Population Trends and Connectivity of Snowy Plovers on the Southern Great Plains of
Texas, New Mexico and Oklahoma

by

Kristen Heath, B.S.

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Approved

Warren Conway, Ph.D.
Chair of Committee

Clint Boal, Ph.D.

Dan Collins, Ph.D.

Nancy McIntyre, Ph.D.

Mark Sheridan
Dean of the Graduate School

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ABSTRACT

According to surveys conducted in 2007-2009, breeding snowy plovers (*Charadrius nivosus*) at saline lakes in Texas experienced a ~75% population decline in the preceding decade. Negative population trends of interior snowy plovers on the Southern Great Plains (SGP) are generally attributed to high predation rates, declining groundwater, stochastic weather events and potentially to heavy metal contamination. The specific objectives of this research were to evaluate current population trends and detection probability of snowy plovers of three separate populations on the SGP and to monitor within-breeding season and migratory movements across the SGP and to wintering grounds on the Gulf coast.

To determine long-term trends of SGP of Texas snowy plovers, weekly summer surveys of saline lakes in Texas were performed in 2017/2018 to compare with survey data from the last two decades. Also, 20-year survey data from Bitter Lake National Wildlife Refuge (BLNWR) in New Mexico and data from annual surveys from 2013-2017 at Salt Plains National Wildlife Refuge (SPNWR) in Oklahoma were used to develop plover trend data for these two NWRs. Finally, to more precisely estimate detection probabilities and density estimates at Salt Plains NWR, weekly distance sampling surveys were performed in 2017/2018. To monitor movements of snowy plovers via the Motus Wildlife Tracking Network, an array of automated telemetry towers were installed at 6 study sites in the SGP. These towers were used to detect nanotag transmitters attached to adult breeding snowy plovers.

Snowy plovers have declined in the last 2 decades, 44% at 2 lakes in Texas ($P < 0.001$) and 63% at BLNWR ($P < 0.001$), whereas snowy plovers at SPNWR appear stable ($P > 0.05$), based on both refuge-level annual surveys and distance sampling

protocol and analyses. Snowy plover detection probabilities were high (0.78) at Salt Plains NWR, which supports earlier estimates of high detection rates of regional snowy plovers. Density at Salt Plains NWR was 0.54 individuals/hectare, resulting in a population estimate of across the entire flats of 3,246 individuals. This estimate is less than previous estimates, but is also the first to employ distance sampling techniques during the breeding season. Further longer term population monitoring would be important to evaluate population trends of plovers at SPNWR during the breeding season.

Within breeding season movements of snowy plovers during 2017 and 2018 suggest that Salt Plains NWR is not connected to Texas nor New Mexico populations. Furthermore, only 2 individuals moved from New Mexico to Texas, revealing these populations are weakly linked and that some degree of isolation exists. Relatively frequent movements of snowy plovers to Lake B in Texas may be indicative of higher-quality breeding and foraging habitat for regional snowy plovers due to the occurrence of consistent freshwater artesian springs. Overall, such potentially low population connectivity may warrant further investigation into the genetic underpinning of small, isolated and potentially threatened subpopulations. Also, the protection of habitat at Lake B may prove crucial in regional snowy plover conservation.

Snowy plovers are most likely nocturnal migrants, and fall migration departures from the SGP are positively correlated to longer photoperiods and low surface wind speeds. Also, although Salt Plains NWR snowy plovers were commonly detected on the Gulf coast of Texas to Florida, no winter-ground resighting or detection confirmed locales of snowy plovers captured and marked in Texas and New Mexico, although some resightings of Texas snowy plovers on the Texas coast have been reported in the past.

Results from this research will prove crucial to long-term conservation and planning efforts relative to understanding regional persistence and dis-connectivity among breeding populations of snowy plovers in the Southern Great Plains. Further efforts should focus upon linking genetic data with movement data to more thoroughly evaluate regional connectivity and persistence probabilities.

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CHAPTER 1
POPULATION TRENDS OF SNOWY PLOVERS ON THE SOUTHERN GREAT PLAINS OF TEXAS, NEW MEXICO AND OKLAHOMA

Introduction

Migratory shorebird populations have declined ~70% in the past four decades according to the North American Bird Conservation Initiative (NABCI) in 2016. These precipitous declines are broadly attributed to the degradation, fragmentation, and human disturbance of virtually all shorebird-relevant habitat types across North America, including coastal shorelines, grasslands, and wetlands (NABCI 2016). Snowy plovers (*Charadrius nivosus*), a rare shorebird widely distributed across North America, have been similarly affected. Recent population estimates from the Southern Great Plains (SGP) of Texas, Oklahoma, and New Mexico have reported declines of >75% in the preceding decade (Andres et al. 2012, Saalfeld et al. 2013). Although inland populations of snowy plovers are spatially disjunct from one another and coastal populations, these mid-continental populations may represent an important pool of genetic diversity (Conway et al. unpublished data) and their breeding habitats—particularly at the Salt Plains National Wildlife Refuge (NWR) in Oklahoma—are also crucial stopover sites for migrating shorebirds (Conway et al. 2005, Andrei et al. 2008).

Snowy plover habitat, regardless of season, includes sparsely vegetated shorelines of ocean beaches, saline lakes, and salt flats, and their geographic range is wide, scattered, and highly localized due to their relatively specific habitat requirements (Page et al. 2009). Pacific Coast populations, listed as federally threatened, have been foci of many studies, but inland snowy plover populations have received considerably less

attention despite their hemispheric significance as the second-largest population in North America (Conway et al. 2005, Thomas et al. 2012, Saalfeld et al. 2013). Salt Plains NWR in Oklahoma is particularly important; it is purported to support ~20% of continental breeding snowy plovers, second only to Great Salt Lake in Utah, and ~90% of the breeding population of the SGP (Thomas et al. 2012).

Across their geographic range, snowy plover population declines are due in part to their proclivity for areas densely inhabited by people, particularly coastal beaches (Gorman and Haig 2002, Andres et al. 2012, Saalfeld et al. 2013). Snowy plover declines on the SGP, however, are more specifically attributed to high nest predation rates, poor adult and juvenile survival, and habitat degradation associated with regional underground water depletion and potentially to heavy metal contamination (Saalfeld et al. 2011, 2013; Thomas et al. 2012; Ashbaugh et al. 2018). Even more exacerbating is the recruitment threshold (minimum number of nestlings to maintain population size) for SGP snowy plovers, previously estimated at an unattainable 5.8-10.0 nestlings per breeding adult (Saalfeld et al. 2013).

Declines in the Ogallala Aquifer on the SGP and in freshwater inflows to Salt Plains NWR in Oklahoma play key roles in regional habitat degradation (Conway et al. 2005, Saalfeld et al. 2013, Duffie 2017, Ashbaugh et al. 2018). Regional saline lakes are fed by Ogallala-origin artesian freshwater springs in the Playa Lakes Region (PLR) of Texas (Brune 1981, Haukos and Smith 1994, Heintzman et al. 2017) and are the key regional nesting habitats for snowy plovers (Conway et al. 2005, Saalfeld et al. 2013). However, reductions in spring flow, surface water duration and extent, coupled with declining water quality, are directly related to ground-water mining by extensive row-

crop farming in the region (Brune 1981, Conway et al. 2005, Heintzman et al. 2017). The resulting greater salinity inhibits growth and reproduction of aquatic invertebrates, an important food-source of snowy plovers (Andrei et al. 2009), and reduced surface water availability inhibits snowy plovers' ability to mitigate heat-stress and thermoregulate during incubation (Saalfeld et al. 2011, 2012b).

Beyond loss of available surface water and deteriorating water quality, nest predation stands as a leading cause of nest failure of snowy plovers on the SGP and elsewhere in their range (Grover and Knopf 1982, Mabee and Estelle 2000, Saalfeld et al. 2011, Sexson and Farley 2012). Although impacts vary depending upon on habitat and predator composition, SGP nest predation rates were comparable to studies in Texas (Saalfeld et al. 2011) but lower than studies conducted in California (Powell 2001, Powell et al. 2002), Puerto Rico (Lee 1989) and one study at the Salt Plains NWR (Winton et al. 2000). Saalfeld et al. (2012a) reported that mean nest success of SGP snowy plovers had decreased by 31% from the preceding decade, where nest predation rates increased between from 27% (17-52% in 1998-1999) to 40% (39-43% in 2008-2009; Conway et al. 2005, Saalfeld et al. 2011). This increase may be caused by increasing populations of avian predators (namely Chihuahuan ravens, *Corvus cryptoleucus*) and vegetation encroachment (Saalfeld et al. 2011; Rosen et al. 2013). Closer proximity of vegetation to nests increases predation risk, potentially due to an impaired ability to detect approaching predators by an incubating adult, or increased risk of interaction with mammalian predators in general (Saalfeld et al. 2011, Ellis et al. 2015).

Metal contaminants in water, sediment and food sources have also been examined in recent studies (Duffie 2017, Ashbaugh et al. 2018). Ashbaugh et al. (2018) found that selenium (Se) concentrations were greater than both background and toxicity thresholds (> 1 ppm) in SGP saline lake sediment and snowy plover blood and feathers. Elevated Se concentrations inhibit avian reproduction, diminish immune response, and cause embryonic malformations in shorebirds (Meador 1996). It is possible that elevated Se levels are contributing to snowy plover population declines, although further investigation into trophic exchange, potential accumulation and interactions are necessary to fully ascertain specific Se effects (Ashbaugh et al. 2018). Similarly, Duffie (2017) revealed detectable levels of mercury (Hg) in snowy plover blood samples and sediment, although Hg levels were not above background levels or thresholds of avian toxicity. Interactions of Se and Hg in biological tissues can be very complex and deserve some further examination in these plover-saline lake systems.

A commonly cited source of shorebird population declines, anthropogenic disturbance (particularly domestic and feral dogs), disrupts breeding behavior and can push birds into marginal breeding and feeding habitat and decrease feeding rates in some geographic regions (Lafferty 2001). Additionally, elevated rates of mortalities of adult, nestlings, and eggs from vehicle collisions or trampling have been reported on beach habitat (Durkin and Cohen 2017, K. M. Heath unpublished data). On the SGP, saline lakes occur in remote, isolated habitats with comparatively little human activity. Many lakes are found on private land and/or near caliche pits and areas with oil mining activities (Conway et al. 2005, Saalfeld et al. 2011) where disruption of behavior and the trampling of nests is possible, but has not been documented. At 3 SGP refuges—Salt

Plains NWR , Bitter Lake NWR and Muleshoe NWR—the likelihood of snowy plover-human interaction may increase with increased vehicle and foot traffic, although walking/driving on the lakes and salt flats is prohibited or discouraged, except at designated "dig sites" at Salt Plains NWR. Overall, excluding human-driven degradation to the landscape, direct anthropogenic disturbance with SGP snowy plovers on their breeding grounds is of less concern than with coastal populations which nest on high-traffic shorelines. There is evidence, however, that direct human disturbance occurs on coastal wintering grounds, which may lead to lower individual fitness (Lafferty 2001, Pearl 2015).

Finally, there is strong evidence supporting the hypothesis that increases in frequency and severity of extreme weather events negatively impact snowy plover populations throughout their geographic range (Crick 2004, Intergovernmental Panel On Climate Change 2007, Frederiksen et al. 2008, U.S. Global Change Research Program 2009). Such events include heavy precipitation, drought and tropical cyclones (Intergovernmental Panel On Climate Change 2007, Frederiksen et al. 2008, Matthews 2008), all of which have the potential to adversely affect SGP snowy plover population persistence (Saalfeld et al. 2013, Pearson and Colwell 2014). The SGP is already characterized as having stochastic weather patterns, which include intense precipitation events, hail, and drought (Haukos and Smith 1994), all of which can negatively affect snowy plover nest success (Paton 1995, Saalfeld et al. 2013, Vincze et al. 2017). Additionally, Frederiksen et al. (2008) claimed that increases in frequency and severity of weather events may lead to greater variability in population survival (for species vulnerable to such events) and subsequently inhibit population growth and increase the

probability of local extinction events. Others have noted that climate change may adversely affect snowy plover habitat, thereby exacerbating already diminished snowy plover survival for both coastal and inland populations (Aiello-Lammens et al. 2011, Convertino et al. 2011, Saalfeld et al. 2013).

Overall, an array of potentially compounding environmental disruptions such as climate change, disruption of breeding behaviors, and water table depletion are negatively influencing snowy plover nest success and survival and contributing to steady population declines in the SGP and elsewhere. Furthermore, non-breeding season weather events and habitat quality may also have carry-over effects and affect inland snowy plover population trends. Regardless of the source, it is crucial to monitor population responses to these environmental perturbations. Obtaining regional estimates of snowy plover survival, detection probabilities and population densities is key to inform future conservation efforts and provide baseline data for future management. Therefore, the objectives of this research were to (1) estimate current regional (SGP) snowy plover population trends and compare to estimates from 10 and 20 years ago and (2) determine detection probabilities and density estimates for snowy plovers on Salt Plains NWR.

