in the Upper Klamath Basin, while contributing to the development

of effective restoration and conservation approaches for colonial waterbirds in general. My use of GPS telemetry to study the fine-scale foraging behavior of Caspian terns will provide new insight into the foraging ecology of this species, such as time spent commuting, actively foraging, and resting during a foraging trip. This technology will also provide a much clearer picture of foraging habitat selection and use by Caspian terns. Finally, my research will help expand the application of this recently developed technology to the study of smaller, more moderate-sized seabirds.

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CHAPTER 2: BREEDING ECOLOGY OF CASPIAN TERNS NESTING ON ARTIFICIAL ISLANDS IN THE UPPER KLAMATH BASIN, CALIFORNIA

Allison Patterson, Daniel D. Roby, Donald E. Lyons, and Ken Collis

ABSTRACT

We investigated the efficacy of using decoys and recorded vocalizations to attract Caspian terns to nest on three artificial islands in the Upper Klamath Basin, California. Caspian terns attempted to breed at all three artificial islands in the first year social attraction was installed. There was a significant increase in the total number of Caspian terns breeding in the Upper Klamath Basin following creation of new nesting islands. In 2010, approximately 258 pairs of Caspian terns attempted to nest on the islands and estimated productivity was 0.65 fledglings/breeding pair. In 2011, approximately 222 pairs attempted to nest on the islands and estimated productivity was 0.11 fledglings/breeding pair. Competition with California and ring-billed gulls (*Larus californicus* and *L. delawarensis*) for nesting space and gull predation on Caspian tern eggs and chicks were the primary factors affecting colony size and productivity on one island, whereas low water levels and depredation by great horned owls (*Bubo virginianus*) were factors affecting colony development and productivity at the other two islands. The immediate occupancy of artificial islands, as well as the increase in the number of breeding pairs and colonies indicates that availability of nesting habitat was limiting breeding by Caspian terns in the Upper Klamath Basin. However, continued management of other potential limiting factors (e.g., control of on-colony predators and competitors) will likely be necessary to promote the development of established, self-sustaining breeding colonies on these artificial islands.

INTRODUCTION

Caspian terns (*Hydroprogne caspia*) in western North America have, over the last century, shifted their breeding habitat from solely interior wetlands, lakes, and rivers to primarily coastal bays and estuaries (Gill and Mewaldt 1983, Wires and Cuthbert 2000, Suryan et al. 2004). By 2000, nesting by the Western North America population had also become concentrated at a single colony site: East Sand Island in the Columbia River estuary, Oregon, which as of the early 2000s accounted for approximately two-thirds of all breeding pairs in this Caspian tern population (Suryan et al. 2004). Concurrent with the shift from the interior to the coast, there has been a shift from nesting in natural habitats to nesting at anthropogenic sites, such as dredge spoil islands and salt pond levees (Gill and Mewaldt 1983, Suryan et al. 2004); this shift has brought Caspian terns into increasing conflict with fisheries, in particular where Caspian tern colonies co-occur with runs of anadromous salmon and steelhead (salmonids; *Oncorhynchus* spp.) that are of conservation concern (Roby et al. 2002, Roby et al. 2003).

Caspian terns nesting at East Sand Island, a 25-ha island near the mouth of the Columbia River, are estimated to consume annually between 4 million and 7 million juvenile salmonids out-migrating to the Pacific Ocean from throughout the Columbia River basin (Roby et al 2002, USFWS 2005). A federal management plan entitled "Caspian Tern Management to Reduce Predation of Juvenile Salmonids in the Columbia River Estuary" (hereafter the Caspian Tern Management Plan; USFWS

2005) was developed by the U.S. Fish and Wildlife Service (USFWS) and the U.S. Army Corps of Engineers (USACE), in consultation with other federal, state, and tribal agencies. The goal of the Caspian Tern Management Plan was to reduce the impact of tern predation in the estuary on survival of juvenile salmonids listed as threatened or endangered under the U.S. Endangered Species Act, while maintaining the viability of the Western North America population of Caspian terns.

As part of this plan, the USACE seeks to provide 3.2 ha (8 acres) of new alternative nesting habitat for Caspian terns in Oregon and California, while reducing the amount of Caspian tern nesting habitat on East Sand Island from 2.0 ha (5 acres) to 0.4 ha (1 acre; USFWS 2005). This reduction in nesting habitat is expected to reduce the number of Caspian terns nesting at East Sand Island from approximately 9,000 – 10,000 pairs to approximately 2,500 – 3,200 pairs (USFWS 2005), thereby substantially reducing predation rates on juvenile salmonids in the Columbia River estuary. Redistributing breeding Caspian terns from one large colony in the Columbia River estuary to several smaller colonies over a broad geographic area could also help reduce the risk to the Western North America Caspian tern population from catastrophic local events (Cuthbert and Wires 1999, Roby et al. 2002).

Prior to the 2010 breeding season, the USACE constructed three artificial islands in the Klamath Basin National Wildlife Refuge Complex, one in Tule Lake National Wildlife Refuge (NWR) and two in Lower Klamath NWR. This area was chosen for construction of artificial tern islands because the Upper Klamath Basin historically supported large numbers of breeding colonial waterbirds, including

Caspian terns (Bailey 1902, Finley and Bohlman 1907). Small numbers of Caspian terns still breed in some years at Clear Lake NWR in the Upper Klamath Basin (Shuford and Craig 2002), and hundreds of non-breeding Caspian terns use the Upper Klamath Basin during the breeding season (Shuford et al. 2004). Because of this history of nesting and continuing use, resource managers believe that the number of Caspian terns breeding in the Upper Klamath Basin is primarily limited by the availability of suitable nesting habitat (USFWS 2009). Most of the natural wetland habitat at Tule Lake and Lower Klamath Lake was lost due to agricultural development during the early 20th Century (NRC 2004), and the wetlands that remain within the Klamath Basin NWR Complex do not provide suitable nesting substrate for Caspian terns (USFWS 2009). Constructing artificial nesting islands for Caspian terns in the Klamath Basin NWRs could help to meet the requirements of the Caspian Tern Management Plan, while restoring a breeding population of Caspian terns to the Upper Klamath Basin (USFWS 2009).

Caspian terns nest in habitats that are naturally ephemeral and will readily colonize new breeding sites when conditions become more favorable (Collis et al. 2002, Suryan et al. 2004). Social attraction techniques (decoys and recorded vocalizations) have been used to attract terns (*Sterna* spp. and *Hydroprogne* spp.) to nest at restored and artificial nesting locations (Kress 1983, Roby et al. 2002). If availability of nesting habitat is limiting the numbers of Caspian terns nesting in the Upper Klamath Basin, then the breeding population of Caspian terns should increase

quickly following the creation of suitable artificial nesting habitat and with the aid of social attraction techniques.

Availability of nesting habitat may not be the only factor limiting breeding Caspian terns in the Upper Klamath Basin and other inland basins. Nest predation by mammalian or avian predators (Hatch 1970, Stienen et al. 2001, Donehower et al. 2007), competition for nesting habitat with gulls (*Larus* spp.; Stienen and Brenninkmeijer 1999, Garica et al. 2010), or low availability of forage fish within commuting distance of potential colony sites (Becker et al. 1997, Davoren and Montevecchi 2003) could also limit the size, number, and reproductive success of Caspian tern colonies in the Upper Klamath Basin. If other factors affect the productivity of Caspian tern colonies that form on new, artificial islands in the Upper Klamath Basin, then using social attraction to encourage nesting at these sites could create an ecological trap for Caspian terns, and serve as a population sink (Battin 2004, Ahlering et al. 2010). Demographic studies estimate that fecundity of approximately 0.65 fledglings/breeding pair (0.32 – 0.74 fledglings/breeding pair) is required to maintain a stable population of Caspian terns within the Pacific Coast region (Suryan et al. 2004).

Recognizing and addressing the initial causes of colony decline and abandonment is an important precursor to any restoration effort for colonial waterbirds (Kress 1983, Anderson and Devlin 1999, Jones and Kress 2012). While creating artificial nesting habitat and providing social attraction should overcome the primary

barriers to the restoration of Caspian tern breeding colonies in the Upper Klamath Basin, there is no way to know in advance of restoration the effects of other potential limiting factors.

The purpose of this study was to test the hypothesis that the numbers of Caspian terns breeding in the Upper Klamath Basin is primarily limited by the availability of suitable nesting habitat. Key objectives of this work were to (1) document tern colony development at restoration sites (artificial islands), (2) compare initial reproductive success of terns at restoration sites to other established Caspian tern colonies within the Pacific Coast region, (3) assess the impact of gulls on the success of tern colony development, and (4) identify additional factors affecting tern colony growth and reproductive success that could be addressed through on-going management at restoration sites. If nesting habitat is limiting the number, size, and productivity of Caspian tern colonies in the Upper Klamath Basin, we expected that: (1) the number of Caspian tern breeding colonies and the total number of breeding pairs in the Upper Klamath Basin would increase as artificial nesting habitat becomes available and (2) the reproductive success of Caspian terns breeding at artificial islands would be comparable to or greater than average nesting success at established colonies in western North America.

METHODS

Study Area

All three artificial tern islands built in the Upper Klamath Basin are located in Siskiyou County, California, along the border with Oregon, and are within Lower Klamath NWR and Tule Lake NWR, parts of the Klamath Basin NWR Complex. Lower Klamath NWR covers 206 km^2 and includes 43 separate permanent and seasonal wetland units and 24.3 km^2 of leased farmland (Mayer 2005). The refuge receives water from Tule Lake NWR and from the Klamath River (NRC 2004). Tule Lake NWR includes two sumps (1A and 1B) totaling 5.3 km^2, which are managed as permanent and seasonal wetlands. Both refuges are managed by the U.S. Fish and Wildlife Service as part of the National Wildlife Refuge System.

One artificial tern island was built in Sheepy Lake, a 3.9 km^2 permanently flooded unit in Lower Klamath NWR, near its western boundary. The Sheepy Lake tern island is a 0.3-ha (0.8-acre; Figure 2.1) anchored floating island constructed from modules of recycled plastic injected with foam and overlain with gravel suitable as nesting substrate for Caspian terns. A second artificial tern island was built in the center of Orems Unit, a seasonally flooded wetland management unit on the eastern edge of Lower Klamath NWR. It is a 0.4-ha (1-acre) silt-core island, surrounded by rocky revetment and topped with gravel substrate. The third artificial tern island was built in the southwestern portion of Tule Lake Sump 1B, a 13.6 km^2 permanently flooded wetland unit in Tule Lake NWR. It is a 0.8-ha (2-acre) rock-core island, topped with gravel substrate.

Four established Caspian tern colonies in the Pacific Coast region (Figure 2.2), where multiple years of monitoring data have been collected, were used as reference sites for reproductive success (productivity) and gull kleptoparasitism rates. The colony on East Sand Island, Oregon, the largest known Caspian tern colony in the world, has been continuously active since 1999, and is located in the Columbia River estuary near the mouth of the river (Roby et al. 2002). Brooks Island in central San Francisco Bay, California, is the site of a moderate-sized Caspian tern colony; Caspian terns have nested at Brooks Island since at least 1988, and it has been the site of the largest Caspian tern colony in the Bay Area since 1997 (Strong et al. 2004, Collis et al. 2012). The Caspian tern colony on Potholes Reservoir in eastern Washington was the third reference site used for comparison purposes. Caspian terns have nested on islands in Potholes Reservoir since the 1950s (Penland 1982). The fourth and final reference colony, a moderate-sized Caspian tern colony on Crescent Island in the mid-Columbia River in south-central Washington, has been active since at least 1991 (Blus et al. 1998). All four reference colonies are located at sites that are either anthropogenic or have been significantly altered by human activities. Data collected at these four Caspian tern colonies between 2000 and 2012 (Roby et al. 2012) were used as reference for comparison with new tern colonies in the Upper Klamath Basin; between 4 and 13 years of data were available for each reference colony. Details of colony size and years when data on nesting success were collected at the four reference colonies are provided in Table 2.1.

Colony Size and Productivity

Social attraction techniques (tern decoys and audio playback systems) were used to attract Caspian terns to breed at the Sheepy Lake tern island during 2010 and at all three artificial tern islands in the Upper Klamath Basin during 2011. Social attraction was not used at the tern islands in Tule Lake Sump 1B or in Orems Unit during 2010 because these two islands were land-bridged due to a drought-related water shortage in the Upper Klamath Basin (NRCS 2010). Social attraction consisted of 220 to 250 Caspian tern decoys arranged over an area of approximately 250 m^2, coupled with four outdoor speakers broadcasting digital recordings of vocalizations from an active Caspian tern colony on a continuous loop. Installation dates for social attraction at each site are reported in Table 2.2.

The number of Caspian tern breeding colonies within the Upper Klamath Basin during 2010 and 2011 was determined using ground, boat, and aerial surveys of all known and potential nesting sites. The three new artificial islands were monitored at least four times per week throughout the breeding season. Historical Caspian tern nesting sites in the Upper Klamath Basin, such as Clear Lake and Meiss Lake, were visited by boat or from land every two weeks during the early breeding season to determine if Caspian terns were nesting. Aerial surveys using fixed-wing aircraft were conducted in May and June to search for Caspian tern colonies on other lakes, marshes, and wetlands throughout the Upper Klamath Basin.

During monitoring visits to the new artificial islands, researchers recorded breeding chronology (pre-laying, incubation, chick-rearing), adult colony attendance

(number of adult Caspian terns present), and the number of nesting pairs (number of active Caspian tern nests containing eggs and/or chicks). For breeding chronology, researchers recorded the first appearance of Caspian terns on the island, as well as the first occurrence of courtship behaviors (mate-feeding, copulation, or nest-scraping), egg-laying, chick-hatching, and chick-fledging. Adult attendance on the colony was estimated as the average of two counts of all Caspian terns on the island at the beginning and end of each monitoring session. The number of Caspian tern nesting pairs was estimated during each colony visit as the number of adults in an incubating/brooding posture, based on counts conducted at least once, but usually an average of two or more counts taken during a monitoring session. Counts at tern colonies on the three artificial tern islands were conducted from observation blinds located on or adjacent to each island. Counts at other tern colonies were conducted from boats or from land at the closest available observation site to the colony, without causing nesting terns to flush from their nests.

The number of breeding pairs at each active Caspian tern colony was estimated from the peak count within a breeding season of the number of active nests. Nesting success at each active Caspian tern colony was measured as the average number of fledglings raised per breeding pair. The number of tern fledglings at colonies with more than 50 pairs was estimated from counts of the number of chicks present on the colony approximately 10 days after the first fledgling was observed. At colonies with less than 50 breeding pairs, the number of fledglings was estimated as the number of chicks that survived to at least 35 days post-hatching, based on monitoring of each

active nest on the colony. Caspian tern nesting success at colonies in the Upper Klamath Basin in 2010 and 2011 was compared to average productivity at the four reference Caspian tern colonies (East Sand Island, Brooks Island, Crescent Island, and Potholes Reservoir) between 2000 and 2011 (Maranto et al. 2010, Roby et al. 2012). Suryan et al. (2004) estimated that average reproductive success between 0.32 – 0.74 fledglings/breeding pair is necessary to maintain a stable population of Caspian terns within the Pacific Coast region.

Competition with Gulls

Ring-billed (*Larus delawarensis)* and California gulls (*L. californicus*) commonly nest in the Upper Klamath Basin. Use of the new artificial tern islands by breeding gulls was estimated from regular counts of all adult gulls present on each island. Counts of adult gulls were conducted at least once per week during the breeding period. Researchers recorded breeding chronology of gulls in the same fashion as for Caspian terns. The number of gull breeding pairs was estimated from the average of counts of each gull species attending nests during the week of peak incubation (when the first gull chicks were seen on an island).

Caspian terns returning to a colony with a fish in their bill (bill load) were observed to determine the proportion of bill loads that were kleptoparasitized by gulls. Observations to estimate kleptoparasitism rates were conducted during 3-hour periods at least four times per week. The timing of kleptoparasitism observation periods varied to control for potential variation in kleptoparasitism rates with time of day;

observation periods were evenly distributed among the following 5-hr periods: 05:30-10:30, 10:30-15:30, and 15:30-20:30 PDT. Adult terns with bill loads were selected for observation while they were in the air and within 50 m of the blind to prevent bias towards bill loads consisting of large or small fish. Each bill load was followed until a fate for the fish was observed, five minutes had passed with no fate, or the observer lost sight of the focal bird. Fish fates were classified as self-feed, mate-feed, chick-feed, pirated by another tern, kleptoparasitized by a gull, or unknown final fate. Kleptoparasitism rates were calculated as the proportion of fish of known fate that were kleptoparasitized. Data from Upper Klamath Basin colonies were compared to data collected following the same protocol at the four reference Caspian tern colonies between 2008 and 2011.

Predation

Throughout the breeding season, researchers recorded any instance of gull predation on Caspian tern eggs or chicks that was observed during monitoring sessions. The total numbers of gull predation events observed during all hours of colony monitoring were recorded from the initiation of the first tern nest to the median date of tern fledging during each year of the study. This was used to measure any change in the intensity of gull predation at the Sheepy Lake tern colony from 2010 to 2011.

A federal depredation permit (MB209988-0) was issued to the USACE to lethally remove California and ring-billed gulls that were habitual predators on the

nest contents of Caspian terns at the new artificial tern islands in the Klamath Basin NWRs. This action was considered necessary by the USACE and Refuge managers to ensure successful development of Caspian tern breeding colonies on these islands. Individual gulls were identified as habitual tern nest predators at any of the new artificial islands if they were seen depredating tern eggs or chicks, attempting to attack tern nest contents from the air or ground, or circling and diving over a Caspian tern colony for at least five minutes. Predatory gulls were shot from the observation blind by a sub-permittee under the depredation permit to the USACE using a .22 caliber rifle. This method caused minimal disturbance to nesting Caspian terns and only briefly flushed gulls nesting nearby (A.P., personal observation). Records were kept on the numbers and species of gulls removed from each new island.