Methods

Study Sites

The SGP ecoregion encompasses > 96 million ha of semi-arid short- and mixed-grass prairie stretching north through Nebraska and includes the Southern High Plains (SHP) of Texas and New Mexico (Assal et al. 2015). This research was conducted at 6 saline lakes/alkali flats interspersed across the SGP of Texas, New Mexico and Oklahoma. Study sites included 3 privately owned saline lakes (designated as Lakes A, B

and C) and Muleshoe National Wildlife Refuge (NWR) on the SGP of Texas; Bitter Lake

NWR in eastern New Mexico; and Salt Plains NWR in north-central Oklahoma (Figure

1.1). Surface temperatures at SGP breeding habitats range from 7-54°C (Saalfeld et al.

2012b), with 73% of annual precipitation occurring from April through September, with

450-550 mm occurring on a west-east gradient (Haukos and Smith 1994, Heintzman et al.

2017, NOAA National Weather Service: http://www.srh.noaa.gov/). The landscape has

strong, consistent winds and high evapotranspiration rates of > 200 cm/year (Reeves and

Temple 1986, Rosen et al. 2013, Ashbaugh et al. 2018).

Texas

Approximately 40 saline lakes existed in the Texas SGP, historically fed by

artesian freshwater springs (Brune 1981). The landscape is dominated by row-crop

agriculture, with rangeland and mineral mining (caliche) activities occurring throughout

the region (Brune 1981, Conway et al. 2005, Rosen et al. 2013). Most of the artesian

springs in regional saline lakes have dried up due to mining of the Ogallala Aquifer for

rowcrop irrigation, and currently < 10 lakes have actively flowing springs (Brune 1981,

Rosen et al. 2013, Heintzman et al. 2017). The Ogallala Aquifer replenishes via

precipitation filtered through ephemeral wetlands (playas) in the region, and current

recharge rates (estimated to be 0.25-25.0 mm/yr on irrigated cropland; Gurdak and Roe

2009) are far outpaced by depletion rates (Brune 1981, Haukos and Smith 1994). Thus,

existing saline lakes now rely principally on precipitation runoff for surface water (Rosen

et al. 2013, Heintzman et al. 2017). The lakes that remain are increasingly saline, and

water levels fluctuate stochastically with precipitation within and among years (Andrei et

al. 2008, Rosen et al. 2013, Heintzman et al. 2017, Ashbaughet al. 2018). Further, recent

studies identify declining water quality as a consequence of increased salinity, elevated levels of total dissolved solids (TDS) and concentrations of Arsenic (As), Selenium (Se), Fluoride (Fl), sulfates, and perchlorates (Reeves and Temple 1986; Hudak 2009, 2010; Ashbaugh et al. 2018). Some of these naturally occur in the Ogallala Aquifer (Hudak 2010), although some may be of anthropogenic origin. For example, Hudak (2010) determined that the presence of As in 173 irrigation wells in the nearby Pecos Valley Aquifer was due to pesticide remnants from agricultural activity in the early to mid-20th century. During spring and fall avian migration, these saline lakes serve as stopover sites for shorebirds and waterfowl and provide winter habitat for sandhill cranes (*Antigone canadensis*) and, rarely, endangered whooping cranes (*Grus americana*, Conway et al. 2005, Andrei et al. 2008). During breeding seasons, prominent nesting shorebirds include snowy plovers, American avocets (*Recurvirostra americana*), black-necked stilts (*Himantopus mexicanus*), and killdeer (*Charadrius vociferous*).

New Mexico

Bitter Lake NWR encompasses ~10,000 ha in eastern New Mexico and consists of managed wetland units, streams, sinkhole ponds, cropland, one saline lake and desert uplands (MacRae et al. 2001, Roesler 2016). Bitter Lake is a shallow saline lake surrounded by salt flats and some salt marsh and is recharged via Salt Creek, Bitter Creek, artesian freshwater springs and precipitation runoff (Peterson and David 1998, MacRae et al. 2001). It provides habitat to several species of endemic plants and arthropods, some threatened and endangered (MacRae et al. 2001, Roesler 2016), and the refuge is year-round and stopover habitat for ~350 species of birds, as well as breeding habitat for snowy plovers, endangered interior least terns (*Sterna antillarum athalassos*),

American avocets and others (U.S. Fish and Wildlife Service 2003). Wetland units are flooded seasonally to provide habitat for waterfowl and waterbirds (MacRae et al. 2001).

Oklahoma

Salt Plains NWR was established in 1930 and currently encompasses ~12,900 ha (U.S. Fish and Wildlife Service 2002, Bonner 2008), including salt flats, salt marsh, ephemeral streams, some agriculture, a 4,000 ha reservoir and the Salt Fork of the Arkansas River (U.S. Fish and Wildlife Service 2002, Bonner 2008). The nearly 5,000 ha salt flats provide critical regional nesting habitat for snowy plovers, American avocets and interior least terns (U.S. Fish and Wildlife Service 2006). The Great Salt Plains Reservoir, created in 1941 with a dam of the Salt Fork of the Arkansas River, is shallow (average depth of 1.2 m) and is slowly filling with sediment from the Salt Fork (U.S. Fish and Wildlife Service 2002). It is expected to fill by 2050 (U.S. Fish and Wildlife Service 2002, Bonner 2008). Located on the eastern portion of the Central Flyway, Salt Plains NWR is a critical stopover site for migrating shorebirds and waterfowl and is breeding habitat for the second largest population of snowy plovers (~5000) in North America, second only to Great Salt Lake in Utah (Thomas et al. 2012). The Salt Plains NWR is arguably the most important habitat for interior snowy plovers throughout the Great Plains.

Capture

Nest searching occurred during surveys (see below) and dedicated search times to locate snowy plover nests on all study sites. Once nests were discovered, they were marked using a GPS unit, and clutch size and age were recorded. Eggs were aged using an egg flotation chart created for snowy plovers (Székely et al. 2008; Figure 1.2). After

the maximum clutch size had been laid and nest age was > 5 days old, bownets (Conway

and Smith 2000, Duffie 2017, Ashbaugh et al. 2018) were used to capture both male and

female adult or after hatch-year (AHY) snowy plovers. Nestlings or hatch-year birds

(HY) were captured by hand (Conway et al. 2004). Once captured, a USGS aluminum

band (size 1P) and a unique combination of color bands were attached to each plover

following established protocols (Saalfeld et al. 2011, Duffie 2017, Ashbaugh et al. 2018).

After banding, the following data were collected: mass (g), wing chord (mm for all other

linear measures), tarsus length, tail length, culmen length, forehead patch width, parasite

load (defined as None, Low, Medium, or High) and molt (location—head, body,

primaries, or tail—and feather designation, if a primary or rectrix). All snowy plovers

were captured and handled according to approved institutional animal care and use

protocols (Texas Tech University IACUC 15035-05, 18049-06 and T18049), state

scientific permits (Texas Parks and Wildlife Department SPR-0413-039; New Mexico

Department of Game and Fish 3558; Oklahoma Department of Wildlife Conservation

7104 and 7411) and the USGS Bird Banding Laboratory Master Banding Permit

(Number 23393).

Surveys

Texas

Weekly surveys from 2017-2018 were conducted at Lakes A, B and C beginning

in May and continuing through late July following protocols and survey routes used by

Saalfeld et al. (2013). Observers were consistent within each year, as were surveyed areas

(Figure 1.3, Figure 1.4, Figure 1.5). Surveys began at approximately 08:00 and lasted 1-2

hours depending on the lake; no surveys were conducted in abnormally high winds or

during precipitation events. All snowy plovers observed were recorded, where efforts were made to not recount birds that were "pushed" by the observer. Individual birds that were uniquely marked were "resighted" during these surveys using unique color-band combinations and were collected only during surveys. Individuals resighted during other field work activities (beyond the formal surveys) were used only in movement analyses (see Chapter II).

Lake A snowy plover surveys began at the caliche pad on the northwestern shoreline (Figure 1.3), where one observer walked north to the northern and eastern shoreline, ~3.75 km. This transect included ~1 km of eastern shoreline not included in Saalfeld et al. (2013a).

Lake B surveys began at the base of the berm on the northern shoreline. Observer 1 walked the caliche berm, then east ~3.5 km along the shore to the mound on the southern shoreline (Figure 1.4); this was the same transect used by Saalfeld et al. (2013a).

Lake C surveys began on the northern shore near the mound and continue south along the eastern shoreline to the fence line near the southern tip of the lake, ~3.2 km (Figure 1.5). This survey followed Saalfeld et al. (2013).

<div align="center">Oklahoma</div>

<u>Annual Population Estimate</u>

Annual snowy plover surveys were conducted on a single survey day in early May from 2013-2017 to estimate the snowy plover population for the salt flats at Salt Plains NWR (Thomas et al. 2012, Hensley et al. 2014). Prior to each annual survey, the entire salt flat area of Salt Plains NWR was overlaid with a 300 x 300 m^2 grid, where 100 of these cells were randomly selected to be surveyed (Figure 1.6, Figure 1.1). These

surveys were performed by professional biologists and volunteers, who were paired and assigned 10-12 cells each to survey. Before the beginning of the surveys, each observer's pace was calibrated to improve consistency among survey teams relative to following survey protocols.

To begin, observers approached each grid cell without traveling through the cell to avoid displacing snowy plovers. Starting at the northwest corner, the two observers walked due east. The first observer stopped after 75 m; the second observer stopped after walking another 150 m. Both observers then turned due south and began walking at the same time and at a steady pace, counting all snowy plovers within 75 m of either side of their transect. Specific attention was made to not count birds outside of this area, particularly in the other observers' area. Plovers that moved from one observer's area to another were not counted by the second observer (this required extreme attention and coordination during and after the survey was completed). Observers stopped every 75 m to help calibrate the survey pace and to scan the next survey section. After walking their 300 m transect, observers ended their surveys at approximately the same time. The counts for each transect were totaled together to determine the number of snowy plovers in that grid cell. For each year, all 100 "grid cell" surveys were conducted in 1 day, beginning in the morning and lasting until late morning or early afternoon.

Detection Probability, Density, and Population Estimates

Distance sampling surveys were conducted at Salt Plains NWR during the breeding season (mid-May through July) in 2017 and 2018, and were designed to mirror established protocols used during previous annual snowy plover surveys (see above; Hensley et al. 2014). Three regions designated as "North," "Middle," and "South" were

created, with each region consisting of 75 grid cells (Figure 1.7) using the existing grid-cell distribution used for the annual plover survey (see above). These three regions were selected for their accessibility to all-terrain vehicles (ATVs) and known regular occurrence of snowy plovers (K. M. Heath personal observation). This ensured that two observers would be able to access all grid cells on ATVs before noon and repeat these surveys weekly. Randomly selected grid cells, 4 in each region (*n* = 12), were used in these surveys. However, of these, 3 grid cells occurred in areas dominated by surface water or in unsuitable habitat (e.g., extensive water coverage, or large patches of saltcedar [*Tamarisk* spp.] or other vegetation) and were removed from the surveys. These were not replaced as it required ~ 5 hours for travel and actual survey time to perform surveys in the remaining 9 cells used for this study. Grid cells were surveyed once weekly from mid-May until late July in 2017 and 2018, following protocols used for the annual May snowy plover performed on the NWR in May (see above; Hensley et al. 2014). In addition to counting plovers within 75 m of their transect, linear distance (m) of snowy plovers from the transect (not from the observer) was also estimated for each bird. A survey schedule was created *a priori* to ensure that the 3 regions were surveyed in random order within each region; these were randomized among regions each week to avoid spatiotemporal biases associated with surveying the same grids at the same time and day each week.

Before surveys were initiated each year, observers calibrated their steps to 75 m. Additionally, observer distance estimation was calibrated each year prior to initiating any snowy plover surveys to minimize biases and improve survey accuracy when estimating snowy plover linear distance from the transect. During the survey, if banded birds were

spotted or nests found, observers waited until the end of the survey to mark the nest or attempt to resight those marked individuals.

<center>New Mexico</center>

From 1999-2018, Bitter Lake NWR staff performed annual, bi-weekly surveys as part of a site-specific protocol to track abundance of shorebirds and waterbirds. Surveys were completed on the same weekday by multiple trained observers. Driving surveys began between 07:30 and 08:00 and followed established routes. All waterbirds and shorebirds, including snowy plovers, were counted per "survey unit" and totaled to estimate abundance across the entire refuge (Figure 1.8; Linner et al. 2016). At least 70% of the survey areas were assumed visible. All snowy plovers were counted, and no efforts were made to resight or record individuals that may have been color-banded by researchers.

Data Analysis

Texas survey data analyses were restricted to May, June, and July counts to avoid including migrating plovers; Bitter Lake data were similarly restricted to represent comparable trends between Texas and New Mexico. Further, Lake C (Texas) was omitted from analysis due to infrequent surveys relative to Lakes A and B.

Survey data analyzed (total numbers of individuals observed during transect surveys in Texas and estimated bi-weekly abundance of snowy plovers at Bitter Lake NWR) were modeled using a negative binomial regression distribution (R, package *MASS,* version 7.3-51.1) rather than a Poisson distribution to account for overdispersion of data, or a high variance in relation to the mean (White and Bennetts 1996). Overdispersion was tested using R package *statsr*, version 0.1-0. Regression models

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created included the following parameters: Julian date (defined here as the number of days since 1 Jan 1900) and lake for Texas; and Julian date for Bitter Lake NWR. The Akaike information criterion (AIC) was used to rank models (Akaike 1987), where models with ΔAIC of < 2 were considered competitive (Burnham and Anderson 2004).

Analysis of variance (ANOVA) was used to examine differences in the number of snowy plovers counted per survey among months (May, June, and July) for Texas saline lakes and Bitter Lake NWR. Percent change between 1998/1999 and 2018 for both Texas and New Mexico were calculated using the percent change in predicted values from top-performing negative binomial regression models (see above for details on modeling approach).

For the annual May Salt Plains NWR snowy plover surveys, a NWR-scale population estimate was calculated by averaging the number of snowy plovers observed per grid cell surveyed and multiplying by the total number of grid cells (668) on the salt flats (Hensley et al. 2014). Then, simple linear regression was used to examine trends in Salt Plains NWR annual snowy plover population estimates from 2013-2017 (R, package *car*, version 3.0-2).

In contrast, for the weekly (mid-May through July) snowy plover surveys conducted at Salt Plains NWR in 2017 and 2018 only, survey data were analyzed using program Distance (version 7.2) and a conventional distance sampling analysis engine to fit detection probability models to survey data. Models were ranked using AIC (Burnham and Anderson 2004), where models with ΔAIC of < 2 were considered competitive (Akaike 1987, Burnham and Anderson 2004). I used the top ranked model to calculate

estimates of detection probability, density, and a population size, and estimates of both global (pooled) and stratum (region) were also reported.

Results

Population Trends

Texas

There were 2 top performing models, 'Julian Date + Lake' and 'Julian Date' suggesting that Julian Date was the strongest predictor (contributed the greatest model weight) of snowy plover survey count data (Table 1.1). To avoid biased results and better compare model estimates with Saalfeld et al. (2013), Lake C survey data were omitted, as Lake C was not used in those previous analyses (see Saalfeld et al. 2013). Overall, estimates using the top-performing model indicate a ~ 40% decline in the preceding 2 decades at Texas Lakes A and B ($z_{1,198}$ = -4.39, $P < 0.001$; Figure 1.9), with no 'Lake' effect ($z_{1,198}$ = -1.33, $P = 0.184$). This estimate is markedly lower than a previous estimate of > 75% declines from 1998-2009 (Saalfeld et al. 2013). However, when analyzing survey data from 2008-2018 only, the top performing model indicated there was an interaction between 'Lake' and 'Julian Date' ($z_{1,76}$ = -4.81, $P < 0.001$). During this interval, snowy plover counts increased by 7% at Lake A but decreased by 37% at Lake B. Despite this interaction and despite population decreases at Lake B, population trends at Lakes A and B seem to have stabilized from 2009-2018 as compared to the preceding analyses, which focused upon data from 1998-2009.

Snowy plover survey counts at Lake C from 2008, 2009 and 2018 were similar among years, for all months combined ($F_{3, 25}$ = 0.64, $P = 0.597$), as well as within months among years (May: $F_{3, 8}$ = 0.90, $P = 0.483$; June: $F_{2, 7}$ = 0.29, $P = 0.760$; July: *F*

$_{2, 4} = 0.60$, $P = 0.592$; Table 1.2). For Lake A, snowy plover mean survey counts varied among years for May, with 1998 as the greatest standalone year ($F_{7, 39} = 8.69$, $P \leq 0.001$; Figure 1.10), but did not vary among years in June ($F_{6, 43} = 2.26$, $P = 0.056$) nor July ($F_{6, 27} = 1.70$, $P = 0.106$; Table 1.3). Snowy plover numbers at Lake A varied among years ($F_{7, 115} = 5.48$, $P \leq 0.001$), with the most plovers again counted in 1998, the least in 2008, and a rebound somewhat by 2017 (Table 1.3, Figure 1.11). During May, snowy plover number counts varied at Lake B from a high in 1998 and lowest in 1999-2000, 2008-2009 and 2018 ($F_{7, 17} = 4.81$, $P = 0.004$; Figure 1.12). There was no variation in snowy plovers counted in June ($F_{6, 23} = 2.88$, $P = 0.082$) nor July ($F_{6, 17} = 2.55$, $P = 0.060$; Table 1.4). Similar to Lake A, snowy plovers observed at Lake B varied over years for all months combined ($F_{7, 71} = 3.52$, $P = 0.003$), with high years in 1998, 2000 and 2008-2010, with contrasting low numbers in 1999 and 2017-2018 (Table 1.4, Figure 1.13).

New Mexico

A negative binomial regression model using 'Julian Date' to predict summer snowy plover counts at Bitter Lake NWR estimated a > 65% decline in breeding snowy plovers observed from 1999-2018 (Figure 1.14). This is similar to declines in the Texas saline lakes during a comparable temporal window (Figure 1.15, Figure 1.16). Snowy plovers observed varied among months from 1998-2018 (May: $F_{19, 28} = 2.97$, $P = 0.004$; June: $F_{19, 30} = 1.95$, $P = 0.049$; July: $F_{19\ 32} = 2.27$, $P = 0.020$; Figure 1.19), and snowy plovers varied among all months combined over time ($F_{19, 130} = 5.12$, $P \leq 0.001$). However, a post-hoc Tukey Honesty Significant Difference (HSD) test showed no differences among years in June. The greatest mean survey count for May-July was in 2001 and the lowest in 2017 (Figure 1.14, Table 1.6, Figure 1.20, Figure 1.21).

Oklahoma

Salt Plains NWR population estimates of snowy plovers from the annual May

surveys in 2013-2017 and in 2007 by Thomas et al. (2012) ranged from 3,086-5,280

individuals ($\bar{x}$ = 4672 ±302, Figure 1.22). The fewest number of snowy plovers estimated

occurred in 2014 (3086 ±721), and the Thomas et al. (2012) estimate from 2007 was the

greatest population estimate (5280 ±1588). Snowy plover population estimates from this

annual May survey were consistent over time (R^2 = 0.04, $F_{1,3}$ = 0.12, P = 0.756).

Detection Probability, Density and Population Estimates

Distance sampling surveys were conducted at Salt Plains from 18 July to 8

August in 2017 and 12 June to 31 July in 2018. There were 2 competing (ΔAIC <2)

detection probability (*p*) models for snowy plovers at Salt Plains NWR in 2017 and 2018

(Table 1.7). All models reported high detection probabilities, ranging from 0.77 – 0.82

(Table 1.7). For both 2017 and 2018 surveys conducted at 9 grid cells at Salt Plains

NWR, survey data fit a standard detection curve (Figure 1.23). Using this detection

curve, snowy plover density (D) and population estimates (N) were calculated for each

region (Middle, North, and South) and then combined for all 3 regions (Table 1.8).

Snowy plover density estimates ranged from 0.43 to 0.62 individuals per hectare, and

regional (North, Middle, South) estimates ranged from 292 to 422 individuals (Table

1.8), where the total population estimate for all 3 regions combined was 1085 individuals

(Table 1.8). The highest density and population estimate was in the Middle region, with

N = 422 ± 153 and D = 0.62 ± 0.24 (Table 1.8).

Discussion

Population Trends

The current estimated decline of ~40% for breeding snowy plovers on the SGP of Texas since the late 1990s is not nearly as severe as previously reported. Saalfeld et al. (2013) reported a >75% decline between the late 1990s and late 2000s. The lack of clear, continued declines in snowy plover surveys during the past decade may indicate that the rate of decline has slowed or stabilized, and has possibly been buffered by population increases, or recoveries, in years between survey efforts. Indeed, temporal patterns suggest that snowy plovers breeding on the SGP of Texas may undergo "boom and bust" years or exhibit a cyclical population dynamic. However, an overall decline of ~40% since 1998 is still noteworthy and reasons for this are likely a complicated assemblage of several factors. Although the rate has apparently slowed, a long-term decline of ~40% remains a key underpinning to regional snowy plover conservation and management approaches.

Declines of snowy plovers are often attributed to habitat loss, habitat degradation, and increasing rates of nest predation. In addition to these causes, Saalfeld et al. (2013) suggested that severe weather events outside of the breeding season (during winter or migration) may have been possible reasons driving declines observed between 2007 and 2008. For example, Saalfeld et al. (2013) reported a decline of > 100 individuals between surveys conducted in 2007 and 2008 (from 123 to 20 mean individuals per survey at Lake A). There is mounting evidence that suggests shorebirds are strongly and negatively affected by hurricanes in multiple ways, even during the non-breeding season, which have carry-over effects into the subsequent breeding season, and may have been the

driving influence for the differences documented by Saalfeld et al. (2013) for SGP snowy plovers. To provide some context and support for this notion, Wunderle (2018) found that 80% of 15 shorebird species declined (presumably from mortality) in northeastern Puerto Rico following Hurricanes Irma and Maria which made landfall in late August 2017 and mid-September 2017, respectively. In addition to direct exposure to wind and precipitation, others have suggested that hurricanes and other tropical storms may have a significant impact on foraging grounds and microhabitats of wintering shorebirds (Marsh and Wilkinson 1991, Schulz 2015). Direct evidence of this correlation between fall and winter weather events and breeding SGP snowy plovers provide some compelling evidence that these populations are not solely regulated during the breeding season (see Chapter II). For example, 4 hurricanes made landfall on the Gulf coast during the 2007-2008 migration and winter period. These landfalls occurred in areas where many SGP snowy plovers are known to overwinter, the impact of which may have been detected during breeding season snowy plover surveys in 2008 and 2009 (see Saalfeld et al. 2013). Similarly, a > 50% breeding season decline was recorded in this study between 2017 and 2018 at Lake A, where there were not any unusually harsh environmental conditions during those years on the SGP. However, Hurricane Harvey, considered the second costliest hurricane in U.S. history, made landfall on 8 August 2017 at Rockport, Texas, and was a sustained storm for nearly two weeks along the Texas coast (National Centers for Environmental Information 2018). A tagged snowy plover from Salt Plains NWR was detected just a week earlier via a Motus tower near the storm surge location and was never detected again (see Chapter II). Both the upper and lower Texas coast are known wintering locales for SGP breeding snowy plovers, and departure dates from SGP saline

lakes (see Chapter II) suggest that a substantial number of SGP-associated snowy plovers may have succumbed to the impacts from Hurricane Harvey.

Snowy plovers occurring in Texas saline lakes have not continued to decline during the last decade at rates comparable to prior decadal estimates (see Saalfeld et al. 2013). Lake C in particular showed little to no fluctuations in survey counts but consistently had fewer individuals recorded per survey (21 individuals) than Lakes A and B, which averaged 56 and 42 birds, respectively, from 1998-2018. Several active springs at Lake C were observed on the south side of the lake in 2018 on foot and using satellite imagery; one or more springs were inaccessible due to lack of landowner access permission and not included in surveys. It is possible, even likely, that the south section of Lake C supports more snowy plovers than were present in surveyed areas, which may mask, or buffer localized fluctuations. Consistency in Lake C survey counts may also suggest that snowy plovers on the SGP landscape are relatively vagile. Birds from other lakes of presumed lesser habitat quality may immigrate to Lake C for its consistent active springs, potentially bolstering local breeding bird abundances. This same pattern may also be true of Lakes A and B, which were similarly consistent in snowy plover counts from 2008-2018. Also, this may be particularly valid as springs of local saline lakes dry or fluctuate in surface water stochastically within and among years and local snowy plovers lose surrounding habitat (Brune 1981, Rosen et al. 2013, Heintzman et al. 2017).

In short, population declines at these three saline lakes may be masked or even buffered by the loss of suitable snowy plover nesting habitat and surface water in other regional saline lakes, resulting in some influx of individuals and greater numbers of snowy plovers at these 3 lakes. For example, Saalfeld et al. (2013) used survival

estimates of adult and juvenile snowy plovers at Lake A and B from 2008-2010 to

calculate recruitment thresholds, the results of which were biologically unattainable

levels (5.8-10.0 hatchlings per adult), and if true, population stability and even

persistence would have been unlikely by 2017-2018,which obviously did not happen.

Perhaps these buffered population declines on the SGP may actually be a result of a

constriction of regional snowy plover distribution during the breeding season. This

scenario is supported by satellite imagery that showed that in the past 27 years, over one-

third of the saline lakes in the SGP region of Texas went dry at least once and that the

smallest and shallowest were more likely to be dry than larger saline lakes (Heintzman et

al. 2017). Moreover, all lakes have become more reliant on precipitation, rather than

artesian spring activity for inundation and maintenance of surface water (Heintzman et al.

2017). All three of our focal saline lakes still have multiple active springs (Heintzman et

al. 2017) and are thus considered the best available breeding habitat for regional snowy

plovers. Therefore, as more saline lakes dry up more frequently, it is feasible that snowy

plovers are occurring more and more exclusively at these large, spring-fed lakes and that

other lakes of poorer-quality habitat are experiencing localized snowy plover extinctions

that are linked with the disappearance of reliable surface water. Bart et al. (2007)

described this shift as the "movement hypothesis," in which regional population declines

are not due to actual reduction of the population, but rather to a distribution change. This

movement, relative to these SGP saline lakes, may have masked more severe regional

population declines because these 3 lakes were the only ones being surveyed. However,

regional snowy plover counts are most likely the result of complicated interactions

among effects of distribution change (i.e., moving from disappearing habitat to more

sustaining lakes like A, B and C), winter-ground conditions (e.g., hurricanes), and fluctuating surface water availability (i.e., relatively wet and dry years) on the SGP.