During each visit to monitor Caspian tern colonies, researchers looked for signs that predators had visited the tern islands (i.e., carcasses of birds, scat or pellets, or sudden disappearance of multiple nesting adults, chicks, or eggs). In particular, researchers looked for signs of predation by great horned owls (*Bubo virginianus*; owl pellets and remains of birds that had been decapitated). Also, researchers looked for signs of mammalian predators (including scat and footprints). If terns were nesting on an island, the search for predator sign was conducted using binoculars and a spotting scope, and a description and the location of any predator sign were recorded to avoid double-counting. If nesting birds were not present on the island, researchers would examine, record, and remove any predator sign.

When there were indications that a nocturnal predator was visiting an artificial tern island while Caspian terns were nesting, we conducted overnight observations to identify the predator and quantify the level of disturbance. During overnight observations, 2-3 researchers scanned the colony throughout the night using a night-vision monocular and recorded whether any predators were seen on the colony, whether any predation on nesting terns or their nest contents was detected, and whether adult Caspian terns abandoned their nests during the night. The impact of nocturnal predators on each tern colony was assessed by the pattern of nest failure associated with predator visits.

Statistical Analysis

A Welch's *t*-test was used to compare the average number of breeding pairs of Caspian terns in the Upper Klamath Basin before and after creation of artificial nesting islands. We used logistic regression to compare kleptoparasitism rates between the Upper Klamath Basin colonies and the four reference colonies. Colony, year, and a colony-year interaction term were considered as explanatory variables and the model best supported by the data was selected using a drop-in-deviance test. Wald's tests were used to determine if there were differences between the Upper Klamath Basin colonies and the four reference colonies, after accounting for other factors in the model. Fisher's exact tests were used to determine whether the probability of kleptoparasitism or gull predation at the Sheepy Lake tern island changed between 2010 and 2011.

RESULTS

Caspian Tern Response to Habitat Creation and Social Attraction

In 2010, the first Caspian tern was seen foraging over Sheepy Lake on 9 April and the first Caspian tern was seen resting on the Sheepy Lake tern island on 11 April (Table 2.2). The numbers of Caspian terns observed resting on the island ranged from 0 to 21 during April. Courtship behaviors (mate feeding, copulation, and nest-scraping) were first observed during the week of 26 April. In May, Caspian terns were observed on the island during every visit; an average of 18 Caspian terns were counted on the island (range = 3 to 67 terns, Figure 2.3). The first Caspian tern nest was initiated (eggs laid) on 19 May; however, the Caspian tern colony did not reach 50% of its peak size until 20 June. Maximum colony size of 258 nests was attained on 12 July. During June - August, when most tern nests were active, the average number of Caspian terns on the island ranged from 183 to 312 individuals, followed by a sharp decline in tern numbers during September. The maximum number of Caspian terns observed on the island was 502 on 27 June. The new artificial tern islands in Tule Lake Sump 1B and Orems Unit were not suitable for Caspian tern nesting in 2010 because the islands were land-bridged due to low water.

In 2011, the first Caspian terns were seen flying over the island in Sheepy Lake on 2 April and the first Caspian terns were seen resting on the island on 6 April (Table 2.2). Caspian tern attendance on the island in April and May was highly variable (average of 23 and 67 individuals, respectively; Figure 2.3). The first Caspian tern nest was initiated on 14 May. Similar to 2010, however, the tern colony did not reach 50%

of its peak size until 22 June. Peak colony size was 188 nests, which was reached on 27 June. During June – August, when most tern nesting occurred, average tern attendance on the Sheepy Lake island was relatively constant (average = 126 – 177 individuals). The maximum number of Caspian terns observed on the island at one time in 2011 was 397 on 24 June.

In 2011, the first two Caspian terns were seen resting on the new Tule Lake tern island on 11 April, eight days after social attraction was first installed on the island and five days after the first Caspian tern of the year was seen on the Sheepy Lake tern island. Between 0 and 32 Caspian terns were observed resting on the island during April. In May the average number of Caspian terns resting on the island rose to 39 (range = 1 to 128 terns; Figure 2.3), and terns were present during every visit to the island. Courtship behaviors were first observed during the week of 1 May and the first nest was initiated (eggs laid) on 18 May. The Tule Lake tern colony did not reach 50% of its peak size until 26 June. Maximum colony size was 34 nests, which was first attained on 12 July. Attendance on the island was relatively consistent through June, July, and August; monthly averages were between 49 and 58 adults on the island. The maximum number of Caspian terns observed on the island was 151 on 31 August.

The first Caspian terns were observed on the Orems Unit tern island on 4 May 2011, one day after social attraction was installed, and courtship behaviors (nest-scraping, mate feeding, and copulation) were seen within the first week (Table 2.2). During May the average number of Caspian terns seen on the island was 40, but

attendance on the island was highly variable (range = 0 to 174 adults; Figure 2.3). Caspian terns initiated three nests on the island between 29 May and 26 June; the most long-lived tern nest was attended for 11 days. In June the average number of Caspian terns seen on the island dropped to 11 (range = 0 to 106 terns). No Caspian terns were seen using the island between 26 June and 9 July; monitoring of the island was discontinued after 9 July. The maximum number of Caspian terns observed on the island was 174 on 11 May.

Colony Size and Productivity

The Sheepy Lake tern island was the only site in the Upper Klamath Basin where Caspian terns nested during 2010. Natural islands at Clear Lake and Meiss Lake were land-bridged because of low water levels. Not enough water was available in the refuges to fill the wetland units containing the Tule Lake and Orems Unit artificial islands because of water shortages. Approximately 258 pairs of Caspian terns attempted to nest on the newly created Sheepy Lake tern island and approximately 167 chicks were raised to fledging. Estimated productivity for this colony in 2010 was 0.65 fledglings/breeding pair.

In 2011, Caspian terns attempted to nest at four sites in the Upper Klamath Basin, the three artificial tern islands at Sheepy Lake, Tule Lake, and Orems Unit, plus one island in Clear Lake NWR. The Sheepy Lake tern colony peaked at 188 breeding pairs in 2011, and 21 chicks were raised to fledging age; estimated productivity for the Sheepy Lake tern colony was 0.11 fledglings/breeding pair in 2011. The colony on the

Tule Lake tern island peaked at 34 breeding pairs. Four pairs successfully raised a chick to fledging age, and estimated average colony productivity was 0.12 fledglings/breeding pair. Three nesting attempts by Caspian terns were recorded at Orems Unit; only one nest was active at a time. None of the tern nests on the island in Orems Unit survived to hatching. A maximum of 11 breeding pairs of Caspian terns were recorded at Clear Lake. None of the Caspian tern nests at the colony at Clear Lake survived to hatching.

The Caspian tern colony on Sheepy Lake in 2010 was the only colony/year on an artificial island during the study period when reproductive success was within the estimated range required to support a stable population of Caspian terns in the Pacific Coast region (0.32 – 0.74 fledglings/pair; Suryan et al. 2004). In 2010, the Caspian tern colony on Sheepy Lake had higher productivity than any of the three reference colonies from which data were available. In 2011, the Caspian tern colonies on two of the three artificial island in the Upper Klamath Basin were more productive than the East Sand Island colony, which failed to raise any young, but less productive than the Crescent Island and Potholes Reservoir colonies. Over the two-year study period, average productivity at Sheepy Lake was comparable to long-term productivity at two of the four reference colonies (Brooks Island and Potholes Reservoir), but lower than average productivity at the other two (East Sand Island and Crescent Island; Table 2.3).

There was a significant difference in the number of Caspian terns known to be breeding in the Upper Klamath Basin before and after restoration was implemented in 2010 (Welch's t = -6.0, df = 9.3, $P < 0.001$; Figure 2.4). Between 1997 and 2009, an average of 91 (± 23 SE) breeding pairs of Caspian terns was recorded in the Upper Klamath Basin (J. Beckstrand, USFWS, unpublished data; Shuford et al. 2002). In 2010 and 2011 the average number of breeding pairs recorded in the Basin was 246 (± 13 SE). The numbers of pairs of Caspian terns breeding at Clear Lake NWR in 2000 and 2001 (242 and 201 breeding pairs, respectively) were similar to the number of pairs nesting at artificial islands in 2010 and 2011. Estimates of the total number of Caspian tern breeding pairs in the Basin before 2009, however, were based on a single survey conducted in late June or early July, which may not be during the peak of Caspian tern nesting in all years.

Competition with Gulls

Ring-billed and California gulls were the most numerous species breeding on the Sheepy Lake tern island. In 2010, gulls arrived on the island and initiated egg-laying within five days of Caspian tern arrival and initiation (Tables 2.2 and 2.4); approximately 750 pairs of ring-billed gulls and 150 and California gulls, nested on the island.

In 2011, gulls were already present on the Sheepy Lake tern island at the end of March when monitoring began, 11 days prior to the first observation of Caspian terns for the year. Gulls initiated breeding 16 days before Caspian terns. The first

observation of a gull egg on the Sheepy Lake island in 2011 was 18 days earlier than in 2010. Approximately 1,750 pairs of ring-billed gulls and 550 pairs of California gulls nested on the island, 2.3 times and 3.7 times more, respectively, than in the previous year. During April, May, and June there were on average 1,038 more gulls on the island in 2011 than in 2010 (Figure 2.5).

The numbers of ring-billed and California gulls using the Tule Lake tern island were quite low throughout the 2011 breeding season (monthly averages: 4 – 41 individuals; Figure 2.5), compared to gull numbers at Sheepy Lake tern island. Gulls began roosting on the Tule Lake tern island in mid-April and initiated courtship behavior a week later (Table 2.4). After May, however, the number of gulls using the Tule Lake island declined substantially and the gulls that were seen on the island mostly roosted on the opposite side of the island from the Caspian tern colony. No active gull nests were detected on the Tule Lake tern island throughout the 2011 nesting season.

Ring-billed and California gulls began using the Orems Unit tern island immediately after the installation of social attraction for Caspian terns (Table 2.4). The average number of gulls on the island doubled from 155 gulls during May to 330 gulls during June (Figure 2.5). Gull nests with eggs were first seen on 16 May, and gull chicks began to hatch on 6 June. A maximum of 240 ring-billed gull nests and 10 California gull nests were counted on the island. All gull nests on the Orems Unit

island had failed by 5 July, apparently because of disturbance and predation by great horned owls.

Rates of tern kleptoparasitism by gulls differed between colonies (χ^2 = 581.2, df = 4, $P < 0.0001$) and there was a significant interaction between colony and year (χ^2 = 22.4, df = 6, $P = 0.001$; Figure 2.6). After accounting for differences between years, the probability that a tern bill-load fish would be kleptoparasitzed at the Sheepy Lake tern colony was 0.02 (95% CI = 0.01-0.03). Gull kleptoparasitism rates were much higher at the four reference colonies; the odds of a bill load fish being kleptoparasitized ranged from 5.6 times greater at the East Sand Island tern colony in 2011 to 46.1 times greater at the Crescent Island tern colony in 2010. Between 2010 and 2011, however, the odds that a bill load fish at the Sheepy Lake tern colony would be kleptoparasitized increased 4.9 times (Fisher's exact test: 95% CI = 1.7 - 19.6 odds, $P = 0.001$). There were no observed incidents of gull kleptoparasitism of tern bill loads at either the Tule Lake tern island or the Orems Unit tern island; consequently, these two sites were excluded from the analysis.

Water Availability

In 2010, there was not sufficient water on the Klamath Basin NWR Complex to fill Tule Lake Sump 1B and Orems Unit, so the artificial islands in both these impoundments were unsuitable as nesting habitat for Caspian terns. By 1 April, cumulative precipitation for 2010 was 69% of the long-term average, the snowpack

was 69% of average, and storage at three large reservoirs in the region (Upper Klamath Lake, Gerber Reservoir, and Clear Lake) was 51% of average (NRCS 2010).

In 2011, water was not available to fill the Orems Unit impoundment until May, one month after Caspian terns had arrived in the region. By 1 April, cumulative precipitation for 2011 was 111% of average, snowpack was 136% of average, and storage at the three reservoirs was 88% of average (NRCS 2011). By August, the Orems Unit impoundment no longer contained sufficient water to deter mammalian predators from accessing the island, if Caspian terns had still been nesting on the island.

Predation

Between 2010 and 2011, we witnessed an increase in gull predation on tern nests at the Sheepy Lake island, from four gull predation events during 215 hours of colony observation in 2010 to 25 gull predation events during 458 hours of colony observation in 2011. The odds of witnessing a gull predation event were 2.93 times greater in 2011 than in 2010 (Fisher's exact test: 95% CI = 1.0 to 11.7 odds, $P = 0.04$). In 2010, two California gulls that repeatedly depredated Caspian tern nests were shot on the Sheepy Lake tern island. In 2011, 45 depredating gulls (42 California gulls and 3 ring-billed gulls) were shot on the Sheepy Lake tern island. No observations of gull predation on Caspian tern nests were recorded at the Orems Unit tern island, and gulls were rarely observed in or near the Caspian tern colony at the Tule Lake island.

We conducted 13 overnight observations of the Tule Lake tern colony between 19 July and 22 August, following indications that a nocturnal predator was active on the tern colony. Great horned owls were seen during four different overnight observations between 19 and 30 July; partial or complete abandonment of the colony by adult Caspian terns occurred during 11 of the 13 overnight observation periods. In total, 68% of active Caspian tern nests on the Tule Lake island failed within three days of known nocturnal visits by great horned owls; 10 tern nests with eggs were abandoned and 11 nests containing chicks failed because chicks were depredated or died in the nest, apparently due to exposure. On the Orems Unit island there was evidence that a great horned owl depredated at least seven adult ring-billed gulls between 20 June and 5 July. This coincided with a complete collapse of the gull colony on this island; by 5 July all gull nests had failed and no Caspian terns had been observed on the island for over a week.

DISCUSSION

Caspian terns responded quickly to habitat creation and social attraction, attempting to breed at all three artificial islands and at each island in the first year when suitable nesting habitat was available. There was an increase in the number of Caspian tern colonies and a significant increase in the number of Caspian terns breeding in the Upper Klamath Basin following implementation of nesting habitat restoration. In both years following restoration, the new artificial tern nesting islands supported the only Caspian tern colonies in the Upper Klamath Basin that successfully

hatched and fledged chicks. The creation of multiple nesting sites has increased the potential for Caspian terns to breed successfully in the Upper Klamath Basin; it is more likely that at least one nesting island will be available in low water years and there is less risk that a single factor (e.g., a predator) can limit nesting success for all sites.

The addition of two new nesting islands in 2011 to the one that was available in 2010, however, did not result in an increase in the overall number of Caspian terns breeding within the Basin. This suggests that the population of Caspian terns that could rapidly recruit to these new islands was limited. The similarity between the number of breeding pairs recorded during this study and the number of pairs recorded in the Basin during 2000 and 2001 could indicate that these early recruits were dominated by Caspian terns with some history of breeding at Clear Lake in the Upper Klamath Basin. Future population growth in the Basin could be driven by intrinsic recruitment of terns that fledged from these sites (Kress 1983, Parker et al. 2007) or increased numbers of terns seeking new breeding sites as suitable nesting habitat is lost elsewhere (Kress 1983), such as at East Sand Island in the Columbia River estuary.

Average nest success at the Sheepy Lake and Tule Lake tern islands during the first two years following construction of these islands was lower than the estimated level of productivity required to maintain a stable population (Gill and Mewaldt 1983, Suryan et al. 2004). The Sheepy Lake tern colony reached this threshold for

productivity in one of the two study years, however, indicating that terns nesting at this site were able to attain adequate productivity for replacement in some years. Long-term productivity at Brooks Island and Potholes Reservoir (0.40 and 0.34 fledglings/breeding pair, respectively), two medium-sized Caspian tern colonies in the Western North American population that have persisted, has been as low as the average of the first two years at the Sheepy Lake colony (0.36 fledglings/breeding pair). These two reference colonies indicate that a Caspian tern colony can persist with average reproductive success as low as was observed at the Sheepy Lake island in the first two years. Caspian terns may continue to nest at these sites following the removal of social attraction even if these colonies represent population sinks in most years. Continuing social attraction and active management at these new islands for several years in order to establish breeding site fidelity and an experienced breeding population may be necessary to balance years with poor reproductive success early on. Even if reproductive success at these restored colony sites is lower than average, they may still benefit the Western North American population by providing more breeding colony sites to help offset the negative population effects of low reproductive success and stochastic events at large colonies in some years (Cuthbert and Wires 1999, Suryan et al. 2004).

In both years of this study, peak nest initiation by Caspian terns was delayed until June, and occurred well after courtship behavior began and the first eggs were laid. Timing of breeding has been shown to affect productivity in many bird species. Seasonal declines in reproductive success have been reported for many species of tern

(Nisbet and Welton 1984, Burger et al. 1996, Arnold et al. 2004). New breeding sites are often colonized by younger birds (Tims et al. 2004). Inexperienced breeders have been found to initiate nesting later, both within and between colonies (Burger et al. 1996, Tims et al. 2004), and tend to experience lower reproductive success (Nisbet et al. 1984, Burger et al. 1996). Nest initiation can also be limited by availability of food early in the nesting season, or intense predation on early nests (Burger et al. 1996). Whatever the proximate cause of the apparent late nest initiation at the Upper Klamath Basin colonies, amelioration of those conditions (i.e., recruitment of more experienced breeders, better early season climatic conditions, or increased prey availability) could contribute to higher productivity in future years.