In addition to a possible distribution change locally, Texas' SGP snowy plover populations may be augmented with immigrants from Bitter Lake NWR or more robust populations from Salt Plains NWR (see Chapter II). Instances of such movements by snowy plovers has been documented on the Pacific coast, where several studies on source-sink dynamics of snowy plover populations on the northern coast of California have demonstrated the effects of immigration removal from population projection models (Mullin et al. 2010, Eberhart-Phillips and Colwell 2014). Eberhart-Phillips and Colwell (2014) estimated a 100% likelihood of quasi-extinction of a sink population and a 46% increase in population size of the source without emigration. Mullin et al. (2010) found that low survival (0.55) and fecundity (0.8) estimates were insufficient to maintain a localized coastal population's persistence; however, estimates based on annual counts (λ = 0.96) and modeling suggested that the population was somewhat stable. Additionally, a preliminary study by Durkin and Cohen (2017) found that a diminishing population of northwest Florida snowy plovers is a likely sink for more productive eastern populations, and without immigration from those more productive eastern population, this regional subpopulation of snowy plovers would likely be extirpated. In short, multiple studies have demonstrated that immigrating snowy plovers can bolster surrounding populations in lesser quality habitat, buffering against the elevated risk(s) of extirpation for some sink populations. Collectively, these studies do invoke, assume, and provide evidence of significant movements among sub-populations of 'connected' populations. Persistence or

extinction probabilities can be strongly influenced by source-sink dynamics that might be driven by sub-populations that are not well documented in many scenarios.

Surveys at Bitter Lake NWR in New Mexico indicate much more dramatic declines than in Texas, with a > 65% reduction in number of individuals counted during May-July surveys of snowy plovers from 1999-2018 (see Figure 1.22). Causes of these sharper declines at Bitter Lake NWR remain unknown, but some environmental quality indicators have been investigated. Recent studies were conducted to quantify heavy metal contaminants in snowy plovers and habitat at Bitter Lake NWR and elsewhere on the SGP (Duffie 2017, Ashbaugh et al. 2018). Results revealed detectable levels (DL) of selenium (Se) and mercury (Hg), as well as levels of Se that were greater than known toxicity levels (> 1 ppm; Duffie 2017, Ashbaugh et al. 2018). Further, the greatest concentration of internal total mercury (THg, 0.706 ppm) on the SGP was found in a female snowy plover from Bitter Lake NWR (Duffie 2017). It is possible that elevated levels of Se > 1 ppm (toxicity threshold) and DL of THg may be detrimental to local snowy plover survival and persistence at Bitter Lake NWR. Aluminum (Al), Cadmium (Cd), and Lead (Pb) were also found at elevated levels compared to regional averages in 1996 and 1997 (MacRae et al. 2001). Boron (B), Zinc (Zn), Se, Hg, and Al were also found in plants, invertebrates, fish or eggs on the refuge above thresholds for adverse health effects (MacRae et al. 2001). Additionally, the organic chemical polychlorinated biphenyls (PCBs) were found in marsh habitat on the refuge at concentrations up to 5 ppm, far greater than the 0.1 ppm threshold of adverse health effects on wildlife. Considering this contamination of both heavy metals and organics, it is possible that

adverse effects of their presence may be contributing to more dramatic snowy plover population declines at Bitter Lake NWR than in Texas.

Perhaps more direct impacts (rather than environmental toxicants) on snowy plover population declines at Bitter Lake NWR are declines in the Pecos River and associated underground water sources. Furthermore, winter locales of Bitter Lake snowy plovers and the potential negative effects on breeding populations remain unknown. To date, no resightings, recaptures or reports exist on the exact wintering location of snowy plovers that nest and were marked at Bitter Lake NWR. Therefore, it is difficult to speculate as to where these birds migrate for winter and to make any informed suppositions about winter habitat quality and its potential effects on population declines. Since 2013, 58 snowy plovers have been color-banded at Bitter Lake NWR and 20 have been tagged with VHF-transmitters, but there have been zero resights or detections, which is in stark contrast to dozens of Texas and Oklahoma birds found wintering primarily on the Texas Coast (see Chapter II). It is possible that New Mexico snowy plovers winter on the Mexico coast where resights and Motus tower detections are far less likely. It is also possible that New Mexico snowy plovers winter in southeastern New Mexico, in and around Nash Draw in Eddy County, where winter records do exist for snowy plovers (Williams and Howe 2014). However, similar to other habitat perturbations in other wintering areas, significant potash mining occurs in this area, which can negatively impact individual snowy plover health and condition. These habitats, while seemingly acceptable, have been shown to be detrimental to the survival of many species and may exist as extreme environmental sinks to regional snowy plovers in New Mexico.

Finally, in Oklahoma, the Salt Plains NWR snowy plover population may be holding steady, at least for the past decade. Despite methodological differences in survey techniques, population estimates do reveal remarkable concordance and consistency. Thomas et al. (2012) confirmed that Salt Plains NWR contains hemispherically important breeding (and probably stopover) habitat for snowy plovers. This population is second only to Great Salt Lake in Utah, which Thomas et al. (2012) estimated at 5,511 (95% CI: $2,391 \leq \bar{x} \leq 8,631$) individuals, compared to 5,280 (95% CI: $3,692 \leq \bar{x} \leq 6,868$) individuals at Salt Plains NWR in 2007. With overlapping confidence intervals, it is possible that Salt Plains NWR is at least comparable in snowy plover population size, if not greater. The significance of this lies in the potential hemispheric importance for SGP populations: Salt Plains NWR may represent a substantial pool of individuals and genetic diversity for not only the SGP populations, but all North American populations. As populations decline, genetic diversity is crucial to buffer against risk of extirpation or even extinction.

Detection Probability, Density and Population Estimate at Salt Plains NWR

In the past two decades, there have been multiple attempts at either estimating snowy plover population size or determining long-term population trends on the SGP (Gorman and Haig 2002, Morrison et al. 2006, Andres et al. 2012, Thomas et al. 2012, Saalfeld et al. 2013, Hensley et al. 2014). Multiple sources claim a relatively large range of detection probabilities for snowy plovers, from 0.21 to > 0.95 (Andres et al. 2012, Thomas et al. 2012, Saalfeld et al. 2013). On the Southern High Plains (SHP) of Texas, both Saalfeld et al. (2013) and Thomas et al. (2012) reported high detection rates for snowy plovers on saline lakes due to lack of vegetation and snowy plover behavior

(easily spotted movements and displays in response to perceived danger to nests). Their claims were supported by consistent survey counts (±2 individuals) at saline lakes with low populations (~20 individuals, Saalfeld et al. 2013). High detection rates at Salt Plains NWR (0.78) during the 2017 and 2018 breeding seasons support the claims of Morrison et al. (2006), Thomas et al. (2012) and Saalfeld et al. (2013), all of which either assumed or calculated high (> 80%) probability of detection of snowy plovers on SGP saline lake and salt flat habitat. Using distance sampling methods to calculate density (D) and population estimates (N), these findings support, at least in part, the inferences made, and methods used by these studies – which provides some strength to the long-term population trend data reported for snowy plovers in the SGP of Texas.

Using the high detection probability estimate for Salt Plains NWR surveys conducted in 2017 and 2018, snowy plover estimates of N and D (per survey region on the salt flats), and a pooled estimate, are fewer than previously reported by Hensley et al. (2014) and Thomas et al. (2012). For example, if the global estimate of 0.54 individuals/ha is extrapolated to the entire flats, represented by 668 grid cells and not just the 3 regions sampled (a total of 225 grid cells) the number of snowy plovers is 3,246 individuals. This disparity may be an issue with extrapolating a density estimate across the entire flats, as uniform distribution of snowy plovers across the entire salt flat is very unlikely. In the 2017 and 2018 surveys, the number and location of grid cells chosen, while random, may be inadequate to estimate true plover density. However, the regions that were surveyed likely represent high-quality habitat where plover densities were greater relative to the rest of the flats, thus a higher than expected population estimate may be expected. Another potential influence is that annual surveys for Salt Plains NWR

from 2013-2017 were conducted in early May, which may have coincided with some

migration, as the breeding season had not fully begun (peak nesting season for both 2017

and 2018 was in June, when ~50% of nests were found per season). Thus, inconsistencies

may be due to individuals or groups being distributed differently across the salt flats,

when transient individuals are migrating farther north early in the breeding season.

   Differences between estimates may be due, in part, to study design and analysis

methodology of this study and previous ones. The Salt Plains NWR annual survey

estimates use a mean number of birds seen per grid cell and extrapolate to the total

number of grid cells, resulting in a range of 3,086 to 5,280 individuals. Consequently,

this method did not consider the distribution, detectability or suitability of habitat. It may,

however, shed light on the need for a more robust and conclusive population estimate of

Salt Plains NWR to better inform future management strategies. The current global

population estimate using distance sampling methods is at odds with larger population

estimates of > 5,000 individuals calculated both by Thomas et al. (2012) and Hensley et

al. (2014). It is possible that previous sampling methods may have over-estimated the

snowy plover population due to lack of compensation for the heterogeneous landscape. It

is also possible that this study's relatively low estimate reflects an actual change in

population size at Salt Plains due to habitat degradation on either breeding or winter

grounds. For example, Hurricane Harvey struck Rockport, Texas in August 2017, a

known winter ground for Salt Plains NWR snowy plovers. Furthermore, heavy rains

occurred throughout the breeding season in 2018, which may have led to lower

population estimates if individuals died or made their winter migration before surveys

were conducted.

Despite disparities between this study and previous ones, a population estimate of 3,246 is higher than estimates prior to Thomas et al. (2012). Vastly lower estimates of < 2,000 snowy plovers calculated by Gorman and Haig (2002) appear to underestimate the magnitude of snowy plovers at Salt Plains NWR and thus their significance throughout North America. Large populations like those at Salt Plains NWR—given that they produce an excess of individuals—can therefore become intrinsic buffers for surrounding populations found in lower-quality, risky habitats subject to extirpation. Dias (1996) points out the difficulties of identifying source-sink population dynamics, however, meaning that long term studies are critical to identifying patterns from exceptionally good or bad years. Also, it is important to assess the movement patterns of snowy plovers to determine the existence or degree of population connectivity (see Chapter II).

Beyond its potential as a population source for the surrounding SGP metapopulation, it is important to note that a large population like Salt Plains NWR may support a vital pool of genetic diversity. Considering apparent population declines of snowy plovers in both Texas and New Mexico, the maintenance of genetic diversity is important in terms of conservation genetics. If populations in Oklahoma are also declining, as this study may indicate, it is even more imperative that they be protected. Low levels of genetic diversity can make small, declining populations susceptible to stochastic environmental changes (Frankham 1995). Further research on the genetic structure of the SGP population may shed light on the significance, or not, of Salt Plains NWR in this regard.

Even considering the potential population dynamics underlying the SGP metapopulation mentioned above, it is difficult to ascertain exactly which factor, or set of

factors, is causing some SGP snowy plover declines—only that they are occurring. With the advent of improved and less expensive satellite tracking technologies, more precise measurements of movements can be attained. More rigorous demographic studies, particularly for Bitter Lake NWR, should be conducted to determine the location and quality of non-breeding habitat. Also, the incorporation of models that include potential influencing factors such as regional precipitation or surface water availability may reveal causes of declines. Population viability models specifically designed for metapopulations may also shed light on the potential future of snowy plovers on the SGP, and give biologists a better idea of where, and when, to implement conservation strategies.