Gulls have been reported to out-compete tern species for nesting habitat in many areas (Kress et al. 1983, Blokpoel et al. 1997, Anderson and Devlin 1999, O'Connell and Beck 2003). Populations of California and ring-billed gulls have been increasing in the Pacific Northwest (Conover 1983, Strong et al. 2004, Ackerman et al. 2006); greater numbers of potential breeders and earlier nest initiation enable gulls to outcompete terns for nesting space (Courtney and Blokpoel 1983, Maxson et al. 1996). Between the first and second breeding seasons on the Sheepy Lake island, the number of breeding gulls increased substantially and the timing of gull nesting was at least two weeks earlier in the second year. At the same time, the number of Caspian terns breeding on the island decreased slightly. With more gulls nesting on the island and initiating nesting earlier in the second year of the study, it appears that gulls out-competed terns for nesting space on the island. In 2010, Caspian terns nesting on the

Sheepy Lake island nested in one cohesive group in the center of the area where decoys and audio playback systems had been deployed. In 2011, Caspian terns nested in two groups one on the outer edge of the social attraction area and the other along the edge of the island. This provides further support for the hypothesis that Caspian terns were precluded from nesting on much of the island by large number of nesting gulls that had initiated earlier in the season.

The incidence of gulls exhibiting predatory behavior toward Caspian tern eggs and chicks increased at the Sheepy Lake island in the second year of the study, as indicated by the substantial increase in the number of gulls that had to be removed. Despite more intensive gull control, there was still a sharp decline in Caspian tern productivity in 2011 compared to 2010, indicating that gull predation on tern eggs and chicks may not have been by just a small number of specialist gulls, as described by Guillemette and Brousseau (2001). Control of predatory gulls on Sheepy Lake island likely helped some Caspian tern chicks survive until fledging, but this measure was not sufficient to prevent a decline in productivity between the two years.

Competition with gulls for nesting habitat would contribute to the increased risk of gull predation on Caspian tern nests. Observations of adult gulls preying on chicks of other gulls were common in both years. Chick hatching for gulls and terns that nested on the Sheepy Lake island in 2010 was nearly synchronous; chicks of all three species were of similar size and equally vulnerable to gull predation early in the chick-rearing period (Shealer and Burger 1992, Becker 1995, Whittam and Leonard

2000). In 2010, Caspian tern chicks may have benefited from predator swamping because of the greater abundance of gull chicks (Darling 1938, Ims 1990, Becker 1995). In 2011, however, gulls initiated nesting well before Caspian terns, and gull chicks were too large to be easy prey for adult gulls when tern chicks began hatching. As a result, tern chicks were the most readily available prey on the colony at the time when the food requirements of gull chicks were highest, and at least some gulls had become accustomed to preying on chicks at the colony. Finally, the Sheepy Lake tern colony was more fragmented in 2011 compared to 2010, making more tern nests susceptible to predation at the edge of the tern nesting areas (Spear 1993, Becker 1995, Donehower et al. 2007).

Despite apparent competition with gulls for nesting space and reduction in nesting success due to nest predation by gulls, kleptoparasitism of Caspian terns by gulls at the Sheepy Lake island was substantially lower than at all four reference colonies. This indicates that gulls nesting at the Sheepy Lake island are not limiting Caspian tern provisioning rates to their mates or chicks. If bill load kleptoparasitism is a learned behavior for gulls, it may take more than two years of sympatric nesting for gulls to develop a strong tendency towards kleptoparasitism. This would explain why kleptoparasitism rates were lower at this new tern colony compared to colonies that have persisted for over 10 years. Also, if prey items brought back to the Sheepy Lake tern colony are relatively small or have low energy content, it may not be sufficiently profitable for gulls to steal bill loads from terns. Finally, if there are ample alternative

food sources available to gulls, then there may not be a strong incentive for gulls to develop kleptoparasitic behavior.

On-going management of gulls has been a requirement for success in many tern restoration projects (Kress 1983, Blokpoel et al. 1997). Within-season control of predatory gulls likely provides some enhancement of reproductive success (Guillemette and Brousseau 2001, Donehower et al. 2007) by limiting and preventing predation. Measures to limit the number of gulls breeding on Sheepy Lake island and delay nest initiation by gulls could have greater benefits in helping terns compete with gulls for nesting territory and increasing nesting synchrony between terns and gulls (Courtney and Blokpoel 1983).

There was no evidence that gulls were limiting Caspian tern colony size or nesting success at either the Tule Lake or the Orems Unit islands. The numbers of gulls nesting and resting on these two islands were relatively small compared to the Sheepy Lake island. Given the marked increase in the number of gulls nesting at Sheepy Lake island in the second year, it is possible that gull nesting on the other two new islands will increase as more gulls become familiar with these islands.

Water shortages made both the Tule Lake and Orems Unit islands unavailable as nesting habitat in 2010, and led to delayed availability of the Orems Unit island in 2011, as well as subsequent land-bridging late in the nesting season. Chronic water shortages in the Upper Klamath Basin limit the benefits of artificial nesting islands to colonial waterbirds if the wetland units containing them cannot be flooded. Creating

additional nesting habitat has served to alleviate some of the impacts of water shortages; with three new artificial islands there are multiple potential colony sites and increased potential that one or more islands will be available for colonial waterbird nesting during low water years. This was evident in 2010 when Sheepy Lake island was the only available nesting site for Caspian terns throughout the Upper Klamath Basin. Without the Sheepy Lake island, it is nearly certain that there would have been no breeding by Caspian terns in the Upper Klamath Basin that year.

Water management considerations make Sheepy Lake the most likely wetland unit of the three restoration sites to have water during low-water years, followed by Tule Lake Sump 1B and Orems Unit. Intermittent availability of the latter two artificial islands as suitable nesting habitat for colonial waterbirds could further limit colony development on those islands, as breeding terns will have less opportunity to develop fidelity to those islands as nesting sites. Water shortages could further limit colony size and reproductive success at all three artificial tern islands by limiting forage fish availability within the Upper Klamath Basin.

Predation and disturbance by great horned owls was the most significant cause of Caspian tern nest failure at the Tule Lake island, as well as gull nest failure at the Orems Unit island. For the Orems Unit island, the timing of owl activity (during nest initiation) and the type of predation (on adult gulls) may have resulted in a greater impact on colony development. Predation on adults prior to nest initiation would clearly indicate to potential breeders that a site poses a risk to survival (Montgomerie

and Weatherhead 1988, Spaans et al. 1998, Lima 2009). Disturbances by owls during early chick-rearing at the Tule Lake colony resulted in nocturnal abandonment by adult terns over an extended period of five days following confirmed owl visits, a pattern that has been observed at other tern colonies (Wendeln and Becker 1999, Arnold et al. 2006). Nocturnal abandonment negatively affects tern nest success because young chicks die of exposure and eggs fail to hatch (i.e., Shealer and Kress 1991). At large tern colonies, the effects of nocturnal disturbances can be localized because only the immediate area around predators is affected (Wendeln and Becker 1999, Arnold et al. 2006); therefore, a larger, more established colony may be more resilient to disturbance from nocturnal predators such as great horned owls.

Great horned owl activity could have long-term consequences for the development of tern colonies on artificial islands. Reduced reproductive success, signs of predation (carcasses of adults or chicks), or encounters with nocturnal predators could provide negative social information to Caspian terns prospecting at these sites late in the breeding season (Danchin et al. 1998, Doligez et al. 2003, Lima 2009). Management action to remove or deter nocturnal predators would be most effective early in the chick-rearing period, when chicks are most vulnerable (Nisbet 1975, Catlin et al. 2011). Reducing the frequency and duration of post-disturbance colony abandonment by breeding adults would also reduce rates of unsuccessful hatching, chick death due to exposure, and predation by other predators (Nisbet and Welton 1984, Shealer and Kress 1991). An enhanced understanding of how the risk of predation at tern colonies is influenced by the density of great horned owls and their

territories, distance to active owl nests or preferred hunting habitat, and availability of alternative owl prey (Sergio et al. 2007) would inform management actions to reduce the impact of owl activity on waterbird restoration projects and help site future restoration efforts so as to minimize conflicts with owls.

A prior history of nesting in the Upper Klamath Basin and continuing use of the Basin by Caspian terns suggested that availability of nesting habitat might limit the breeding population in the region. We demonstrated how artificial nesting islands and social attraction could be used to establish new Caspian tern breeding colonies in the Upper Klamath Basin. On-going management will likely be necessary to reduce the impacts of competition and nest predation by gulls and predation by nocturnal predators (e.g., great horned owls, terrestrial mammalian predators) if these sites are to remain productive in the long-term. Over the next few years, management actions that increase reproductive success should help to recruit breeding adults and establish breeding-site fidelity, thereby increasing the probability of creating a larger, persistent breeding population within the Upper Klamath Basin. More established colonies, with higher numbers of breeding pairs and more breeding experience, may be capable of resisting the detrimental effects of some predators and competitors without intensive management. Ultimately, the success of this restoration effort will depend on the number of breeding pairs and long-term reproductive success of Caspian terns that continue to nest at the artificial islands after social attraction is no longer deployed. Even if average productivity remains too low to be self-sustaining while colonies

become more established, having more breeding sites for Caspian terns in western North America contributes to a more resilient regional population.

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Table 2.1. Average number of breeding pairs of Caspian terns at selected reference colonies in the Pacific Coast region of North America[a].

	Breeding Pairs				
	2010	2011	Long-term average	Range	Years
East Sand Island	8,283	6,969	9,034	6,969- 10,668	2000-2011
Brooks Island	--	--	841	681- 1,040	2003-2005, 2008-2009
Crescent Island	375	419	469	349-657	2000-2011
Potholes Reservoir	416	422	310	202- 422	2000-2001, 2003-2011

[a] Data on number of breeding pairs are from Roby et al. 2012.

Table 2.2. Chronology of Caspian tern response to social attraction and colony development at three new artificial islands in the Upper Klamath Basin of California and Oregon.

	Social attraction installed	First tern on island	First courtship	First egg	First chick	First fledgling
Sheepy Lake						
2010	March 24	April 11	April 26	May 19	June 15	July 28
2011	April 2	April 6	April 21	May 14	June 26	Aug 12
Tule Lake						
2011	April 3	April 11	May 1	May 18	July 13	Aug 31
Orems Unit						
2011	May 3	May 4	May 5	May 29	--	--

Table 2.3. Nesting success of selected Caspian tern colonies in the Pacific Coast region of North America[a].

	Productivity (fledglings/breeding pair)				
	2010	2011	Average	Range	Years
Sheepy Lake	0.65	0.11	0.38	0.11 – 0.65	2010-2011
Tule Lake	--	0.12	0.12	--	2011
East Sand Island	0.05	0.00	0.66	0.00 – 1.39	2000-2011
Brooks Island	--	--	0.40	0.14 – 0.62	2003-2005, 2008-2009
Crescent Island	0.52	0.32	0.55	0.28 – 1.00	2000-2011
Potholes Reservoir	0.01	0.27	0.37	0.01 – 0.88	2001, 2003[b], 2005-2007[b], 2010-2011

[a] Nesting success data for East Sand Island, Brooks Island, Crescent Island, and Potholes Reservoir (2001, 2007, 2010, and 2011) are from Roby et al. 2012.

[b] Nesting success data for Potholes Reservoir (2003, 2005, and 2006) are from Maranto et al. 2010.

Table 2.4. Nesting chronology and number of breeding pairs of gulls nesting at three new artificial islands in the Upper Klamath Basin of California and Oregon.

	On colony	Courtship	Eggs	Chicks	Fledglings	Breeding pairs	
						RBGU[a]	CAGU[b]
Sheepy Lake							
2010	April 11	April 20	May 14	June 12	July 18	750	150
2011	<March 28	April 4	April 30	May 26	July 5	1750	550
Tule Lake							
2011	April 18	April 18	--	--	--	0	0
Orems Unit							
2011	May 5	May 5	May 17	June 6	--	240	10

[a] Ring-billed gulls (*Larus delawarensis*)

[b] California gulls (*L. californicus*)

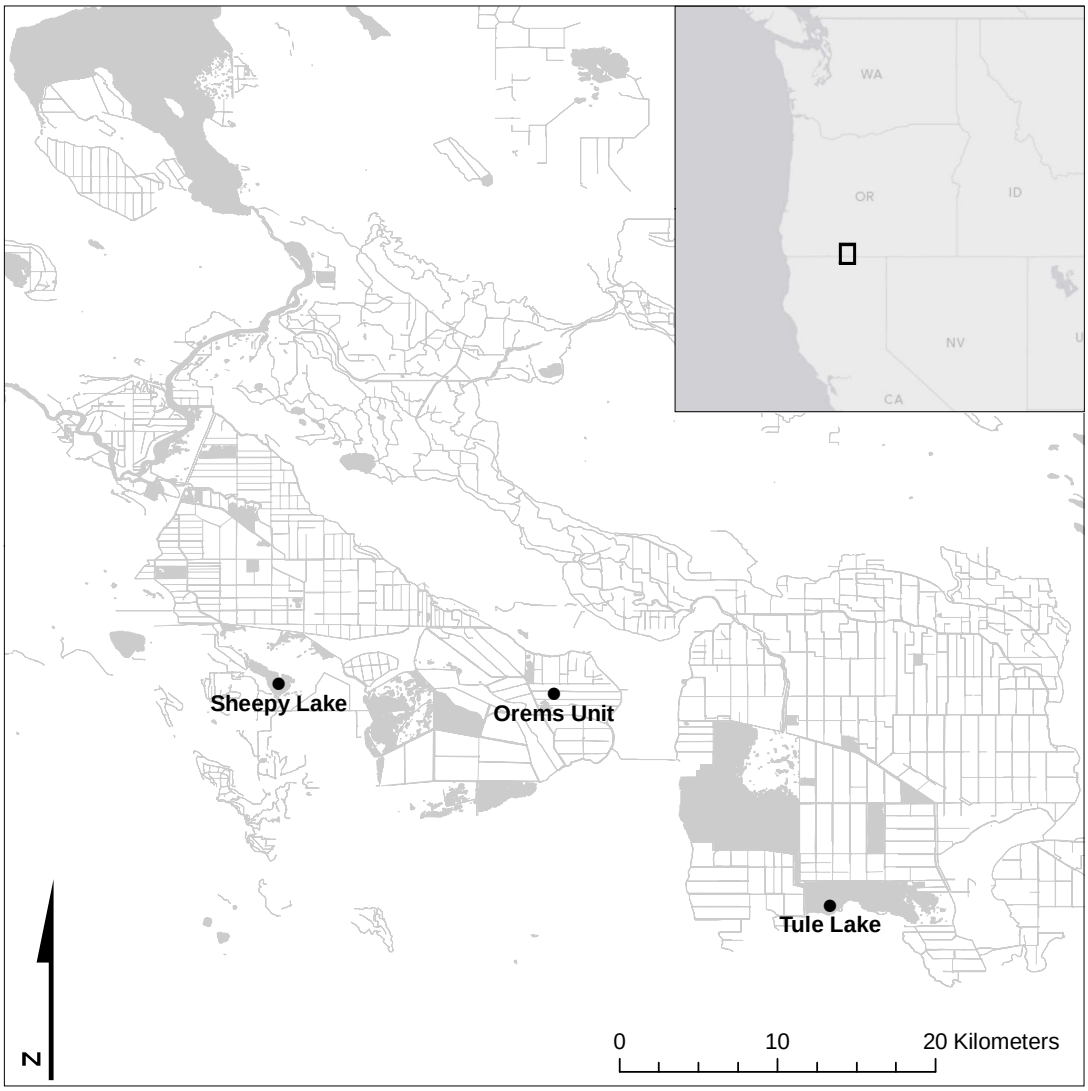

Figure 2.1. Map of the study area in the Upper Klamath Basin of California and Oregon, showing the locations of three new artificial Caspian tern nesting islands.

Figure 2.2. Map of the Pacific Coast region of the conterminous U.S., showing the locations of the three new Upper Klamath Basin Caspian tern artificial nesting islands and four other established Caspian tern colonies used as references.

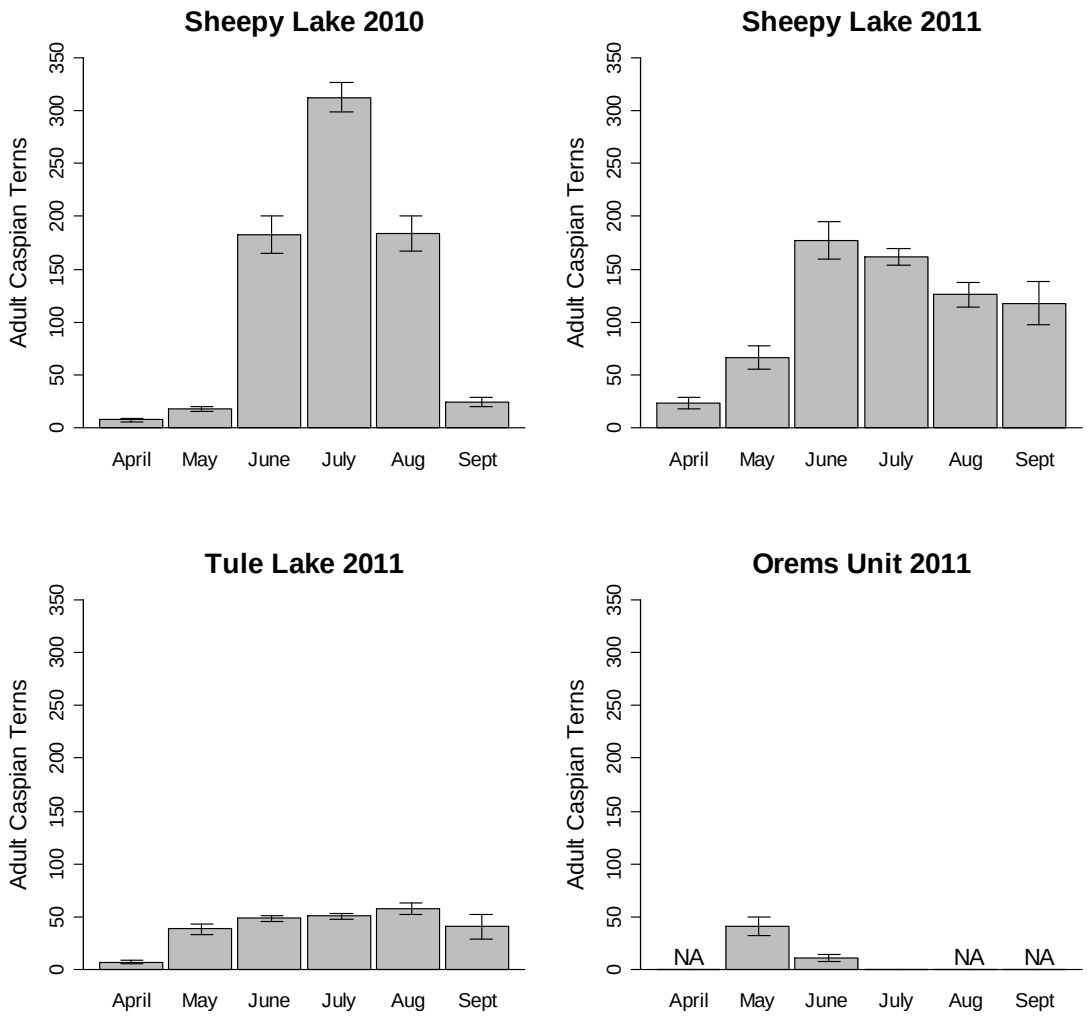

Figure 2.3. Number of adult Caspian terns observed on each new artificial island in the Upper Klamath Basin of California and Oregon, bars indicate average of all counts per month (± SE).

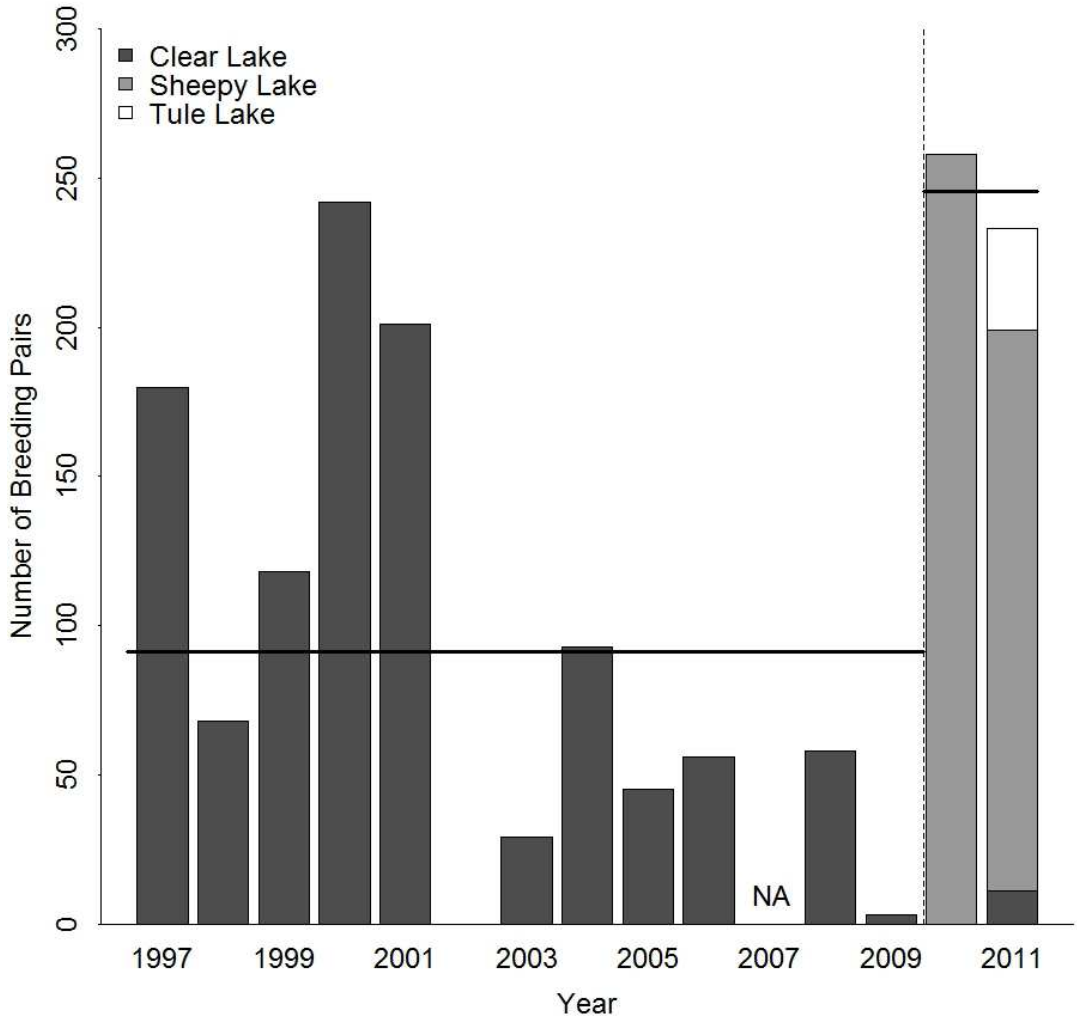

Figure 2.4. Number of Caspian tern breeding pairs in the Upper Klamath Basin of California and Oregon from 1997 to 2011. Dashed vertical line indicates implementation of nesting habitat restoration and social attraction at Sheepy Lake and Tule Lake; before then Caspian terns nested only at Clear Lake. Horizontal lines indicate average number of breeding pairs before and after the creation of artificial nesting islands.

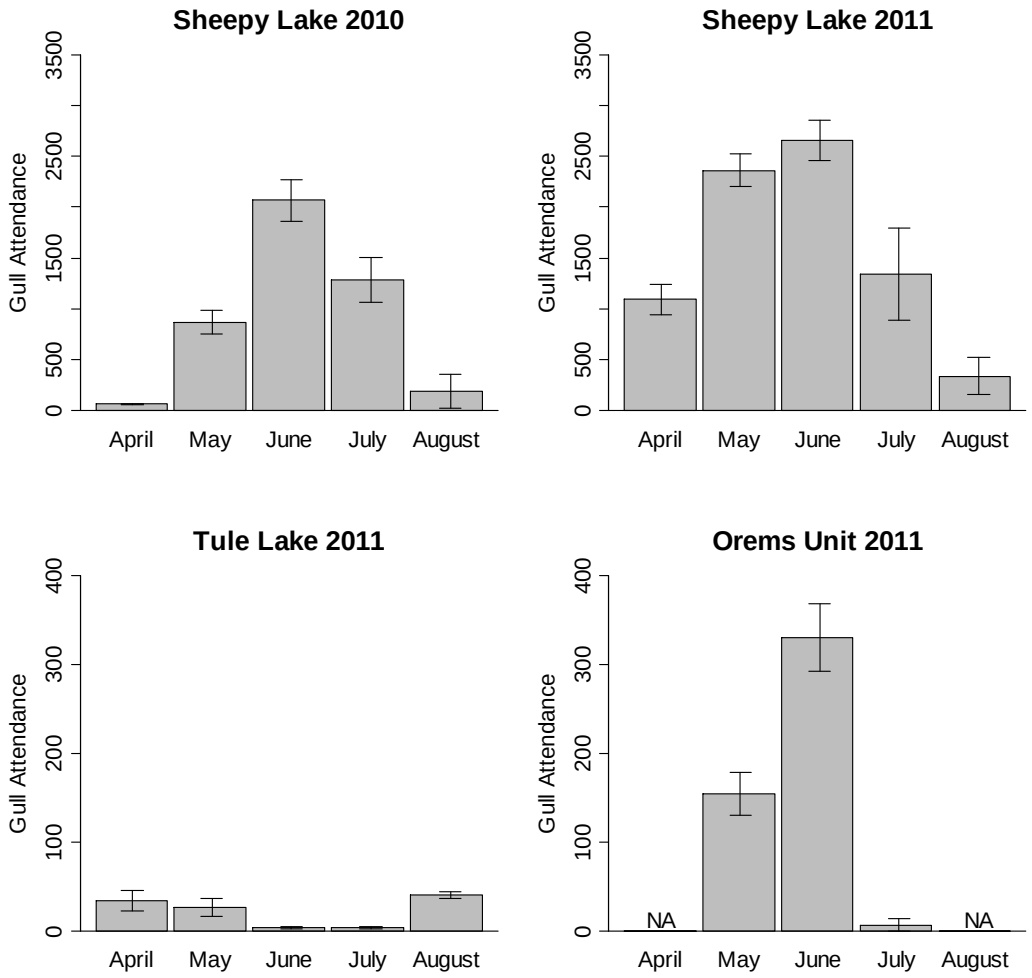

Figure 2.5. Number of adult California and ring-billed gulls on each Caspian tern nesting island in the Upper Klamath Basin of California and Oregon bars indicate average of all counts per month (± SE). Note different scales on y-axis between plots for Sheepy Lake (top row) and the other two islands (bottom row).

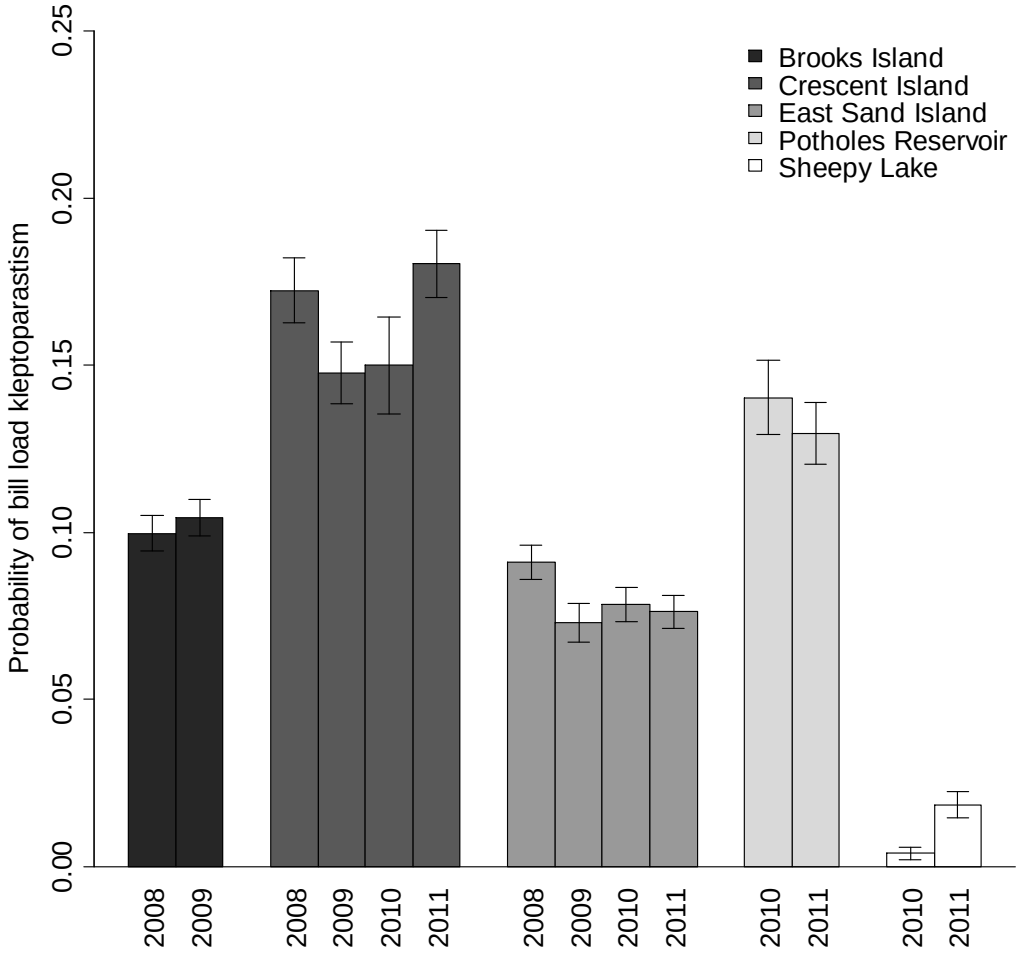

Figure 2.6. Gull kleptoparasitism rates at five Caspian tern breeding colonies in the Pacific Coast region of North America between 2008 and 2011; bars show proportion of fish transported by terns in their bills with a known fate that were kleptoparasitized by gulls (± SE).

CHAPTER 3: FORAGING BEHAVIOR OF CASPIAN TERNS NESTING AT TWO NEIGHBORING COLONIES

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ABSTRACT

Efforts to conserve and restore waterbird colonies can be compromised by low prey availability within foraging distance of the breeding colony. We investigated the importance of local foraging conditions for Caspian terns (*Hydroprogne caspia*) breeding at two newly established colony sites in the Upper Klamath Basin, California (Sheepy Lake and Tule Lake), whose maximum foraging areas largely overlap. We measured adult foraging behavior, adult body mass, and size-adjusted body mass of chicks at these two colonies to determine if prey availability could potentially affect colony development. We used GPS-telemetry to track the movements of breeding Caspian terns; cluster analysis was used to infer behavioral states from movement characteristics. Terns breeding at Sheepy Lake spent less time at the colony (52% of the day) than terns breeding at Tule Lake (74%). Caspian terns breeding at Sheepy Lake foraged more extensively than terns breeding at Tule Lake; Sheepy Lake foraging trips lasted longer (median = 186 min) and went farther from the colony (27 km) compared to Tule Lake foraging trips (55 min and 6 km, respectively). Between-colony differences in foraging behavior corresponded to 4% lower average body mass of breeding adults and significantly lower size-adjusted body mass of chicks at Sheepy Lake compared to Tule Lake. Even though these colonies are separated by only 30 km, local conditions apparently resulted in markedly different foraging behavior; together foraging behavior and body condition indicated that foraging conditions were better for terns breeding at Tule Lake than at Sheepy Lake. Comparisons between these newly established colonies and four older colonies within the Pacific Coast

region of North America indicated that foraging conditions around both colonies were adequate to support persistent colonies that could grow in the future. Assessment of foraging conditions at colony restoration sites immediately following colonization can help predict long-term site potential and inform future management decisions.

INTRODUCTION

As part of a plan to reduce the impact of Caspian tern (*Hydroprogne caspia*) predation on survival of threatened juvenile salmonids (*Oncorhynchus* spp.) in the Columbia River estuary (USFWS 2005), the U.S. Army Corps of Engineers constructed three artificial islands in the Upper Klamath Basin to provide alternative nesting habitat for Caspian terns nesting in the Columbia River estuary, Oregon (USFWS 2009). The Upper Klamath Basin was chosen because the region historically supported large numbers of breeding colonial waterbirds, including Caspian terns (Finley 1907, Finley and Bohlman 1907, Finley 1915). Small numbers of Caspian terns still breed in some years at Clear Lake National Wildlife Refuge (NWR) at the eastern edge of the Upper Klamath Basin (Shuford and Craig 2002), and hundreds of non-breeding Caspian terns use the Basin during migration, as well as during the breeding season (Shuford et al. 2004).

Because of the prior history of nesting and continuing use, resource managers believed that the number of Caspian terns breeding in the Upper Klamath Basin was limited by the availability of suitable nesting habitat. Most of the natural wetland nesting habitat in Tule Lake and Lower Klamath Lake was lost during agricultural

development in the early 20th Century (NRC 2004), and the wetlands that remain within the Klamath Basin NWR Complex do not provide suitable nesting substrate for Caspian terns (USFWS 2009). Constructing artificial nesting islands for Caspian terns in the Klamath basin NWRs could help to meet the requirements of the Caspian Tern Management Plan, while restoring the breeding population of Caspian terns to the Upper Klamath Basin (USFWS 2009).

While availability of nesting habitat is presumably an important factor limiting the numbers of breeding Caspian terns in the Upper Klamath Basin and other inland basins in the American west, it may not be the only limiting factor. Prey availability is an important factor limiting the number, size, and reproductive success of colonial nesting birds (Suryan et al. 2000, Suryan et al. 2002, Ainley et al. 2003, Burke and Montevecchi 2009). When prey availability is low, breeding birds must spend more time foraging and travel further from the colony to find prey, which reduces provisioning rates, growth rates, and survival rates of chicks (Davoren and Montevecchi 2003, Boersma and Rebstock 2009, Burke and Montevecchi 2009).

During the breeding season Caspian terns are central-place foragers; their foraging behavior is constrained by the need to return to the nest (Orians and Pearson 1979). For birds acting as-central place foragers, habitat availability is inversely related to distance from the central location (Matthiopoulos 2003, Wakefield et al. 2009). As the distance to suitable foraging habitat increases, breeding birds face trade-offs between allocating energy to themselves vs. their offspring and between spending

time foraging vs. spending time at the nest. Colonial nesting waterbirds can be further constrained because suitable nesting habitat may not be available close to readily available prey resources.

Caspian terns are piscivorous colonial waterbirds that nest at sparsely-vegetated sites on coastal and inland islands (Gill and Mewaldt 1983, Wires and Cuthbert 2000, Suryan et al. 2004). Breeding Caspian terns may be especially susceptible to the negative effects of low prey availability because of their foraging mode; as plunge-divers they can only access fish in the top meter or so of the water column and as single-prey loaders they can only transport one prey item to the nest site per foraging trip. Foraging success of terns can be affected by a variety of environmental factors, including wind, sea surface conditions, tides, and water clarity (Dunn 1975, Baptist and Leopold 2010). Foraging may be further constrained at inland colonies because the absolute amount of potential foraging habitat available within foraging range (ca. 80 km from the nest; Adrean 2011) is likely to be small compared to coastal colonies.

It is difficult to accurately measure availability of forage fish prey, especially for a plunge-diving bird, because measures of prey abundance may not be representative of the prey that are available near the surface (Cairns 1989, Suryan et al. 2002, Ainley et al. 2003). Adult colony attendance, foraging effort, foraging distance, and chick body condition can be useful indicators of foraging conditions

when direct measurement of prey availability is not feasible (Cairns 1987, Davoren and Montevecchi 2003).