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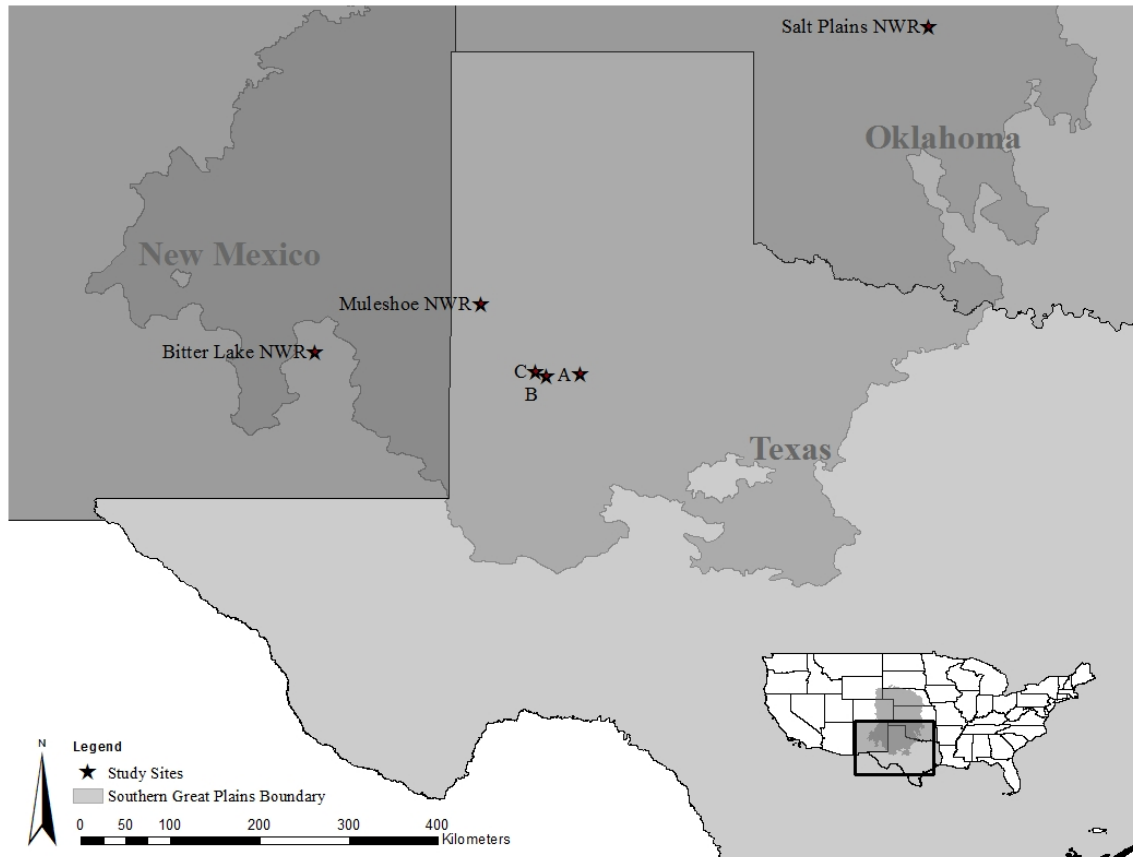
Figure 1.1. Study site locations of snowy plover surveys, snowy plover captures and Motus telemetry tower locations on the Southern Great Plains of Texas, New Mexico and Oklahoma.

	position of egg and angle of its longitudinal axis horizontal	stage of floating
	lays on the bottom of the dish 0	A
	the pointed edge approaches the bottom, but the blunt edge has not risen < 45	AB
	the pointed edge is on the bottom, the blunt edge takes off < 45	B
	the pointed edge is on the bottom, the blunt edge erected 45 < és < 90	C
	the egg stands at the bottom on the pointed edge 90	D
	the egg takes off and floats	E
	the blunt egg appears on the water surface	F

Incubation stage	A	AB	B	C	D	E	F
Number of days incubated (mean ± SE)	0 ± 0	0.8 ± 0.3	2.4 ± 0.4	5.0 ± 0.7	8.0 ± 0.7	10.0 ± 0.8	11.2 ± 1.2
Number of eggs used for calibration	5	7	7	6	3	3	3

Figure 1.2. Egg flotation chart used to determine the age of snowy plover eggs on the Southern Great Plains of Texas, New Mexico and Oklahoma, calibrated using Kentish plover eggs in southern Turkey (Szekely et al. 2008).
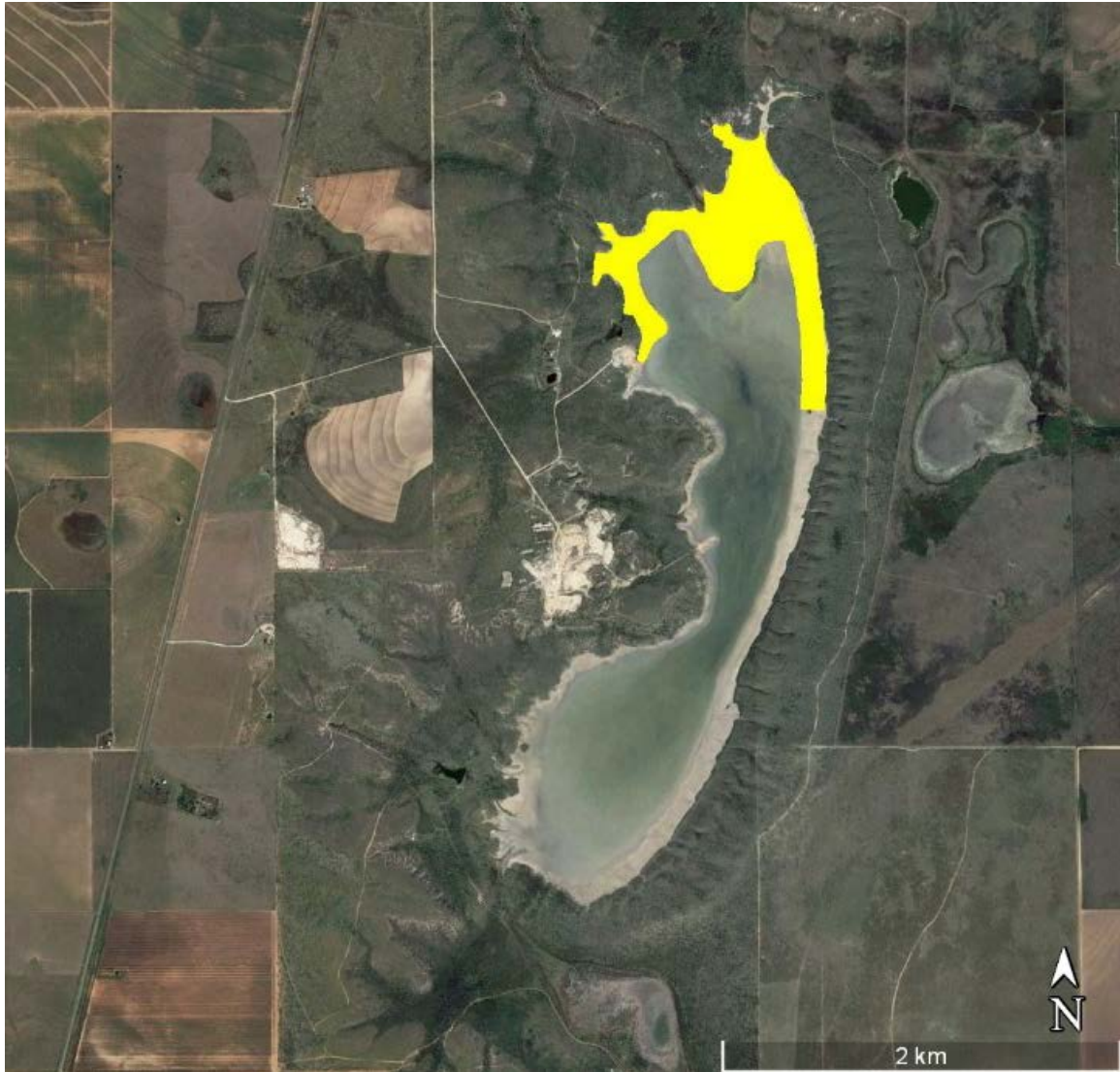
Figure 1.3. Snowy plover survey area (0.59 km^2) at Lake A in Texas from 1998-2018.

Figure 1.4. Snowy plover survey area (0.32 km^2) at Lake B in Texas from 1998-2018.

Figure 1.5. Snowy plover survey area (0.34 km^2) at Lake C in Texas from 2008-2018.
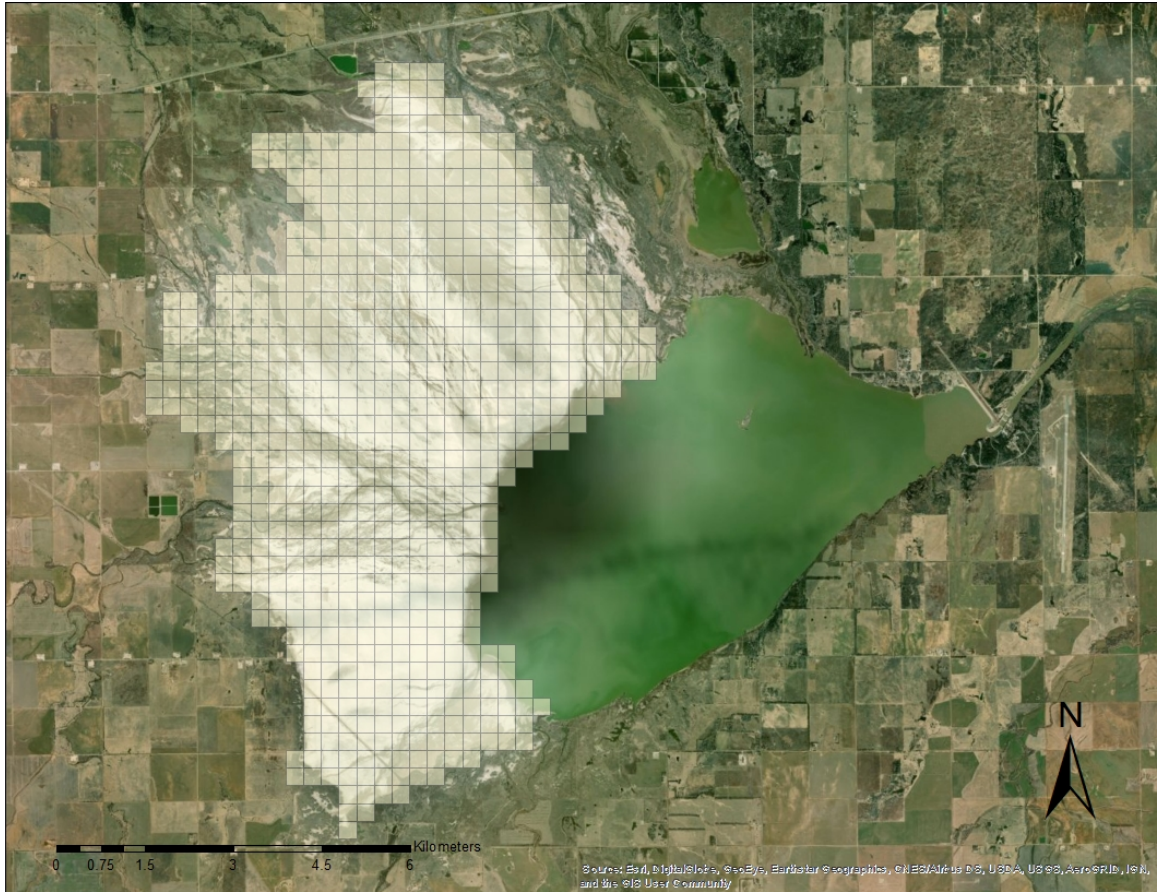
Figure 1.6. Layout of 668 survey grid cells (300 x 300 m) at Salt Plains National Wildlife Refuge in north central Oklahoma used during annual snowy plover surveys, 2013-2017 and snowy plover distance sampling, 2017-2018.
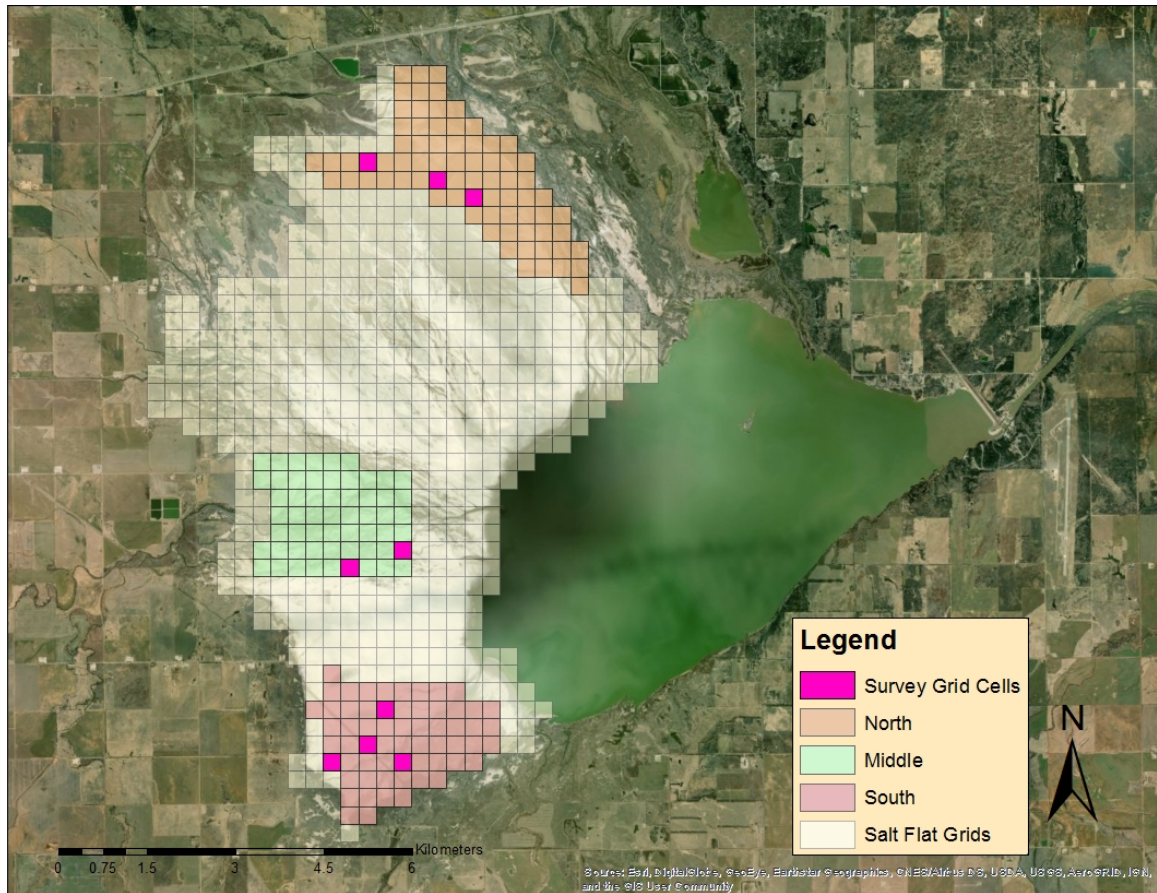
Figure 1.7. Salt Plains National Wildlife Refuge salt flats overlaid with grid cells (300 x 300 m) with highlighted regions (North, Middle and South) and survey grid cells used for snowy plover distance sampling surveys in 2017-2018.
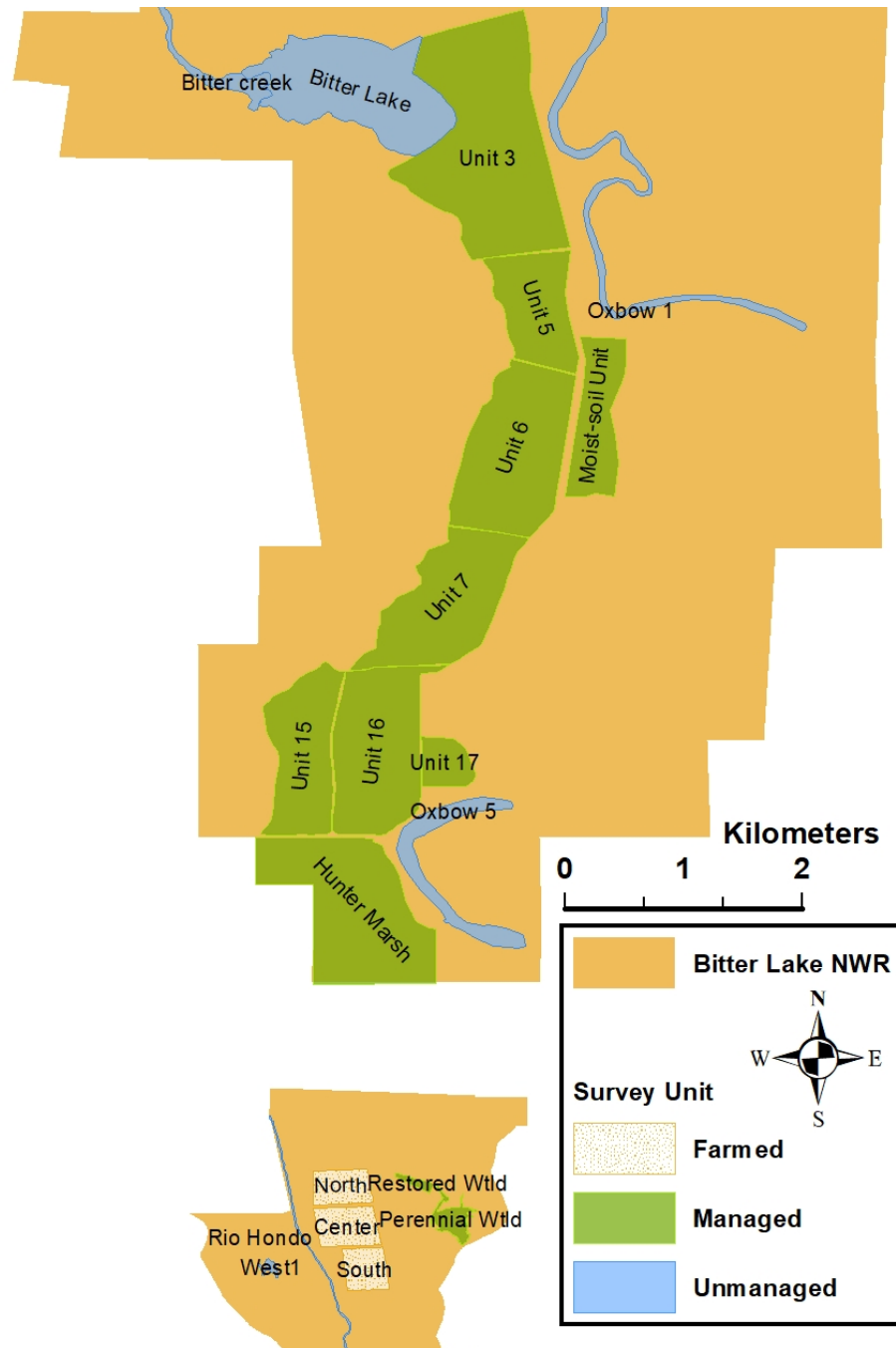
Figure 1.8. Bitter Lake National Wildlife Refuge, with associated wetland management units (Linner et al. 2015).