Radio telemetry studies of Caspian tern foraging behavior in the Columbia River estuary, Oregon, and in San Francisco Bay, California, showed that lower forage fish availability was associated with greater average foraging distance off-colony, longer foraging trips, and lower colony attendance; which were all associated with lower reproductive success (Anderson et al. 2007, Lyons et al. 2007, Adrean 2011). The foraging activity of Caspian terns nesting in the Columbia River estuary during 1998 and 1999 was concentrated near the colony; 50% of foraging and commuting terns were located within 8 km of the colony, and at least 95% were located within 27 km (Lyons et al. 2007). During 1999 and 2001, Caspian terns nesting in the Columbia River estuary were detected on average 11.2 km and 13.9 km from the colony, respectively, and productivity in those two years was 1.20 and 1.40 fledglings per breeding pair, respectively (Roby et al. 2002, Lyons et al. 2005, Anderson et al. 2007). When off-colony detections averaged farther from the colony (20.2 km in 2000 and 19.6 km), productivity was significantly lower, 0.57 and 0.55 fledglings/pair, respectively (Roby et al. 2002, Lyons et al. 2005, Anderson et al. 2007). The location of suitable nesting sites relative to profitable foraging areas will have important consequences for foraging behavior and chick body condition of terns breeding at those sites.

Investigations of the foraging behavior of breeding Caspian terns have so far been limited to studies using radio-telemetry because of the relatively small average body size of Caspian terns (ca. 650 g) and the difficulty of recapturing individual terns on the breeding colony. Radio-telemetry studies have provided valuable information about colony attendance and foraging trip duration, and limited data on off-colony foraging distribution (Sirdevan and Quinn 1997, Lyons et al. 2005, Anderson et al. 2007, Adrean 2011). Without continuous tracking of individual movements, radio-telemetry cannot be used to study the fine-scale foraging behavior of Caspian terns. The recent development of micro-GPS data loggers (< 15 g) with remote data retrieval are creating new opportunities to research the foraging strategies and habitat use of smaller waterbird species (McLeay et al. 2010).

The goal of this study was to determine whether prey availability could be a factor limiting the success of restored Caspian tern colonies in the Upper Klamath Basin. We investigated the foraging behavior of breeding adults and the physical condition of adults and chicks as indicators of prey availability. Here we report on the first use of GPS telemetry to study the fine-scale foraging behavior of Caspian terns. We compared foraging behavior of Caspian terns breeding at two newly established colonies during late incubation and early chick-rearing. We predicted that, if Caspian tern nesting at colonies in the Upper Klamath Basin were food-limited, their foraging behavior would be consistent with colonies experiencing food limitation and the physical condition of chicks would be lower at Upper Klamath Basin sites relative to other established colonies.

METHODS

Study Area

A 0.3-ha (0.8-acre) artificial tern nesting island was built in Sheepy Lake, a 3.9-km^2 permanently flooded unit in Lower Klamath NWR, just prior to the 2010 nesting season. This island was first colonized by nesting Caspian terns in 2010, soon after island construction was completed. In 2011, 188 pairs of Caspian terns nested on the Sheepy Lake island. A second 0.8-ha (2-acre) artificial tern nesting island was built in nearby Tule Lake NWR, in Sump 1B, a 13.6-km^2 permanently flooded wetland unit. Caspian terns bred at the Tule Lake island for the first time in 2011, when 34 pairs nested on the island. These two artificial tern islands are 30 km apart, separated by a patchwork of seasonal wetlands and agricultural land (Figure 3.1).

GPS Tracking

Caspian terns were captured during late incubation using walk-in dome traps and noose mats placed around nest scrapes. Eleven terns were captured at each colony and a GPS data logger (Telemetry Solutions, Concord, California) was attached to ten terns from each colony. Loggers included a UHF transmitter for remote transmission of GPS location data; this allowed us to retrieve tracking data without recapturing tagged birds. Average unit weight was 13.4 g, which is approximately 2% of average body mass for adult Caspian terns (Cuthbert and Wires 1999). Unit dimensions were 53 mm x 13 mm x 22 mm, with a 160-mm flexible antenna. Transmitters were attached to the base of the central four rectrices using two 10-cm cable ties and

superglue gel. Each tern was also banded with a field-readable alphanumeric, colored leg band on one leg to allow for individual identification, and two colored leg bands and a numbered metal USGS leg band on the other leg. We collected 5-7 breast feathers from each bird for DNA-sexing; analysis was conducted by Avian Biotech International (Tallahassee, FL). Locations of nests belonging to tagged terns were identified during the first day of tracking and breeding status was monitored until tag failure or nest failure. Breeding status for each individual was classified as incubating eggs, attending chicks, or failed, depending on the status of its nest at the end of each day.

GPS units were programmed to acquire fixes at 4 min intervals during daylight hours, 05:00 to 21:00 PDT, and to begin collecting data two days after initial capture. Data loggers were programmed to attempt to obtain a fix for 1 min; if a location was not acquired within this interval, the unit turned off until the next scheduled attempt. Based on prior testing of the data loggers we expected to collect approximately four days of foraging data from each GPS units under this programming.

Before deployment, we tested the accuracy of the GPS data loggers. Seventeen GPS data loggers were deployed at fixed locations under the programming described above for three days. A Garmin etrex handheld GPS simultaneously recorded fixes at 5-sec intervals over the same period. The true location was determined from the average location of all positions from the Garmin GPS. We calculated error for each location as the distance between fixes recorded by the GPS data loggers and the true

location. Using the programming described above, 95% of all fixes were within 39 m of the true location.

Behavioral Classification

GPS data were filtered to remove missed fixes, fixes that require velocities greater than 80 km/hr, and fixes that were less than 90 sec apart. We chose 80 km/hr as a threshold for excluding points based on visual examination of a histogram of all velocities, and mapping locations with velocities greater than 70 km/hr. There were few fixes with velocities greater than 80 km/hr. When mapped these locations appeared to represent an anomalous change in direction or speed relative to the previous and subsequent locations. In total, 1.33% of all location fixes were filtered out using this filtering criterion.

Locations were classified as "active" if there were three or more consecutive fixes at least 39 m apart. Locations were classified as "resting" if there were two or more consecutive fixes less than 39 m apart. Resting locations were classified as "on-colony" if they occurred within 500 m of the breeding colony, or "off-colony" if they occurred more than 500 m from the colony. This threshold was chosen to incorporate frequently used loafing sites that were visible from each colony.

For all "active" locations we used k-means cluster analysis to identify patterns of movement that represent distinguishable behavioral states, following the technique proposed by Van Moorter et al. (2010). Cluster analysis uses multivariate data (e.g., velocity and turning angle) to identify clusters of observations with similar

characteristics (Steinley 2006). We performed cluster analysis 10 times for all possible numbers of clusters between 1 and 10, and we used the gap statistic (Tibshirani et al. 2001) to identify the optimum number of clusters in the data set (Van Moorter et al. 2010). The gap statistic approach estimates the number of groups within a data set by comparing the change in within-cluster dispersion for each number of clusters to the dispersion expected from simulated reference null distributions (Tibshirani et al. 2001). This technique allowed us to objectively classify locations into behavioral states using multivariate measurements of movement characteristics, without making any *a priori* assumptions about the number of discernible behavioral states in the data or the characteristics of movements (Van Moorter et al. 2010).

Velocity and turning angle at each "active" location were used as measures of movement characteristics (Calenge et al. 2009). We calculated velocity as the distance between the current location and the next location, divided by the time between locations. Turning angle was calculated as the change in direction, in degrees, between the previous location and the subsequent location. Values of velocity ranged from 0 to 80 km/hr, and values of turning angle ranged from 0^o to 180^o. We performed range standardization on both variables before analysis so that differences in range between variables would not affect the contribution of each variable to the clustering (Steinley 2006). Turning angle could not be calculated for the first and last locations in a series of active locations; therefore, the start and end points of any movement bout were not classified to behavioral state. The gap statistic was calculated from 50 simulated data sets and the tolerance level was set to 2, higher tolerance values increase the evidence

necessary to include additional clusters (Van Moorter et al. 2010). K-means analysis was repeated 100 times with different random starting values to ensure that the number of states chosen and state assignment were not sensitive to starting values.

Foraging Behavior

We calculated daily activity rates as the proportion of all locations recorded for an individual during a day in each of the behavior category: (1) time spent on colony, (2) time spent foraging, (3) time spent commuting, and (4) time spent resting off-colony. Only days when at least 50% of location attempts were successful were included in the analysis of daily activity rates, this was done to exclude data that did not represent a significant portion of a day. We used mixed-effects models to examine how colony (Sheepy Lake or Tule Lake), breeding status (eggs, chicks, or failed), sex (male or female), and the interaction of colony x breeding status influenced daily activity rates. Individual bird identity was included as a random effect, to account for multiple days of data collected from the same individual. Residual variance was larger for failed breeders than for terns with eggs or chicks; therefore, we included a variance structure to allow for different residual variance among the categories of breeding status (Zuur et al. 2009). Behavioral activity rates were logit-transformed to approximate a Gaussian distribution (Warton and Hui 2010); a nominal value (0.001) was added to zero values in any category prior to transformation. Significance of model terms was determined using extra-sums of squares *F*-tests; non-significant ($\alpha > 0.05$) terms were sequentially dropped from the final model.

We examined the off-colony distribution of breeding Caspian terns (tending either eggs or chicks) in two stages. First, we assessed factors influencing the probability that a Caspian tern was active or resting while away from the colony. Then, for all locations where terns were considered active, we assessed factors influencing the probability that a location was classified as foraging versus commuting. Because behavioral state for both models could be categorized as a 1 or 0, we fit generalized linear mixed models (GLMMs) with a binomial distribution and a logit link function. Main effects for full models were colony (Sheepy Lake or Tule Lake), breeding status (eggs or chicks), sex (male or female), and distance from colony (km). The full model also included two-way interactions for colony x distance and colony x breeding status. Models included a random effect of day nested within individual bird identity, and assumed a continuous first-order autoregressive correlation structure to account for temporal correlation between consecutive locations (Zuur et al. 2009). We used Wald's *t*-tests to sequentially remove non-significant terms from the full model and identify the simplest model that adequately described behavioral patterns. GLMMs were fit using penalized quasi-likelihood with the glmmPQL function in the MASS package in R (Venables and Ripley 2002; R version 2.13.2, <http://www.r-project.org/>).

Central-place foraging trips were defined as any trip which began and ended at the colony and included at least 5 off-colony locations. Three foraging trips where the tern was moving away from the colony when the tag started collecting data or moving towards the colony when the tag stopped collecting data were also included in this

analysis. Missing start and end times for these three trips were not extrapolated. For each foraging trip we calculated total trip duration (min), time spent foraging (min), time spent commuting (min), and the maximum distance from the colony to any location during the foraging trip (km). We used mixed-effects models to examine how colony, breeding status, and sex influenced trip characteristics. Individual bird identity was included as a random effect, to account for multiple foraging trips taken by the same individual. All measures of foraging trip characteristics were log transformed prior to analysis. Significance of model terms was determined using extra-sums of squares *F*-tests; non-significant terms were sequentially dropped from the final model.

Foraging Areas

We delineated the foraging area(s) used by each individual GPS-tagged tern based on the biased random bridge approach for calculating utilization distributions (Benhamou and Cornelis 2010, Benhamou 2011). Unlike traditional kernel density estimators, which treat each location as independent, the biased random bridge approach calculates the utilization distribution based on pairs of serially correlated locations, thus incorporating the movement process into the estimate of space use (Horne et al. 2007). Utilization distributions were calculated for each tagged breeding individual using all locations classified as foraging. Only pairs of locations less than 12 min apart were included in these calculations; the 12-min threshold was chosen to avoid using foraging locations separated by missing data, or pairs of locations that were not part of a sustained foraging bout, in estimating utilization distributions. The minimum smoothing parameter was set to 40 m, and the diffusion coefficient for each

individual was estimated using a maximum likelihood approach (Calenge 2006). We arbitrarily chose the 50% contour interval to represent the foraging area(s) of each GPS-tagged tern (Hyrenbach et al. 2002). We evaluated the cumulative distribution of foraging areas for terns from each colony as a function of distance from the colony, based on the mean proportion of all foraging areas located within each 10-km interval from the colony.

Body Mass of Adults and Chicks

All 22 adult Caspian terns captured during GPS tagging were measured prior to release. Caspian tern adults were weighed the nearest 10 g using a 1,000-g capacity Pesola spring scale. Wing length measurements were taken to the nearest 1 mm on the flattened and straightened wing from the wrist joint to the tip of the longest primary. The difference in body mass of adult terns was tested using ANOVA, with colony, sex, and breeding status as predictors. Significance of model terms was determined using extra-sums of squares *F*-tests; non-significant terms were sequentially dropped from the final model.

We examined differences in chick body condition for the two Caspian tern colonies in the Upper Klamath Basin and for four persistent colonies within the range of the Pacific Coast population of Caspian terns (East Sand Island, OR; Crescent Island, WA; Brooks Island, CA; and Potholes Reservoir, WA). Chicks were captured at each colony during the late chick-rearing period, approximately 10 days after the first fledgling was observed, by herding flightless chicks into a cloth corral. A

subsample of all chicks captured was chosen to represent a range of wing lengths. If fewer than 30 chicks were captured at a colony in one year, then all chicks captured were measured. Caspian tern chicks were measured in the same fashion as adults. Caspian tern chicks whose mass was less than 600 g were weighed to the nearest 5 g using a 600-g capacity Pesola spring scale; all other chicks were weighed to the nearest 10 g.

We used mixed effects models to examine differences in chick body mass as a function of wing length (Lyons and Roby 2011) and colony. The full model included wing length (mm), colony, and the interaction between wing length and colony. A random slope and intercept terms for year were also included. Only chicks with wing length between 175 mm and 350 mm were included in the analysis. This represented the range of wing lengths measured at both the Sheepy Lake and Tule Lake colonies, and ensured that the model did not estimate chick mass outside the range of chick ages sampled at the two colonies of interest. Akaike's information criterion (AIC) was used to identify the most parsimonious random model structure (Zuur et al. 2009). After determining the appropriate random structure, the significance of fixed model terms was determined using extra-sums of squares *F*-tests; non-significant terms were sequentially dropped from the final model.

RESULTS

GPS Tracking

We retrieved GPS tracking data from 16 of the 20 adults that were fitted with GPS tags. Data were recovered from eight terns tagged at each colony, three females and five males from the Sheepy Lake colony (Figure 3.2a) and four females and four males from the Tule Lake colony (Figure 3.2b). Data could not be retrieved from two GPS units on terns that continued to attend active nests on their colony; two GPS-tagged terns were not relocated after release. There was considerable variation in the length of time individual birds were tracked, ranging from six hours to six days. Median tracking time was two days. Ages of chicks attended by GPS-tagged adults ranged from one day to four days, for those terns that were tracked while provisioning chicks (n = 7). Failures of nests attended by GPS-tagged adults at the Sheepy Lake colony were attributable to nest predation by California and ring-billed gulls (*Larus californicus* and *L. delawarensis*), and at the Tule Lake colony to predation by great horned owls (*Bubo virginianus*). Data from one GPS-tagged individual at the Sheepy Lake colony were censored after the first day, when we confirmed that the bird's mate had abandoned the breeding attempt.

Behavioral Classification

The gap statistic identified three movement states as the optimal clustering of the behavioral data. The three movement states differed in both velocity ($F_{2,2506}$ = 2520, $P < 0.001$) and turning angle ($F_{2,2506}$ = 6940, $P < 0.001$). Based on the characteristics of the three movement states, we classified them as "commuting," "extensive search," and "intensive search" (Figure 3.3). Commuting movements were

characterized by high velocities (median = 43 km hr^{-1}, range = 27 – 79 km hr^{-1}) and low turning angles (median = 11^{o}, range = 0 – 94^{o}); these fast, directed movements occur when a tern is commuting between areas. Extensive search movements were characterized by low velocities (median = 17 km hr^{-1}, range = 0 – 38 km hr^{-1}) and moderate turning angles (median = 32^{o}, range = 0 – 92^{o}); these slow, directed movements occur when a tern is searching an area slowly, without doubling back on itself. Intensive search movements were characterized by even lower velocities (median = 11 km hr^{-1}, range = 0 – 43 km hr^{-1}) and high turning angles (median = 151^{o}, range = 80 – 180^{o}); these tortuous movements occur when a tern is making slow, tight turns over a small area. For all subsequent analysis, intensive search and extensive search were considered collectively as foraging behavior.

Foraging Behavior

The proportion of time that adults spent on-colony (colony attendance) was significantly different between colonies ($F_{1,13}$ = 9.14, P = 0.01) and different between adults whose breeding status differed ($F_{2,20}$ = 12.14, P < 0.001), but not between the sexes ($F_{1,12}$ = 0.18, P = 0.68). Colony attendance was higher at the Tule Lake colony than at the Sheepy Lake colony. For terns incubating eggs, time spent on colony averaged 64% of the day at the Sheepy Lake colony (95% CI = 48% – 80%) and 82% of the day at the Tule Lake colony (95% CI = 70% – 90%). For terns raising chicks, colony attendance was 52% at the Sheepy Lake colony (95% CI = 40% – 64%) and 74% at the Tule Lake colony (95% CI = 65% – 81%). Colony attendance was much

lower for terns whose nest had failed (Sheepy Lake colony: 4%, 95% CI = 1% – 17%; Tule Lake colony: 10%, 95% CI = 2% – 34%).

The proportion of time terns spent foraging per day was independent of colony location ($F_{1,13} = 1.53$, $P = 0.24$) or sex ($F_{1,12} = 1.51$, $P = 0.24$). There was weak evidence that the proportion of time spent foraging was related to breeding status ($F_{2,20} = 2.86$, $P = 0.08$), with a lower proportion of time spent foraging during incubation (9%, 95% CI = 5% – 17%) than during chick-rearing (19%, 95% CI = 16% – 23%) or after nest failure (18%, 95% CI = 14% – 23%).