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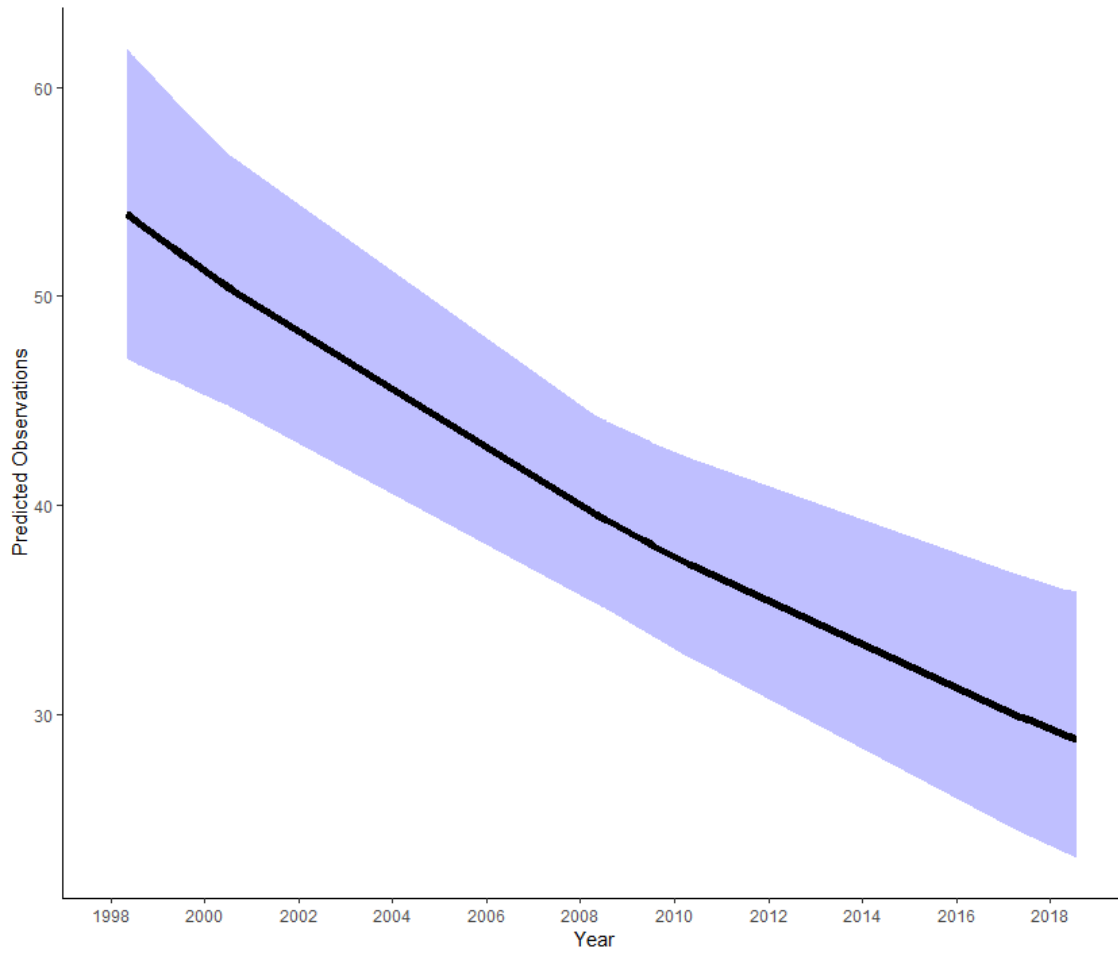
Figure 1.9. Negative binomial regression model of predicted weekly snowy plover survey counts at Lakes A and B in Texas from May-July, 1998-2018. Purple band around prediction line represents the 95% confidence interval.
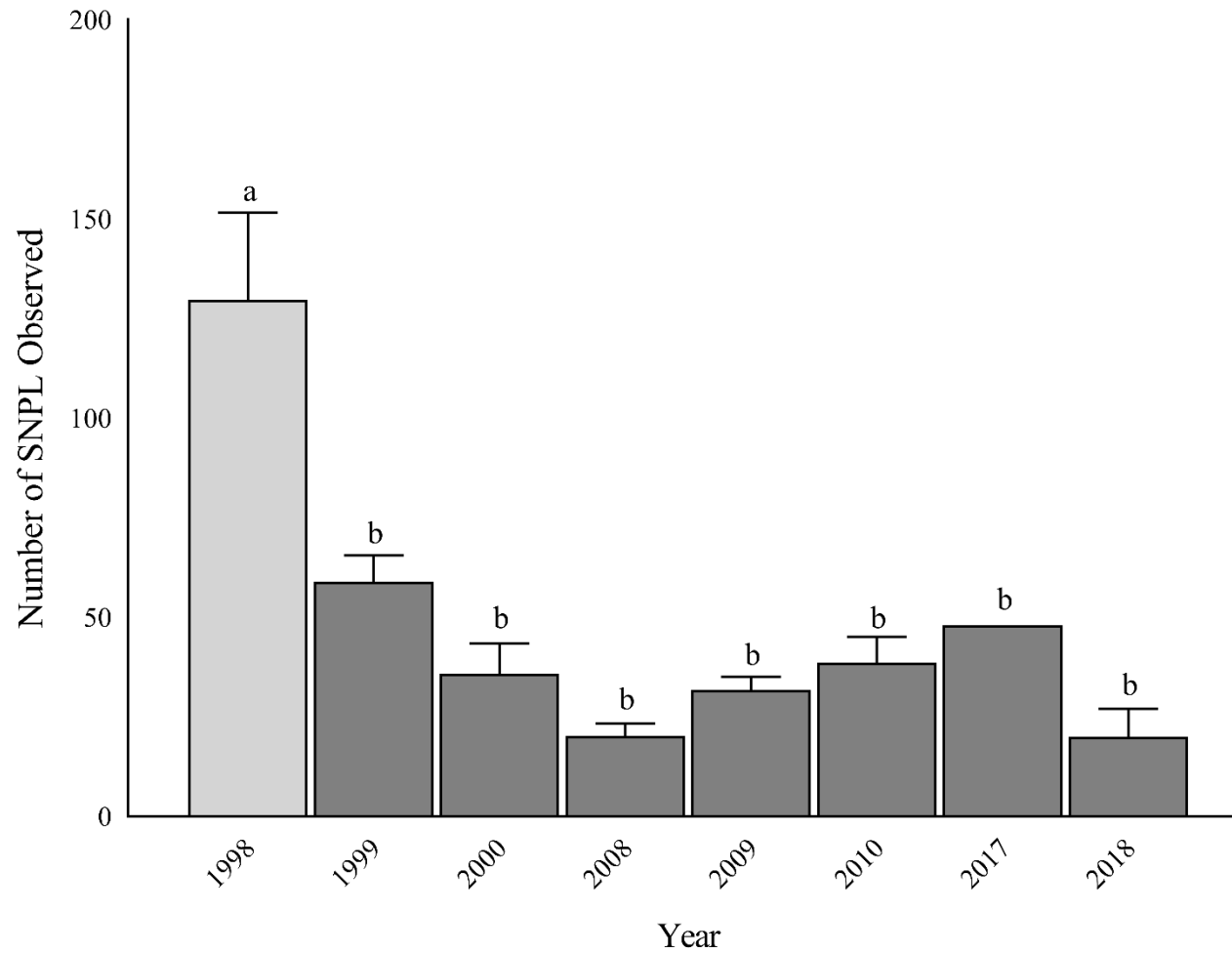
Figure 1.10. Number of snowy plovers (SNPL) observed at Lake A in May from 1998-2000, 2008-2010 and 2017-2018. Bars with the same letter are not different ($P > 0.05$) using Tukey post-hoc comparisons.
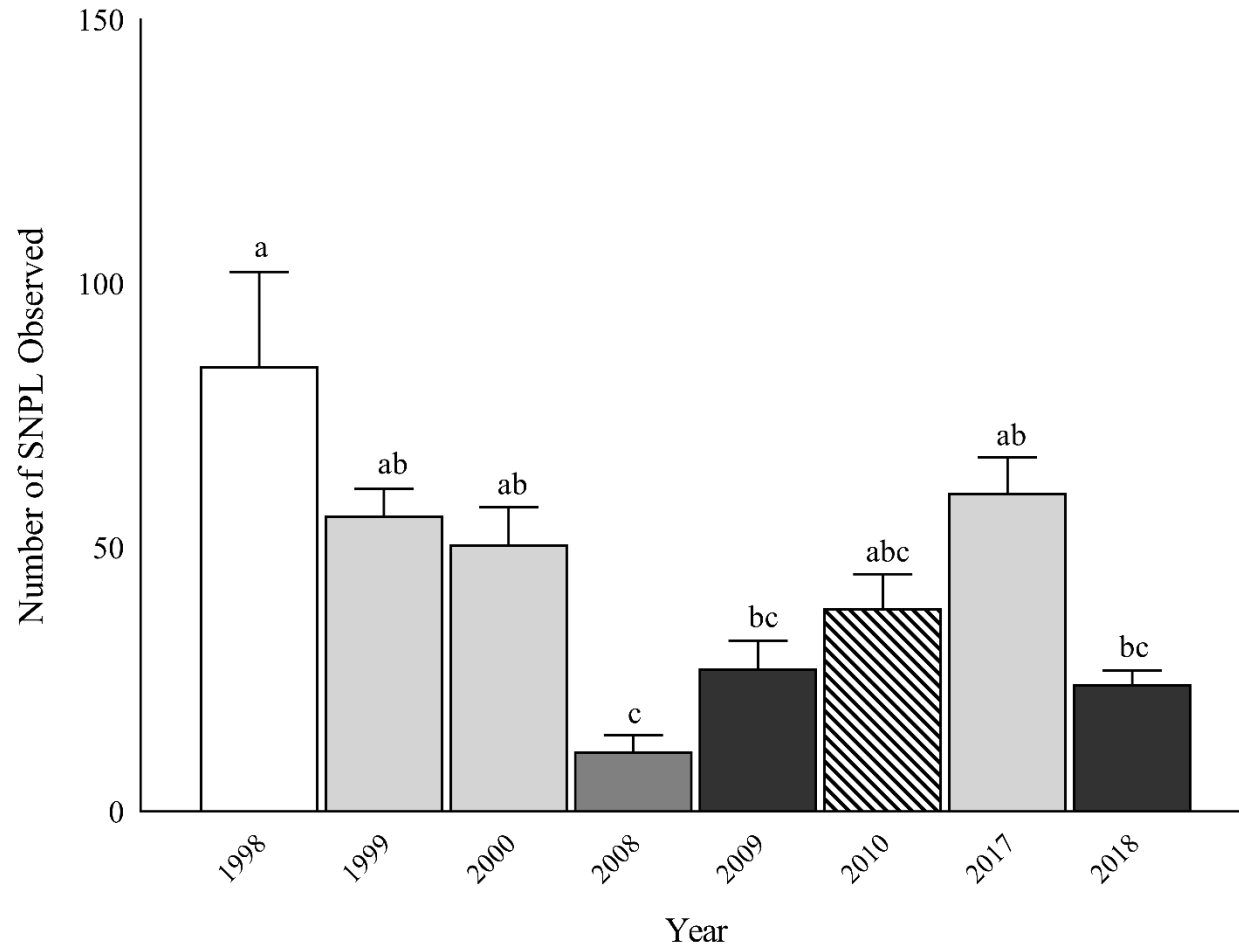
Figure 1.11. Number of snowy plovers (SNPL) observed during surveys in May-July at Lake A from 1998-2000, 2008-2010 and 2017-2018. Bars with the same letter are not different ($P > 0.05$) using Tukey post-hoc comparisons.
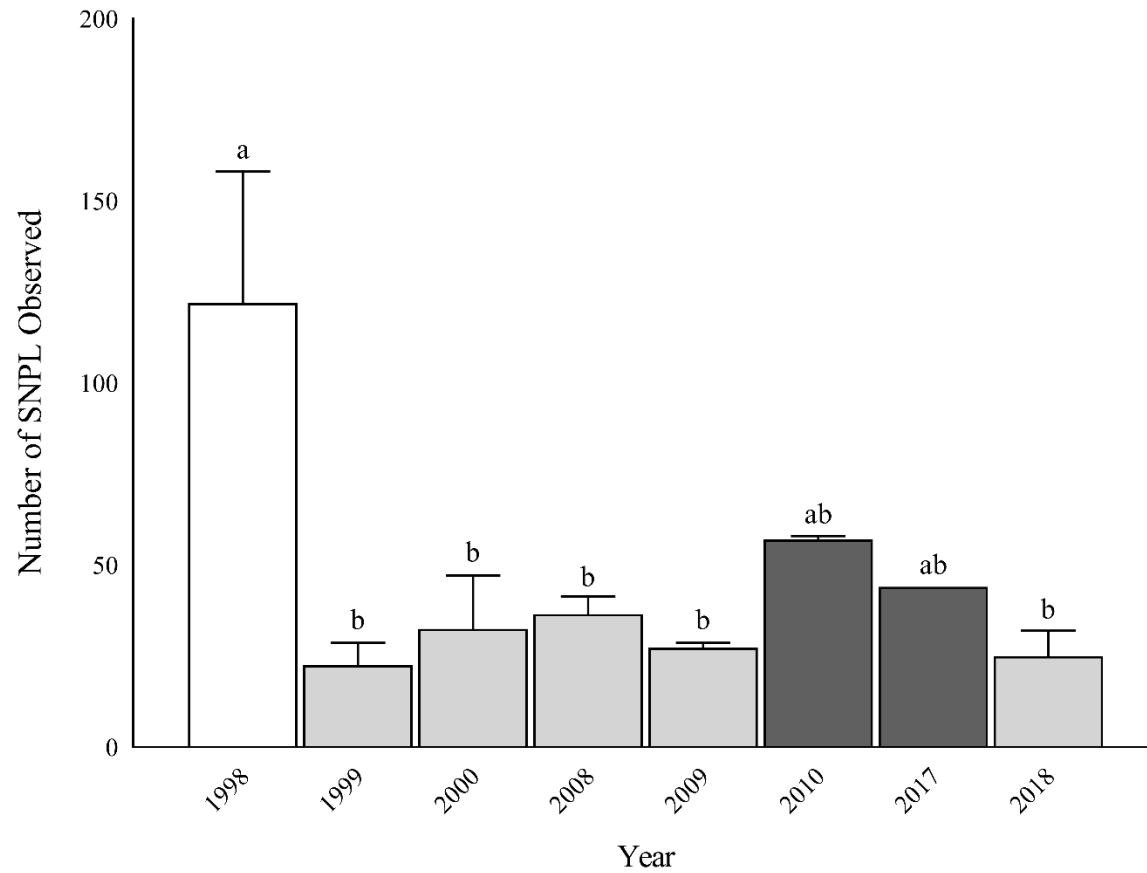
Figure 1.12. Number of snowy plovers (SNPL) observed during surveys in May at Lake B from 1998-2000, 2008-2010 and 2017-2018. Bars with the same letter are not different ($P > 0.05$) using Tukey post-hoc comparisons.
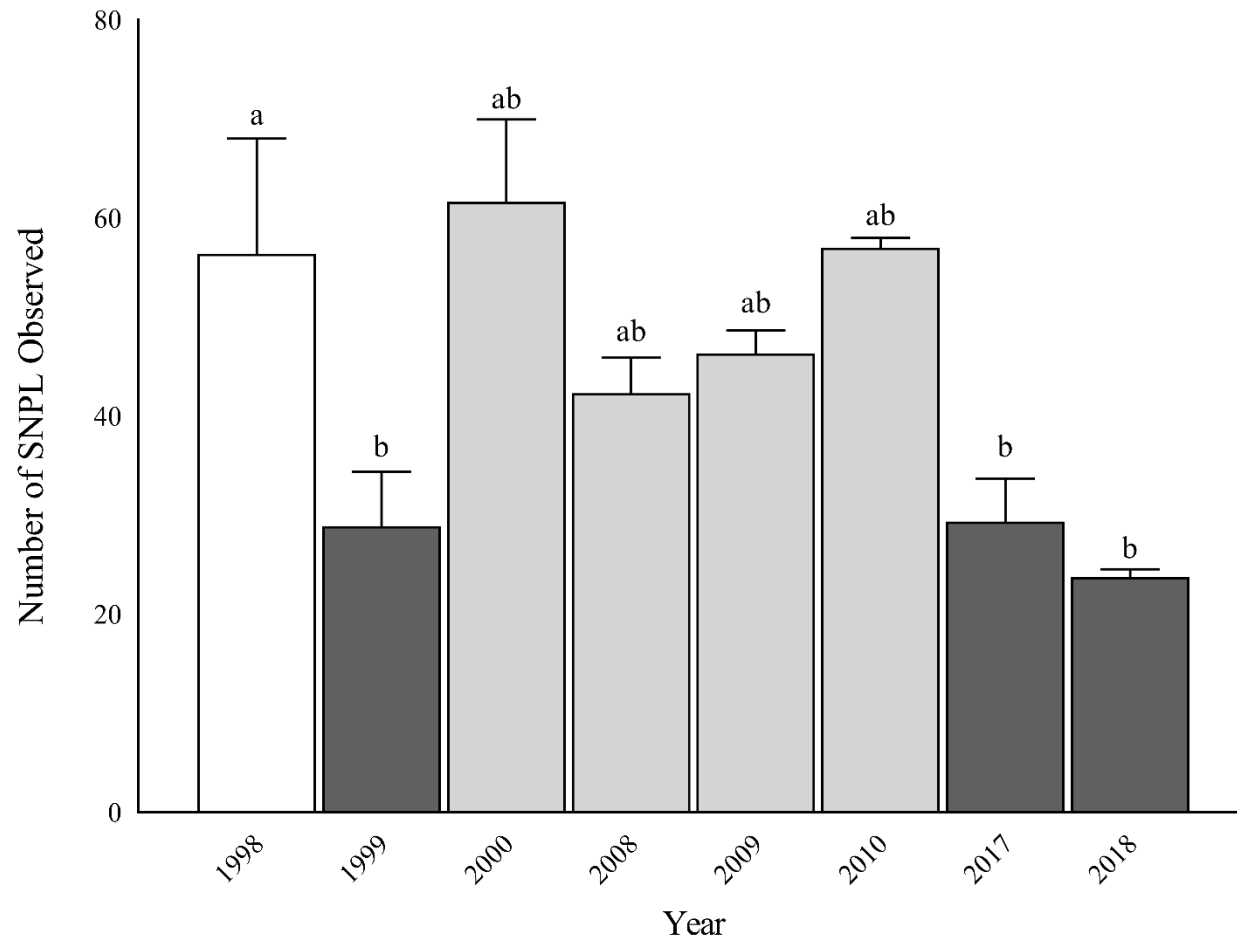
Figure 1.13. Number of snowy plovers (SNPL) observed during surveys in May-July at Lake B from 1998-2000, 2008-2010 and 2017-2018. Bars with the same letter are not different ($P > 0.05$) using Tukey post-hoc comparisons.
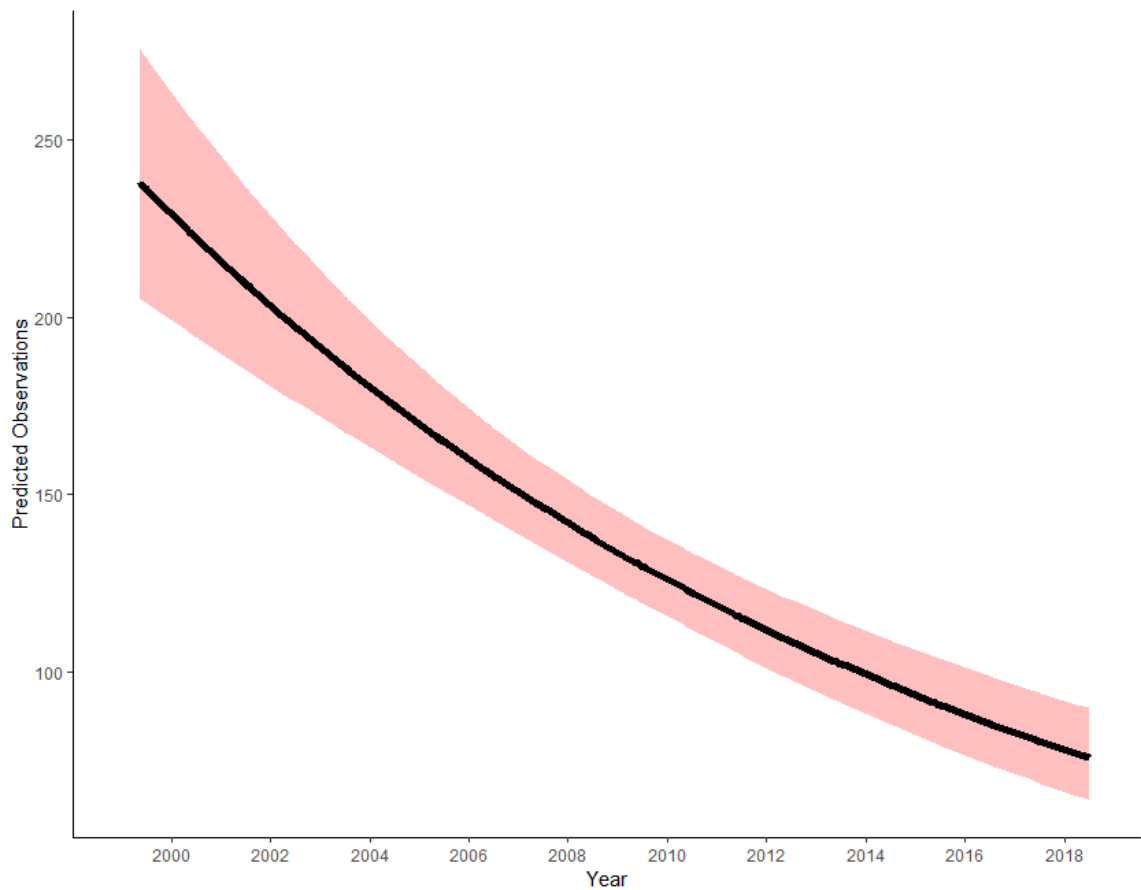