The proportion of time spent commuting was significantly different between colonies ($F_{1,13} = 6.71$, $P = 0.023$), but was not associated with differences in breeding status ($F_{2,20} = 1.91$, $P = 0.17$) or sex ($F_{1,12} = 1.27$, $P = 0.28$). Terns from the Sheepy Lake colony spent 8% of the day commuting (95% CI = 5% – 14%) while terns from the Tule Lake colony spent only 3% of the day commuting (95% CI = 2% – 6%).

There were significant differences in the proportion of time spent resting off-colony related to breeding status ($F_{2,18} = 27.62$, $P < 0.001$), and a significant interaction between breeding status and colony ($F_{2,18} = 9.44$, $P = 0.002$). During incubation, the proportion of time spent resting off-colony was similar for terns from the Sheepy Lake colony (5%, 95% CI = 0% – 43%) and terns from the Tule Lake colony (1%, 95% CI = 0% – 4%). For terns raising chicks, however, those from the Sheepy Lake colony spent more time resting off-colony (11%, 95% CI = 2% – 38%) than terns from the Tule Lake colony (0%, 95% CI = 0% – 1%). Failed breeders,

regardless of colony, spent much more time resting off-colony (Sheepy Lake colony: 31%, 95% CI = 13% – 56%; Tule Lake colony: 53%, 95% CI = 19% – 85%).

There was a significant negative relationship between distance from colony and the probability of being active, and a significant interaction between breeding colony and distance from colony (Table 3.1). GPS-tagged terns breeding at the Sheepy Lake colony were estimated to have a greater than 90% probability of being active within 13 km of the colony; at distances further than 40 km Sheepy Lake terns were more likely to be resting than active (Figure 3.4a). For GPS-tagged terns breeding at the Tule Lake colony there was an estimated > 90% probability of being active within 13 km of the colony; at distances further than 25 km from the colony Tule Lake terns were more likely to be resting than active (Figure 3.4b).

For terns breeding at the Sheepy Lake colony, the probability of foraging as opposed to commuting increased with distance from the colony (Table 3.2). Terns breeding at the Sheepy Lake colony were less likely to be foraging close to the colony; the probability of foraging continued to increase with increasing distance from the colony (Figure 3.5a). For all distances from the colony, terns from the Tule Lake colony had between a 65% – 80% probability of foraging (Figure 3.5b). Terns breeding at the Tule Lake colony had a higher probability of foraging within 15 km of their colony than terns breeding at the Sheepy Lake colony.

Colony was the only factor that was significantly associated with characteristics of foraging trips (Table 3.3); there was no evidence that breeding status

or sex had an effect on foraging trip characteristics. Foraging trips by terns from the Sheepy Lake colony were longer than trips by terns from the Tule Lake colony ($F_{1,10}$ = 18.59, P = 0.002; Table 3.3). During foraging trips from the Sheepy Lake colony, terns spent more time commuting than terns from the Tule Lake colony ($F_{1,10}$ = 18.24, P = 0.002). There was weak evidence that terns from the Sheepy Lake colony spent more time foraging per foraging trip than terns from the Tule Lake colony ($F_{1,10}$ = 4.16, P = 0.069). Maximum distance from the colony was significantly greater for terns from the Sheepy Lake colony than for terns from the Tule Lake colony ($F_{1,10}$ = 25.05, P < 0.001).

Foraging Areas

Foraging areas for the five GPS-tagged terns breeding at the Sheepy Lake colony were dispersed among five different areas (Figure 3.6a): Sheepy Lake (n = 3 terns), Tule Lake Sump 1A (n = 3), Klamath River (n = 2), Copco and Iron Gate reservoirs (n = 1), and agricultural canals around Tule Lake and Lower Klamath NWRs (n = 1). Foraging areas for the seven GPS-tagged terns breeding at the Tule Lake colony were largely concentrated within Tule Lake NWR (Figure 3.6b): Tule Lake Sump 1A (n = 6 terns), Tule Lake Sump 1B (n = 7), agricultural canals around Tule Lake NWR (n = 2), and Clear Lake (n = 1). All overlap in foraging areas between terns from the two colonies occurred at Tule Lake Sump 1A. Eighty-nine percent of the foraging areas of GPS-tagged terns nesting at the Tule Lake colony occurred within 10 km of the colony, while only 17% of the foraging areas of GPS-

tagged terns nesting at the Sheepy Lake colony occurred within 10 km of the colony. All foraging areas for Tule Lake terns were within 28 km of the colony; all foraging areas for Sheepy Lake terns were within 54 km of the colony.

Body Mass of Adults and Chicks

We were unable to confirm the breeding status of three terns captured at the Sheepy Lake colony and GPS-tagged that did not return to the colony after capture, these individuals were excluded from this analysis. There was a significant difference between colonies ($F_{1,16}$ = 7.12, P = 0.017) and sexes ($F_{1,16}$ = 7.75, P = 0.013) in the average total body mass of captured adult Caspian terns. There was no relationship between breeding status (egg stage vs. chick stage) and adult mass ($F_{1,53}$ = 0.26, P = 0.616). On average, body mass of adult terns captured at the Sheepy Lake colony (mean = 586 g) was 29 g less (95% CI = 8 – 50 g) than the body mass of adult terns captured at the Tule Lake colony (mean = 611 g). Male terns were on average 30 g (95% CI = 9 – 51 g) heavier than female terns. Results were similar when the three adult terns whose breeding status was unknown were included in the final model.

Size-adjusted chick body mass differed among nesting colonies ($F_{5,1569}$ = 107.48, P < 0.001; Figure 3.7). Average size-adjusted mass of tern chicks from the Sheepy Lake colony was 36 g greater than that of tern chicks from the Crescent Island colony in south-central Washington (P < 0.001), but 41 g to 89 g less than chicks from the Tule Lake colony and the other three comparison colonies (P < 0.001). Size-adjusted body mass of chicks from the Tule Lake colony was the highest of all 6

colonies and averaged 125 g greater than that of chicks from the Crescent Island colony ($P < 0.001$) and 89 g greater than that of chicks from the Sheepy Lake colony ($P = 0.001$).

DISCUSSION

Our results indicated that the foraging behavior of Caspian terns breeding at two neighboring colonies in the Upper Klamath Basin were surprisingly divergent. The distance between the two colonies in our study (30 km) was far less than the maximum foraging range for breeding Caspian terns (80 km; Adrean 2011). Despite the proximity of the two colonies, terns nesting at Sheepy Lake had markedly longer foraging trips, lower colony attendance, and greater commuting distances to foraging areas compared to terns nesting at Tule Lake. These inter-colony differences in foraging behavior were associated with lower body mass of adults and lower size-adjusted body mass of pre-fledged chicks at the Sheepy Lake colony. Our results highlight the importance of foraging conditions in close proximity to the colony for central place foraging waterbirds during the breeding season.

Colony attendance by Caspian terns nesting at the Tule Lake colony was consistently much higher than that of terns nesting at the Sheepy Lake colony, with Tule Lake terns spending considerably less time commuting or resting off-colony. Average colony attendance by Sheepy Lake terns with young chicks (52%) is just enough for one adult to be present at the nest throughout the day. Caspian terns exhibit lower colony attendance as the breeding season progresses (Anderson et al. 2005,

Lyons et al. 2005). If parents need to increase their foraging effort as the energy requirements of their growing chicks increase, terns breeding at the Sheepy Lake colony may only be able to increase foraging effort by leaving chicks unattended and exposed to the risks of predation by gulls and harassment by other adult terns. All tracking data for this study were collected while chicks were less than five days old, when the energy requirements of small chicks are relatively low; this probably explains why we did not detect a clear increase in foraging effort between terns with eggs and those with chicks.

We found strong relationships between distance from the colony and foraging behavior and this relationship was different for the two colonies (Figure 3.5). Terns nesting at the Tule Lake colony generally foraged immediately upon leaving the colony. Conversely, Sheepy Lake breeders had a low probability of foraging within 10 km of the colony, and the probability of foraging increased with distance from the colony. The Upper Klamath Basin consists of a fragmented patchwork of wetlands, lakes, rivers, and agricultural canals. Even though these two colonies share broadly overlapping potential foraging habitat, the distance to foraging areas from the Sheepy Lake colony made them less accessible to terns breeding at this colony. Sheepy Lake breeders had to adopt a more extensive foraging behavior, which consequently increased foraging effort and decreased physical condition and time spent at the nest.

Foraging trips from the Sheepy Lake colony lasted, on average, more than three times longer (186 min) than foraging trips from the Tule Lake colony (55 min).

Average duration of foraging trips by Sheepy Lake breeders was longer than that of terns nesting in the Columbia River estuary (136 min in 2000 and 97.5 min in 2001; Anderson et al. 2007) or in San Francisco Bay (125 min, Adrean 2011). Conversely, average foraging trip duration of Tule Lake breeders was as low or lower than that observed in the Columbia River estuary and in San Francisco Bay. Longer foraging trips by Sheepy Lake breeders were characterized by more time spent commuting, a higher proportion of foraging trips that included a resting bout, and greater maximum distance from the colony. Long foraging trips reduce the time spent at the nest and limit the number of fish deliveries to chicks, which can have a negative impact on both the growth rate and survival of chicks (Suryan et al. 2002, Davoren and Montevecchi 2003, Boersma and Rebstock 2009).

The difference in distribution of foraging areas for breeding terns from the two colonies reflects the between-colony differences in foraging behavior described above. Tule Lake terns concentrated their foraging within Tule Lake NWR. Sheepy Lake terns used foraging areas that were dispersed to the north, east, and west of the colony; the majority of foraging areas were more than 10 km from the colony, with four of the five terns using foraging areas closer to the Tule Lake colony than the Sheepy Lake colony. Terns from both colonies foraged in Tule Lake Sump 1A; this was clearly a foraging hot spot for Caspian terns in the Upper Klamath Basin. Given the small size of both the Sheepy Lake and Tule Lake colonies (188 pairs and 34 pairs, respectively), it seems unlikely that there was competition for foraging areas during this study. As these colonies become more established, particularly if the Tule Lake colony increases

in size, this could provide an opportunity to examine how foragers from different colonies compete for shared foraging areas (Gremillet et al. 2004).

The body mass of adult terns breeding at Sheepy Lake was, on average, 4% lower than that of adults breeding at Tule Lake. Lower adult body mass during breeding was associated with lower reproductive success in Arctic terns (*Sterna paradisaea*; Monaghan et al. 1989) and common terns (*S. hirundo*; Wendeln and Becker 1999). We cannot determine whether the between-colony difference in adult body mass of Caspian terns was biologically significant, or whether this difference was a physiological response to stress or an adaptive response to reduce flight costs and enhance foraging efficiency (Jones 1994). Regardless, the between-colony difference in adult body mass suggests that differences in prey availability close to the two colonies were significant enough to affect the physical condition of adults. There was no affect of breeding status on adult mass, however, so it is unlikely that the observed between-colony differences were a result of the GPS-tagged terns from the two colonies being at different stages of the nesting cycle.

Size-adjusted body mass of Sheepy Lake chicks was approximately 25% less than that of Tule Lake chicks. Tule Lake chicks had as high or higher average size-adjusted body mass as did any colony in the Pacific Coast population; however, this estimate is based on a very small sample size from only a single breeding season. Nevertheless, chicks from the Sheepy Lake colony had lower average size-adjusted body mass than either chicks from the Tule Lake colony or chicks from three of the

four comparison colonies. Lower chick condition at the Sheepy Lake colony could have immediate consequences for reproductive success through reduced chick survival; there could also be secondary effects on post-fledgling survival, recruitment to the breeding population, and future reproductive potential if under-nutrition during the chick stage has persistent negative effects on fitness (Lindström 1999, Metcalfe and Monaghan 2001, Kitaysky et al. 2006, Morrison et al. 2009).

Accurately describing behavior based on tracking data is a major objective of animal movement studies. In some studies this has been accomplished by arbitrarily defining a threshold in speed to distinguish foraging from commuting (Gremillet et al. 2004, Kotzerka et al. 2010, McLeay et al. 2010). More sophisticated approaches to distinguishing foraging from commuting behavior based on movement tracks include first passage time (Fauchald and Tveraa 2003, Suryan et al. 2006), fractal dimension (Tremblay et al. 2007), and state-space modeling (Morales et al. 2004, Jonsen et al. 2005, Breed et al. 2009). Of these techniques, only state-space modeling assigns locations to behavioral states; however, state-space models are complex to implement and require assumptions about the movement process being estimated. In the present study, we have successfully applied a cluster analysis approach to objectively infer three types of movement behavior. This approach is simple to implement, does not make any assumptions about the number of movement types or characteristics of those behaviors, and can be adapted to incorporate multiple measures of movement behavior (Van Moorter et al. 2010). This methodology allowed us to identify different movement states, quantify time spent foraging, and test hypotheses about foraging

effort, the spatial distribution of off-colony behavior, and the locations of foraging areas.

Caspian terns demonstrated flexible foraging behavior in response to local prey availability; breeding behavior and parental effort appear to be strongly influenced by foraging conditions close to the colony. Foraging behavior of Caspian terns from the Sheepy Lake colony was consistent with that of terns from other colonies experiencing food limitation (Lyons et al. 2005, Anderson et al. 2007, Adrean 2011). Greater foraging effort came at the expense of colony attendance, self-maintenance, and chick condition, which are all likely to have impacts on overall productivity. There was no evidence that prey availability limited productivity at the Tule Lake colony.

This study was conducted during the first year that the Tule Lake island was available to breeding Caspian terns and the colony was quite small (34 breeding pairs). The Sheepy Lake colony was substantially larger (188 breeding pairs), but it was in its second year of development; the Sheepy Lake island had been used by 258 breeding pairs of Caspian terns the year before. This prior history of nesting likely explains the difference in colony size between the two islands during our study. Given the apparent higher forage fish availability close to the Tule Lake island, it seems likely that this colony will attract more breeding Caspian terns in future nesting seasons unless other factors, such as predation, strongly limit reproductive success. Some Caspian terns breeding at Sheepy Lake used foraging areas that were closer to the Tule Lake island, if other factors do not limit recruitment to Tule Lake we would expect some terns that

nested on Sheepy Lake to switch to the Tule Lake island because it is closer to preferred foraging areas (Cairns 1979). Despite pronounced differences between the two colonies in the foraging behavior of breeding terns, productivity was similar at the two colonies. At least in 2011, predation played a more significant role than foraging conditions in limiting the reproductive success for Caspian terns nesting at these two new colonies in the Upper Klamath Basin (see Chapter 2).

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Table 3.1. Estimated coefficients, standard errors, and significance tests from a binomial generalized linear mixed model estimating the probability that a Caspian tern was active while off-colony, as a function of breeding colony and distance from colony. Coefficients and standard errors are on a logit scale. Degrees of freedom, *t*-values, and *P*-values are for Wald's *t*-tests of the significance of each covariate.

	Coefficient	Standard Error	df	*t*-value	*P*-value
Intercept	3.22	0.83	1226	3.86	<0.001
Colony: Tule	1.11	1.09	10	1.02	0.330
Distance	-0.08	0.03	1226	-2.90	0.004
Colony x Distance	-0.09	0.04	1226	-2.19	0.029

Table 3.2. Estimated coefficients, standard errors, and significance tests from a binomial generalized linear mixed model estimating the probability that an active Caspian tern was foraging vs. commuting, as a function of breeding colony, breeding status, and distance from colony. Coefficients and standard errors are on a logit scale. Degrees of freedom, *t*-values, and *P*-values are for Wald's *t*-tests of the significance of each covariate.

	Coefficient	Standard Error	df	*t*-value	*P*-value
Intercept	-0.53	0.38	914	-1.38	0.1681
Colony: Tule	1.89	0.43	10	4.37	0.001
Distance	0.06	0.02	914	2.84	0.005
Colony x Distance	-0.08	0.03	914	-2.80	0.005

Table 3.3. Summary of central-place foraging trips of Caspian terns breeding at Sheepy Lake and Tule Lake in the Upper Klamath Basin, California. Values for duration, foraging, commuting, and maximum distance from colony are medians (± 95% confidence intervals) as estimated by mixed-effects models.

	Sheepy Lake	Tule Lake
Number of trips	8	35
Proportion of trips with commuting	1.00	0.69
Proportion of trips with resting	0.63	0.09
Duration of trip (min)	186 (105 – 329)	55 (42 – 72)
Commuting time (min)	48 (18 – 122)	5 (3 – 10)
Foraging time (min)	72 (39 – 134)	39 (29 – 52)
Maximum distance (km)	27 (15 – 47)	6 (4 – 8)

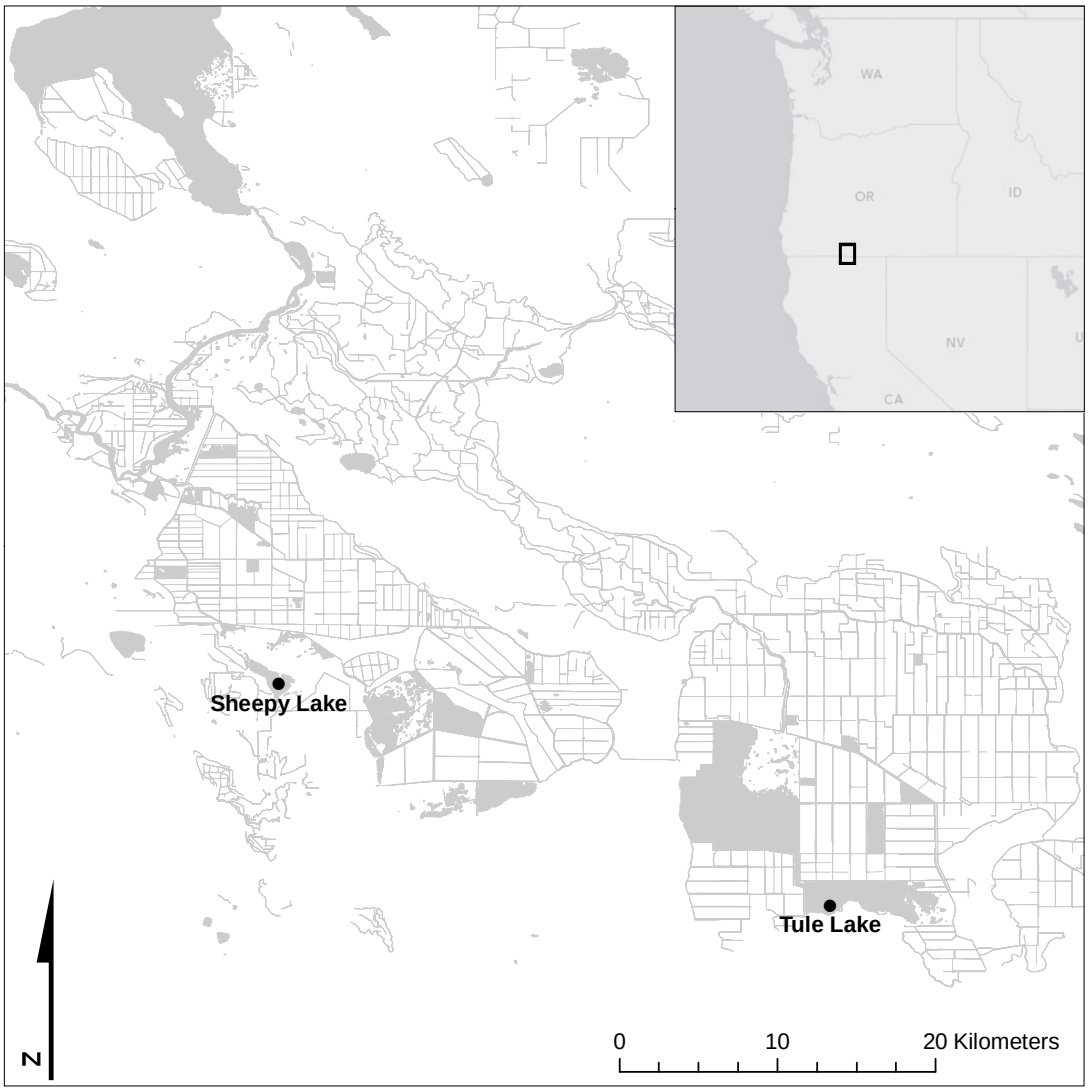

Figure 3.1. Map of the study area in the Upper Klamath Basin of California and Oregon, showing the locations of the new artificial Caspian tern nesting islands in Sheepy Lake and Tule Lake.

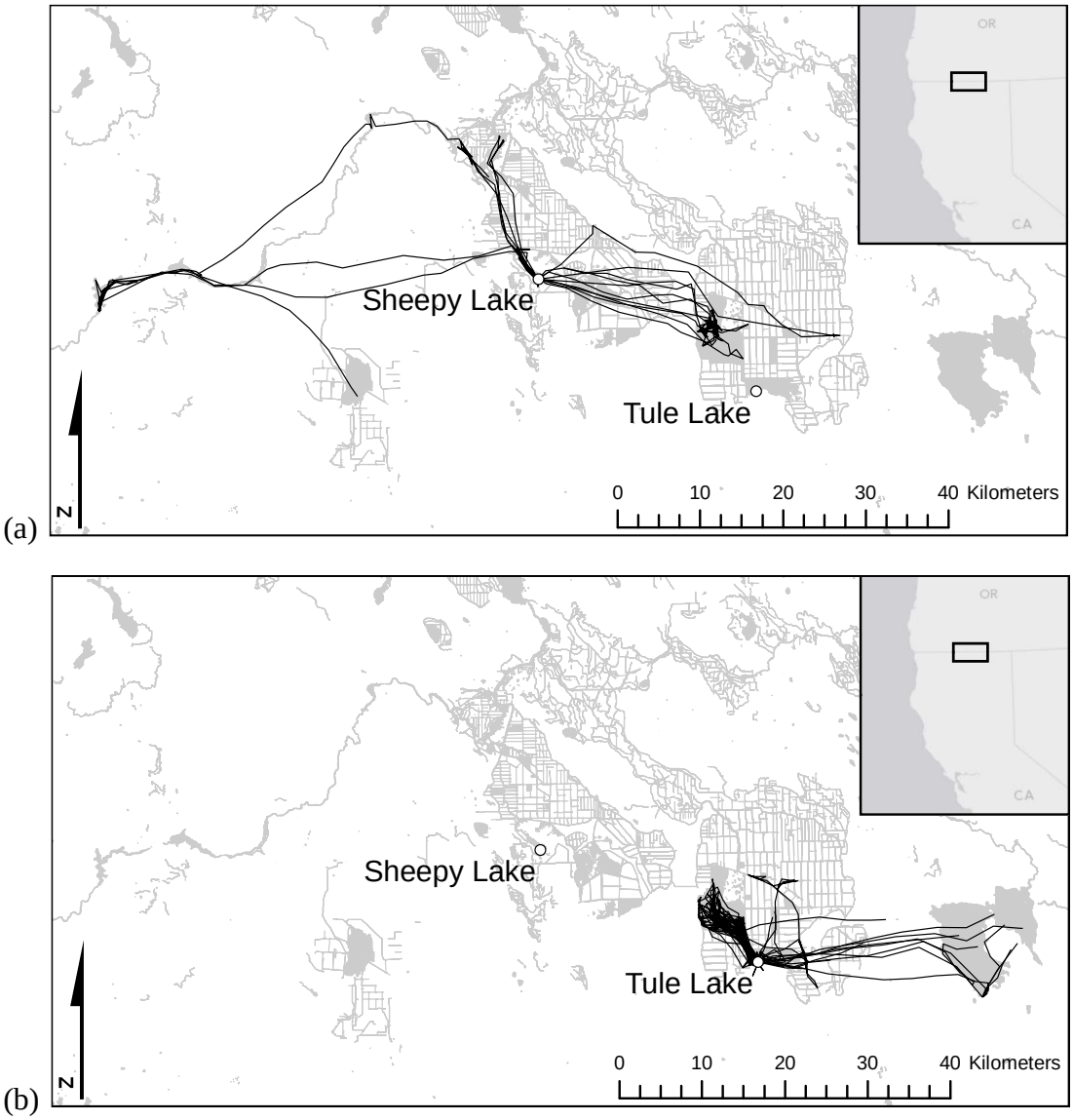

Figure 3.2. Maps showing all movements by GPS-tagged Caspian terns breeding at (a) the Sheepy Lake colony and (b) the Tule Lake colony in the Upper Klamath Basin of Oregon and California, USA. Open circles indicate colony locations. Grey areas indicate lakes, rivers, and canals.

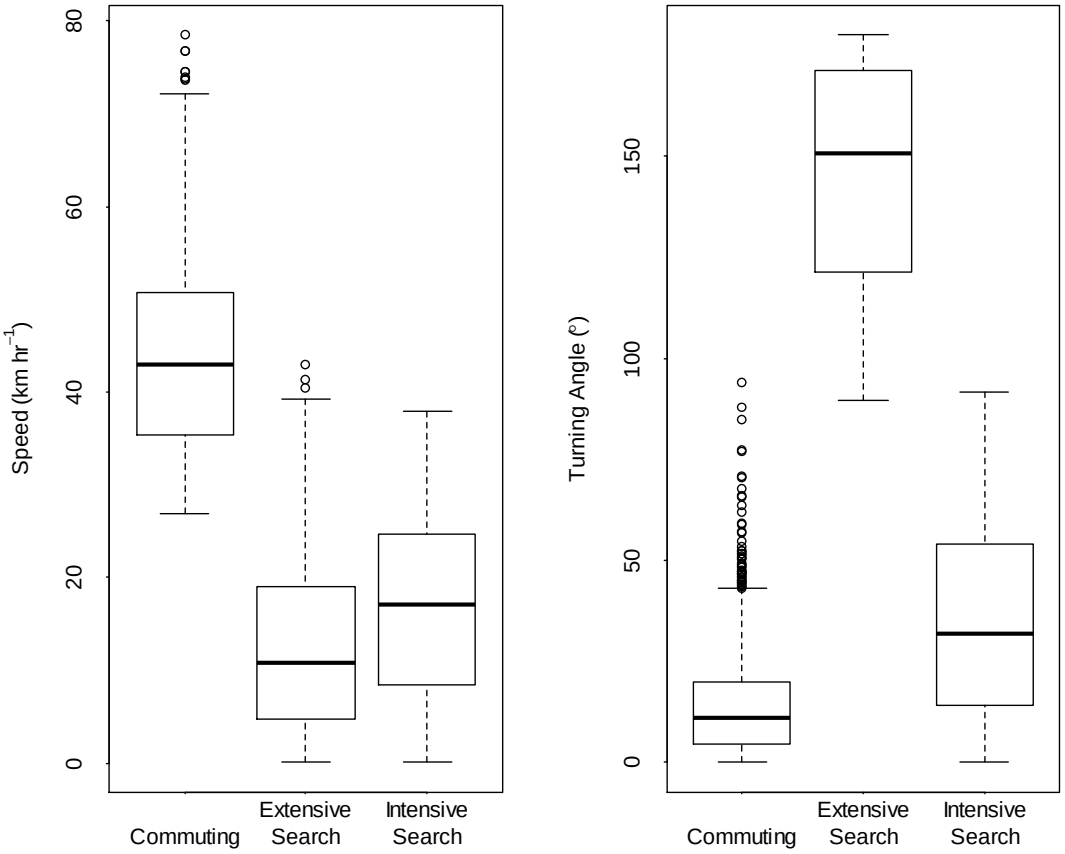

Figure 3.3. Values of velocity and turning angle for the three movement states as defined by cluster analysis. Data on movement characteristics are for Caspian terns equipped with GPS-loggers and nesting at either the Sheepy Lake colony or the Tule Lake colony in the Upper Klamath Basin of Oregon and California, USA.

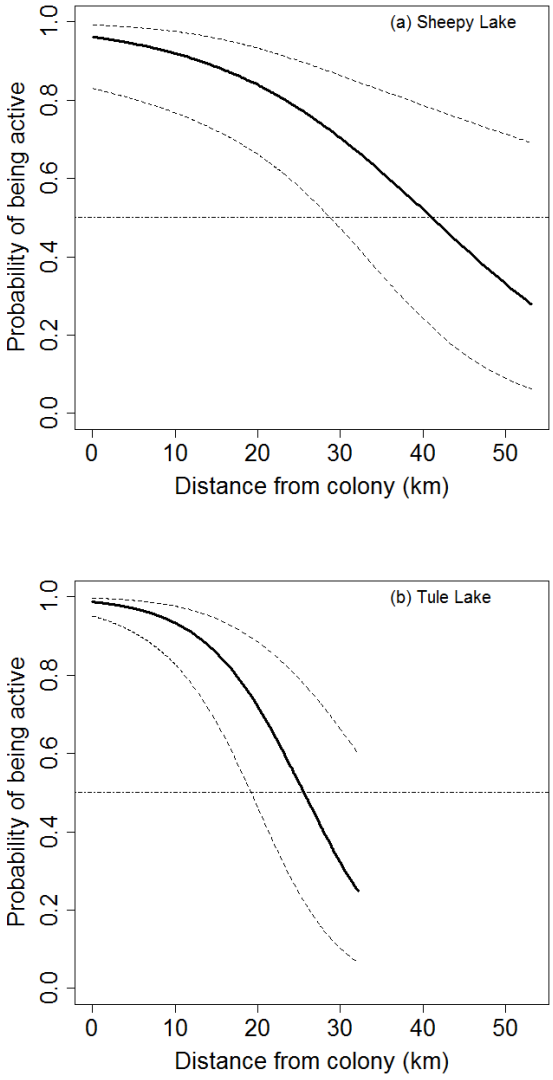

Figure 3.4. Estimated probability that a Caspian tern breeding at (a) Sheepy Lake or (b) Tule Lake in the Upper Klamath Basin, California, was active vs. resting while off-colony as a function of colony and distance from the colony. Solid lines indicate estimated mean probabilities and dotted lines indicate 95% confidence intervals. Dashed horizontal lines depict the 0.5 probability.

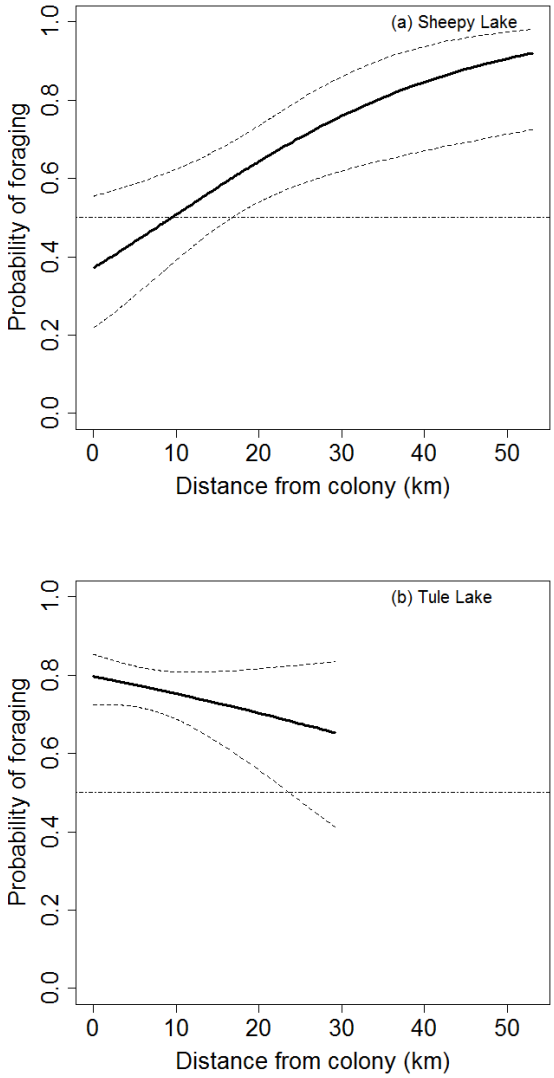

Figure 3.5. Estimated probability that a Caspian tern breeding at (a) Sheepy Lake or (b) Tule Lake in the Upper Klamath Basin, California, was foraging vs. commuting as a function of colony and distance from the colony. Solid lines indicate estimated mean probabilities and dotted lines indicate 95% confidence intervals. Dashed horizontal lines depict the 0.5 probability.

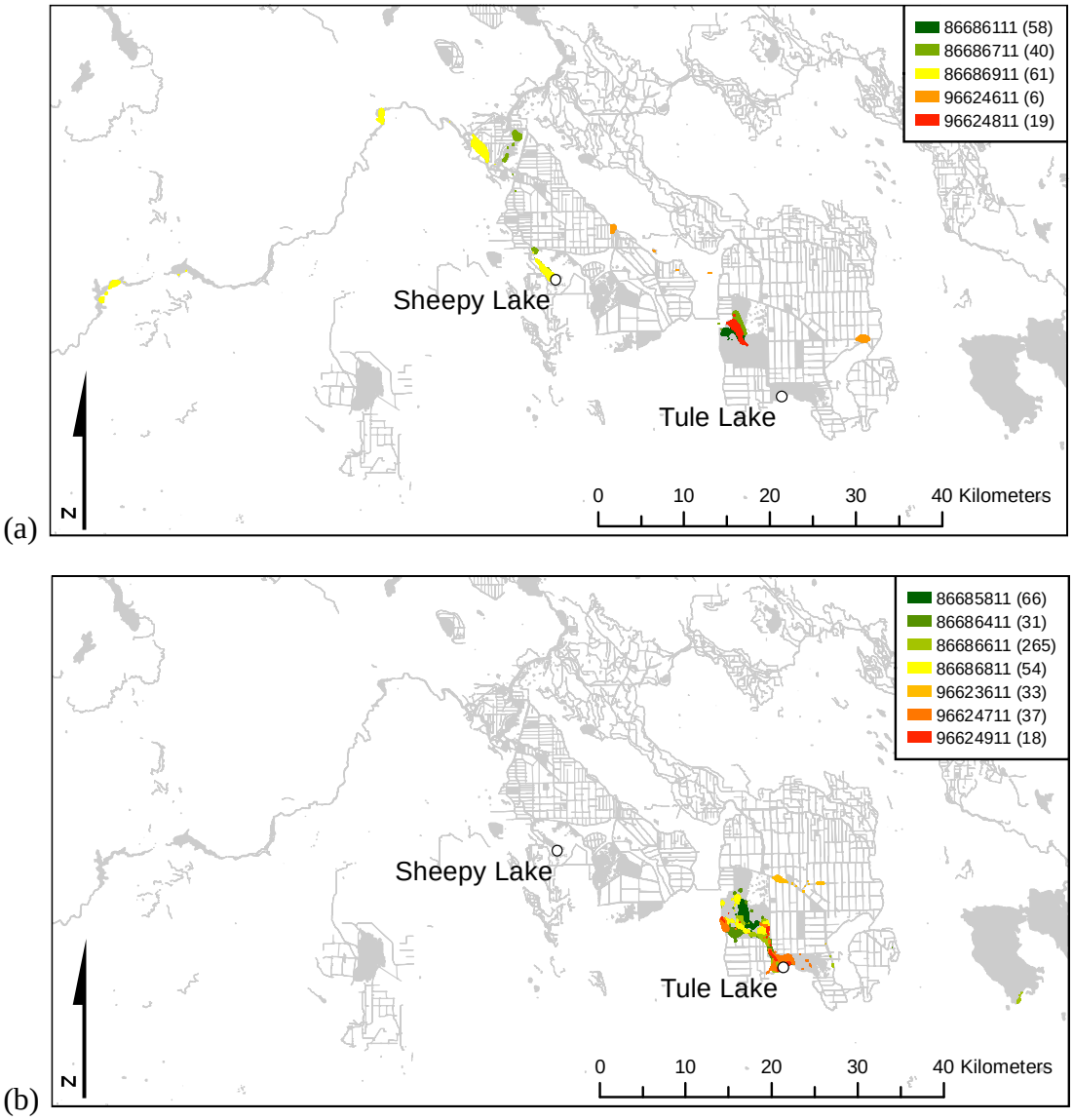

Figure 3.6. Foraging areas of Caspian terns breeding at colonies on (a) Sheepy Lake and (b) Tule Lake in the Upper Klamath Basin of Oregon and California. Foraging areas are based on the 50% utilization distributions of all foraging locations for each individual tern, estimated using the biased-random bridge approach. Legend indicates tern identity, and the number of foraging locations used to estimate foraging area is in parentheses.

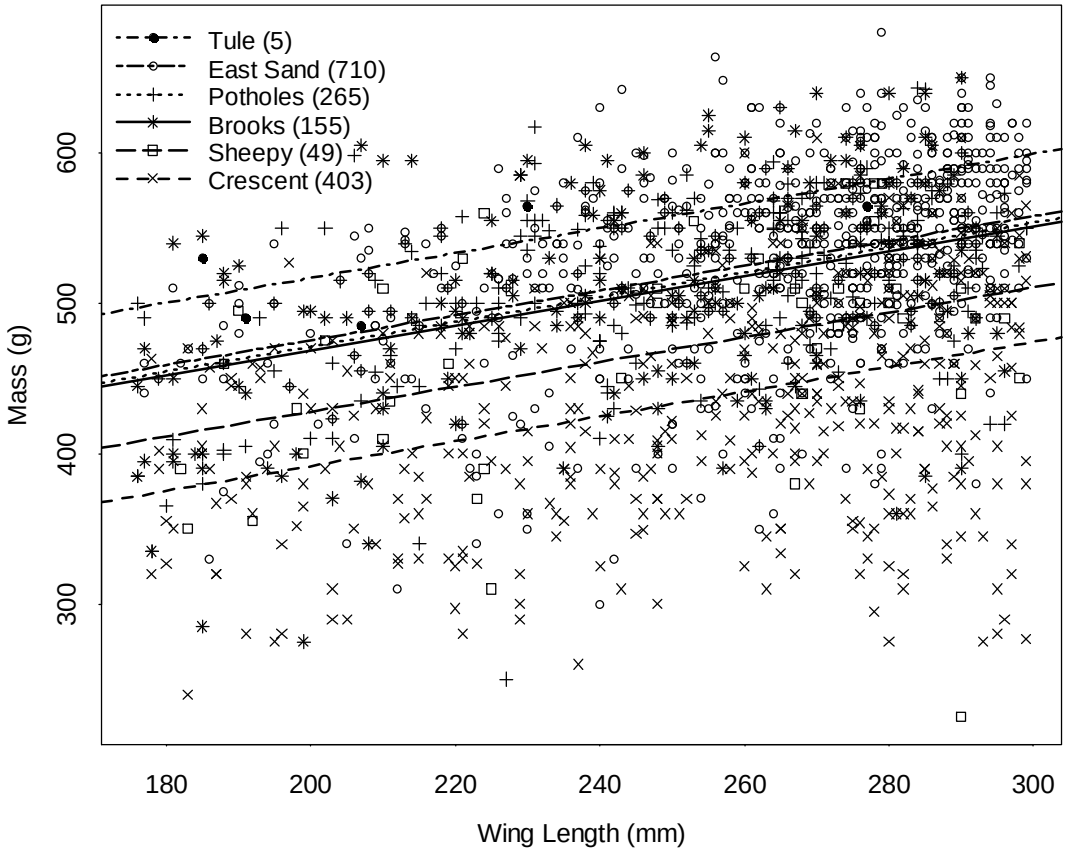

Figure 3.7. Body mass of Caspian tern chicks as a function of wing length from six colonies in the western North America population. Colony names in the legend appear in the same order as regression lines on the graph. Numbers in parentheses next to colony names indicate the number of chicks measured at each colony.

CHAPTER 4: SYNOPSIS AND CONCLUSIONS

Allison Patterson

The primary objectives of this study were to (1) evaluate the initial success of constructing artificial nesting habitat (new islands) and providing social attraction (decoys and audio playback systems) in order to restore Caspian terns (*Hydroprogne caspia*) as a breeding species in the Upper Klamath Basin and (2) identify those factors that could limit the future growth and productivity of Caspian tern breeding colonies that might form on these islands. Here, I place my results in the context of the broader Caspian Tern Management Plan (USFWS 2005), recommend an approach for moving forward with effective monitoring and management of alternative Caspian tern nesting habitat created as part of the Plan, and describe how lessons learned from this study can inform future restoration and management of waterbird colonies. Habitat enhancement and social attraction have become important tools for the conservation and management of waterbird colonies in the last 40 years, and will continue to play an important role, especially as more colonies face challenges from human development and the negative effects of anthropogenic climate change (Jones and Kress 2012).

Caspian terns responded rapidly to the construction of artificial nesting islands and deployment of social attraction in the Upper Klamath Basin, attempting to breed at all three newly-constructed islands in the first year and establishing successful breeding colonies at two of the three sites. Despite drought and exceptionally cool conditions during the breeding season (NOAA 2010, NRCS 2010, NOAA 2011), these restoration activities increased the number of Caspian terns breeding in the Upper Klamath Basin in 2010 and 2011 relative to the preceding fifteen years. In both years

of my study, new islands built as part of the restoration effort were the only sites in the Basin where Caspian terns experienced some reproductive success and produced fledglings. The addition of two artificial Caspian tern nesting islands in 2011 did increase the number of breeding colonies in the Basin, but did not increase the total number of breeding pairs compared to 2010. The total number of breeding pairs that attempted to nest at all three sites declined slightly from 2010 to 2011, suggesting that there were limitations on the number of Caspian terns that could be attracted to breed in the Upper Klamath Basin. The failure of additional acreage of available nesting habitat at multiple islands to attract more terns to the Basin suggests in 2011 that the availability of nesting habitat was no longer the main factor limiting the size of the Caspian tern breeding population in the Basin.

Productivity at the restored Caspian tern colonies was variable in the first two years following island construction. At Sheepy Lake in 2010, reproductive success was 0.65 fledglings/breeding pair, while in 2011 tern colonies on Sheepy Lake and Tule Lake both experienced relatively low reproductive success, 0.11 and 0.12 fledglings/breeding pair, respectively. Over both years of my study, average productivity at these colonies was low relative to levels suggested as necessary to maintain a stable Pacific Coast population of Caspian terns (Suryan et al. 2004). Other moderate-sized colonies within the Pacific Coast region have persisted despite occasional years of low reproductive success, below 0.32 fledglings/breeding pair. Chronically low productivity, however, would lower site fidelity of birds that have

nested at these sites, negatively affect recruitment of prospecting birds from other areas, and reduce the potential for future recruitment to the natal site.

A two-year study is too short to draw strong conclusions about the longer-term potential for reproductive success at these new Caspian tern colony sites. However, the first two years have shown that terns nesting at Sheepy Lake can achieve reasonable rates of reproductive success in some years, but fledging rates and total number of fledglings produced may be variable depending on factors such as water availability, interspecific competition for nest sites, and nest predation. Favorable foraging conditions at the Tule Lake colony indicate that this could be an attractive site for a breeding colony of Caspian terns, if nest predation and nocturnal disturbance can be managed.

I identified three main factors potentially limiting colony size, development, and reproductive success of Caspian terns on these artificial islands; the importance of each limiting factor varied among sites and years. Water shortages made the Tule Lake and Orems Unit islands unavailable as nesting habitat in 2010, and resulted in land-bridging of the Orems Unit island in the midst of the 2011 nesting season, which would have caused colony failure had a Caspian tern colony formed there. Competition with gulls (*Larus* spp.) for nest sites and gull predation on tern eggs and chicks contributed to smaller colony size and lower reproductive success of the Sheepy Lake tern colony in 2011. Predation and nocturnal disturbance by great horned owls (*Bubo virginianus*) resulted in abandonment of the Orems Unit island by Caspian

terns during the nest-building stage, and caused most of the nest failures at the tern colony on the Tule Lake island. Management actions to minimize the negative impacts of these factors would aid the development of these nascent Caspian tern colonies. Long-term management actions, including persistent use of social attraction techniques and predator management measures, have been recommended to maintain successful seabird colonies at restoration sites (Hall and Kress 2004, Parker et al. 2007, Jones and Kress 2012).

Terns respond quickly to social attraction compared to other species with higher breeding site fidelity (Kress and Nettleship 1988, Parker et al. 2007, Jones and Kress 1012). Given this vagility, however, long-term management to create a history of successful breeding may be required to promote site fidelity among terns that recruit to these colonies. Individual breeding success and local breeding success have been associated with higher breeding site fidelity in colonial seabirds (Naves et al. 2006, Boulinier et al. 2008). Tims et al. (2004) found that common terns (*Sterna hirundo*) from an established colony did not relocate to newer colonies in large numbers even though productivity was higher at the newly established sites; they concluded that breeding site selection is conservative and common terns prefer to stay at a known site with lower breeding success than take on the risk and costs of establishing a territory at a new site. Suryan and Irons (2004) proposed that long-term colony growth by black-legged kittiwakes (*Rissa tridactyla*) within Prince William Sound, Alaska, was driven by natal recruitment more than movements among colonies by breeding adults.

The regular banding of Caspian tern adults and pre-fledged chicks at colony restoration sites would generate valuable information about the retention of breeders and natal site recruitment to these colonies. This would provide insight into the dynamics of new colony development, such as whether colony growth is intrinsic or driven by recruitment from other colonies, and how local productivity influences dispersal rates. From a management perspective, this could provide valuable information to guide decisions about the need for on-going management of these colonies. High breeding and natal site philopatry would be strong indicators that new Caspian tern colonies had become self-sustaining.

In both years of my study, Caspian tern nest initiation was delayed; the peak in egg-laying did not occur until almost two months after the initiation of courtship behavior and at least one month after the first tern eggs were laid. The delay in nest initiation may have resulted from the newness of the colonies; new colony sites tend to recruit less experienced breeders, and terns that recruit to new sites may take longer to establish pair bonds and nesting territories. If this were the case, then we would expect the peak in egg-laying to occur earlier and nest initiation to be more synchronized as new colonies become more established. An alternative explanation is the unusually cold weather during the early stages of both the 2010 and 2011 nesting seasons. Average May temperatures recorded at Klamath Falls, Oregon were 3^{o}C lower than the 30-year average in both 2010 and 2011 (NOAA 2010, NOAA 2011). If the delayed onset of nesting by Caspian terns was driven by climatic conditions, then nesting should be initiated earlier in years with average spring temperatures. Earlier,

more synchronized breeding should benefit these Caspian tern colonies in several ways: (1) by attracting breeders that had not previously recruited to these sites because of poor conditions early in the season; (2) by promoting higher reproductive success, which is generally associated with earlier nesting; (3) by allowing terns to better compete with gulls for nesting territories at sites where nesting gulls are abundant; and (4) by providing better defenses against avian nest predators, either through predator swamping or enhanced cooperative nest defense.

The three artificial islands in the Upper Klamath Basin are only part of a larger scale Caspian tern management program (USFWS 2005). In fulfillment of this plan, the U.S. Army Corps of Engineers has constructed artificial islands in four other areas of interior Oregon: Fern Ridge Reservoir, Warner Valley, Summer Lake basin, and Malheur NWR. By the 2012 breeding season, the amount of suitable habitat available for nesting Caspian terns at East Sand Island in the Columbia River estuary had been reduced from 2 ha (5 acres) to 0.6 ha (1.6 acres), and further reductions are being considered to achieve the desired colony size of 2,500 to 3,125 breeding pairs, down from 9,000 to 10,000 breeding pairs. Preliminary data indicate that there is high connectivity among the colonies developing on artificial islands in interior Oregon and California, specifically those in the Upper Klamath Basin, Warner Valley, and Summer Lake basin (Suzuki 2012). Monitoring the movements of individual terns amongst these colony sites will be necessary to assess whether growth of any one colony is driven by (1) recruitment of terns displaced from the East Sand Island colony, (2) movements of breeding adults among the artificial islands, or (3)

recruitment to the natal site. My study focused on assessing the initial success of habitat creation in the Upper Klamath Basin and providing information that would be useful to inform management of those sites. In the long-term, the increase in size and productivity of Caspian tern colonies in the Upper Klamath Basin should be evaluated within the context of all colonies in interior Oregon and California at least, but preferably within the context of the entire meta-population of Caspian terns in western North America.

Caspian terns breeding at Sheepy Lake expended greater foraging effort than terns breeding at Tule Lake. Sheepy Lake terns spent less time at the colony, took longer foraging trips, commuted farther to foraging areas, and spent more time resting away from the colony than Tule Lake terns. The observed differences in foraging behavior between terns breeding at the Sheepy Lake colony and the Tule Lake colony highlighted the benefits of access to high-quality foraging habitat in close proximity to the colony. Breeding Caspian terns can adapt their foraging behavior to exploit prey patches that are far from the colony; in my study three terns breeding at Sheepy Lake had foraging areas that included habitat more than 30 km from the colony. In San Francisco Bay, breeding Caspian terns were detected as far as 80 km from their nest site (Adrean 2011). But foraging at long distances from the breeding colony comes at the expense of nest attendance, nest defense, chick provisioning rates, and resource allocation for self-maintenance. Only high-quality individuals are likely to successfully raise chicks under these conditions.

The Caspian tern colony at the Tule Lake island experienced favorable foraging conditions in 2011, comparable to the foraging conditions experienced by Caspian terns nesting in the Columbia River estuary during years of higher than average nesting success (Lyons et al. 2005, Anderson et al. 2007). These favorable nesting conditions were apparently due to the proximity of high-quality foraging areas, particularly in Tule Lake Sump 1A. Eighty-nine percent of the foraging areas of GPS-tagged Caspian terns breeding at the Tule Lake colony occurred within 10 km of the colony. In 2011, there was twice as much potential foraging habitat (areas covered by water) within 10 km of the Tule Lake colony (38 km^2) than within 10 km of the Sheepy Lake colony (19 km^2; A. Patterson, unpublished data).

Increasing the amount of high-quality foraging habitat in proximity to a breeding colony should, in theory, increase the number of breeding pairs a colony can support and increase average reproductive success. This would be especially true for inland colonies, where the amount of potential foraging habitat is generally much lower than at coastal sites. Becker et al. (1997) showed that common terns nesting at a freshwater site experienced more favorable foraging conditions compared to terns nesting at a coastal site because of more consistent prey availability at the limnetic site. This benefit of consistency, however, can become a disadvantage for inland colonies when there is a shortage of potential foraging habitat in close proximity to the colony; a shortage of proximal foraging habitat appears to be a constraint for the Sheepy Lake Caspian tern colony.

The area covered by water within 30 km of an existing or potential colony site could be used as an index of the availability of foraging habitat when considering where to implement restoration efforts for piscivorous colonial waterbirds on a regional scale. The value of such an index could be enhanced by including only permanently-watered areas and the available information on local distributions and abundances of forage fish populations. An index to the availability of foraging habitat within 10 km of a prospective colony site could be used to prioritize island placement within an intended restoration area, such as the Upper Klamath Basin.

My study was the first to use GPS transmitters to track movements of Caspian terns. I obtained, for the first time, a complete picture of the movements of breeding adult Caspian terns during foraging trips and throughout the day. Foraging effort was strongly related to the distance between the breeding colony and preferred foraging areas; the position of each colony within the fragmented wetland landscape of the Upper Klamath Basin resulted in significant inter-colony differences in foraging behavior. Breeding Caspian terns displayed considerable variation in foraging behavior, in part to accommodate variation in commuting distance to foraging areas as central-place foragers during the nesting season. But this variation in foraging effort was strongly associated with variation in parental care. As GPS transmitters become smaller, longer-lasting, and more reliable, there is greater potential to answer questions about the foraging behavior of Caspian terns and other smaller seabirds. The greatest opportunities are in combining movement data with individual-level data, such as prey selection, body condition, reproductive effort, and chick growth rate.

The justification for creating additional nesting habitat for Caspian terns in the Upper Klamath Basin, namely the prior history of nesting in the Basin and the continued use by non-breeding terns during the breeding season (USFWS 2009), was correct in assuming that breeding numbers were limited by availability of nesting habitat. This was borne out by the rapid attraction of Caspian terns to all three newly-constructed islands and successful colonization of two of the three islands in the first year of availability. However, during this study I identified several additional factors, each of which could limit colony development and sustainability for one or more of these islands; some of these limitations could have been avoided or at least mitigated with more strategic island placement within the Upper Klamath Basin.

Artificial tern nesting islands are best situated at sites that are (1) not land-bridged during minimum water levels, (2) maximally inaccessible to mammalian and avian predators, and (3) most proximal to foraging habitat where patches of high-quality prey are likely to persist. Research on what factors are associated with sites that are more accessible and attractive to potential predators or competitors would be helpful in guiding island design and placement in the future. A better understanding of the relationship between colony size and the area available for foraging could help predict the relative potential of competing prospective sites. There are, of course, other constraints on where artificial nesting islands can be built; these constraints include considerations of expense, logistics, and potentially competing management objectives for other species and the overall ecosystem. To assure that restoration of breeding sites for colonial waterbirds is successful and cost-effective, we must strive to optimize the

trade-offs between the biological potential of a site and the practical constraints for creating habitat at that site.

Some potential limitations of specific colony sites (e.g., disturbance by predators) can be addressed through persistent management, but the management solution may be expensive and a challenge to sustain. Other potential constraints of prospective colony sites (e.g., proximity to high-quality foraging habitat) may be very difficult to remedy, and could seriously, or potentially permanently, compromise prospects for colony restoration at the site. Future efforts to create or enhance Caspian tern habitat should consider the full costs of potential restoration sites facing these biological constraints, which could include the on-going costs of persistent management or a failure to meet restoration objectives.

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