Figure 1.14. Negative binomial regression model of biweekly snowy plover survey counts at Bitter Lake National Wildlife Refuge from May-July in 1999-2018. Red band around prediction line represents the 95% confidence interval.
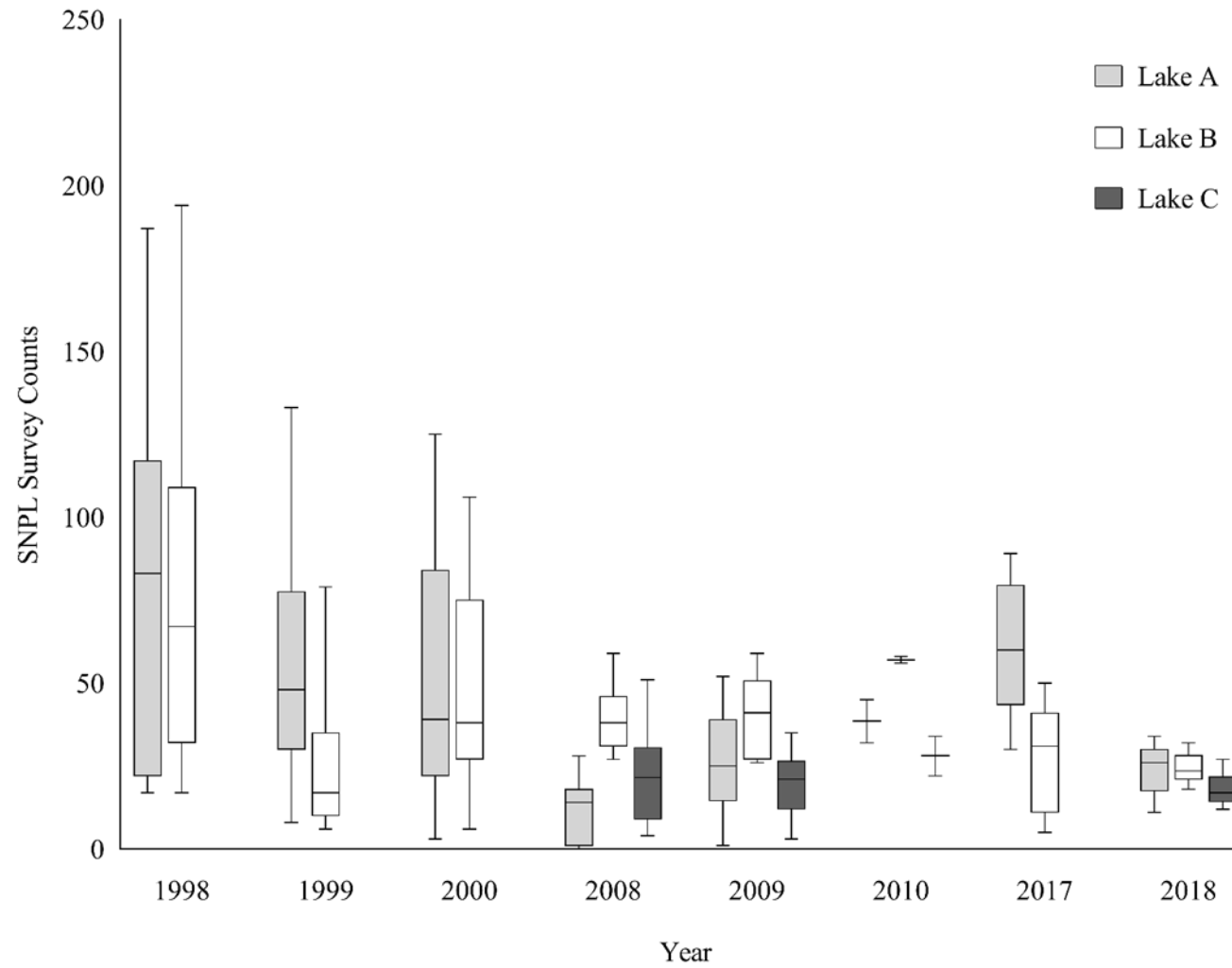
Figure 1.15. Raw snowy plover survey count data at Lakes A, B and C in Texas from 1998-2000, 2008-2010 and 2017-2018
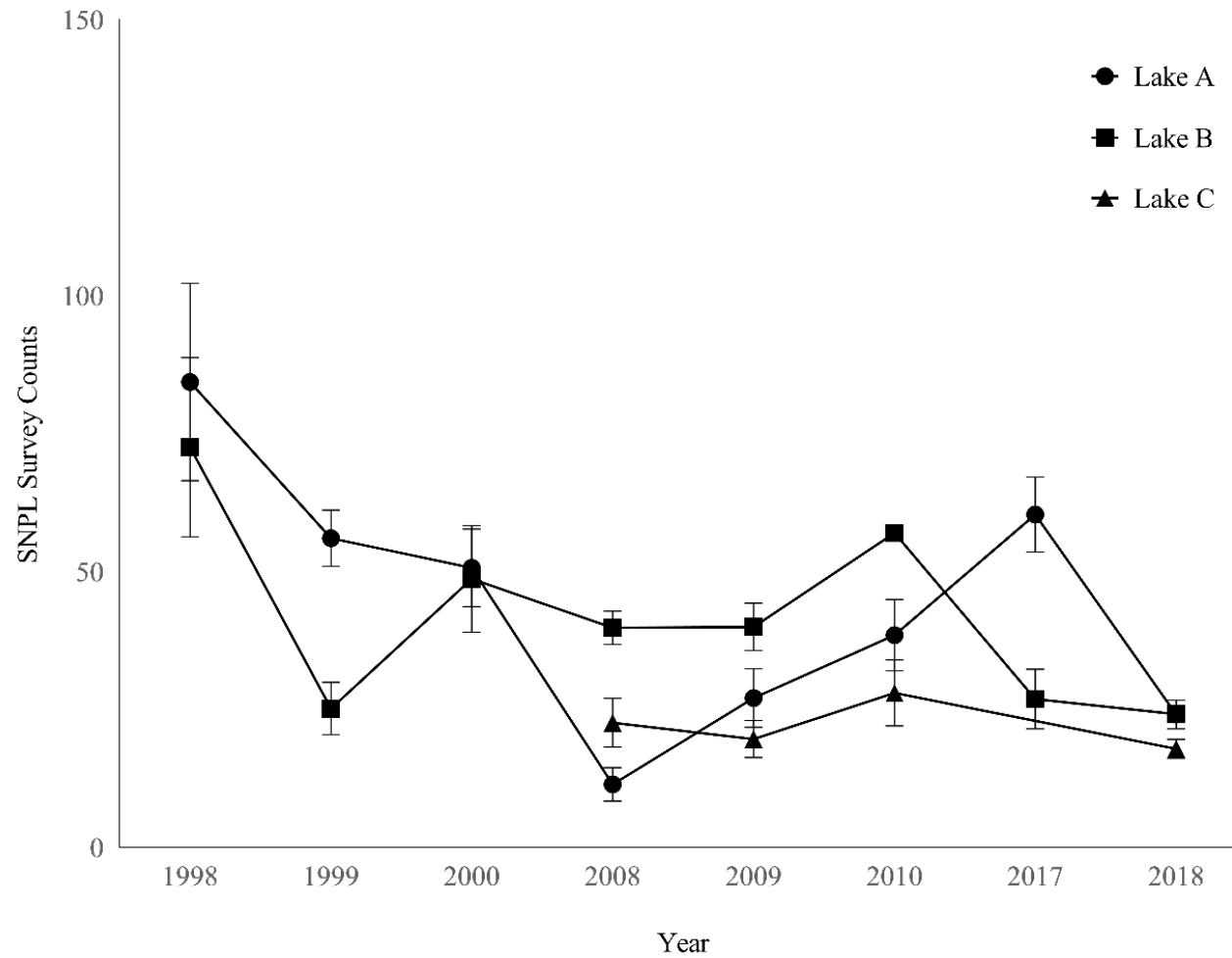
Figure 1.16. Mean snowy plover survey count data with standard error (SE) at Lakes A, B and C in Texas from 1998-2000, 2008-2010 and 2017-2018.
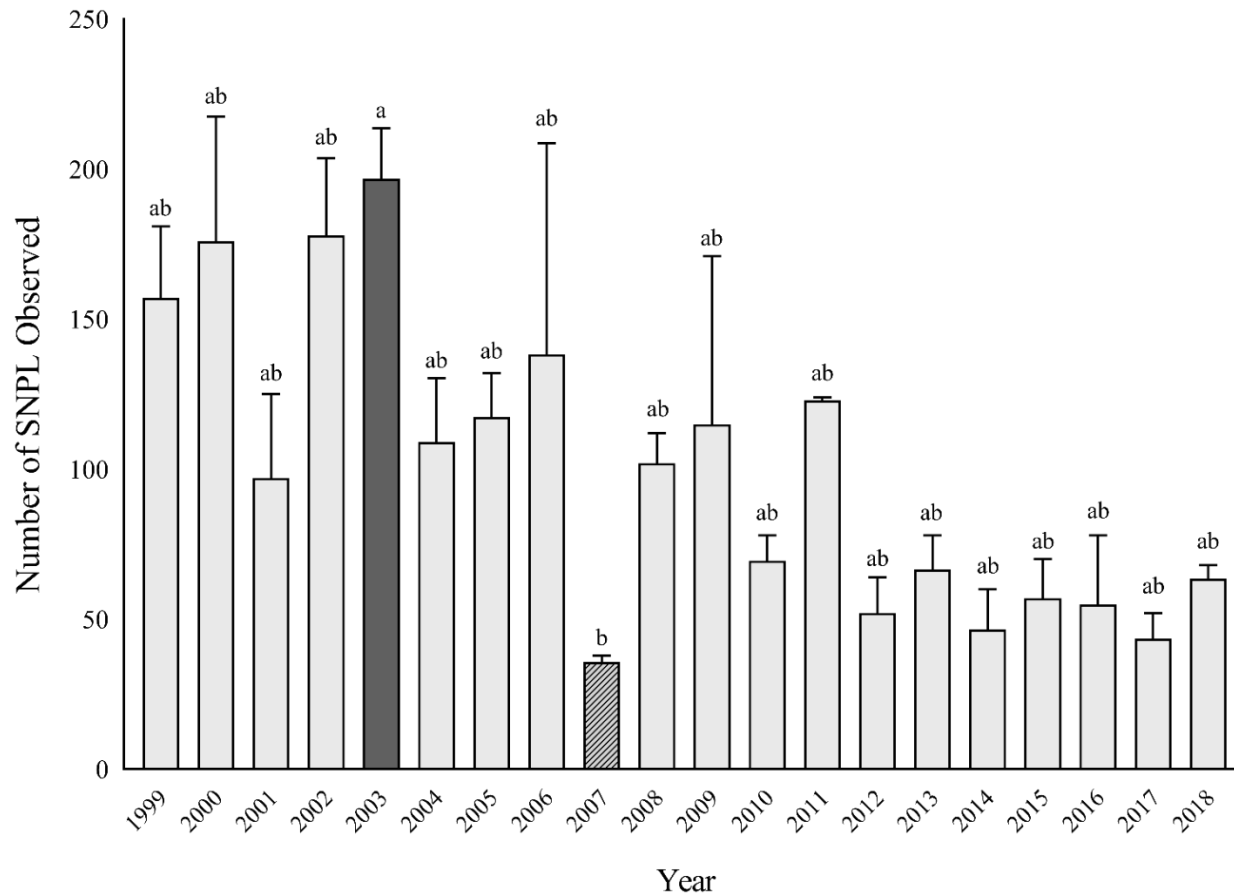
Figure 1.17. Number of snowy plovers (SNPL) observed during biweekly surveys in May at Bitter Lake National Wildlife Refuge from 1999-2018. Bars with the same letter/color are not different ($P > 0.05$) using Tukey post-hoc comparisons.
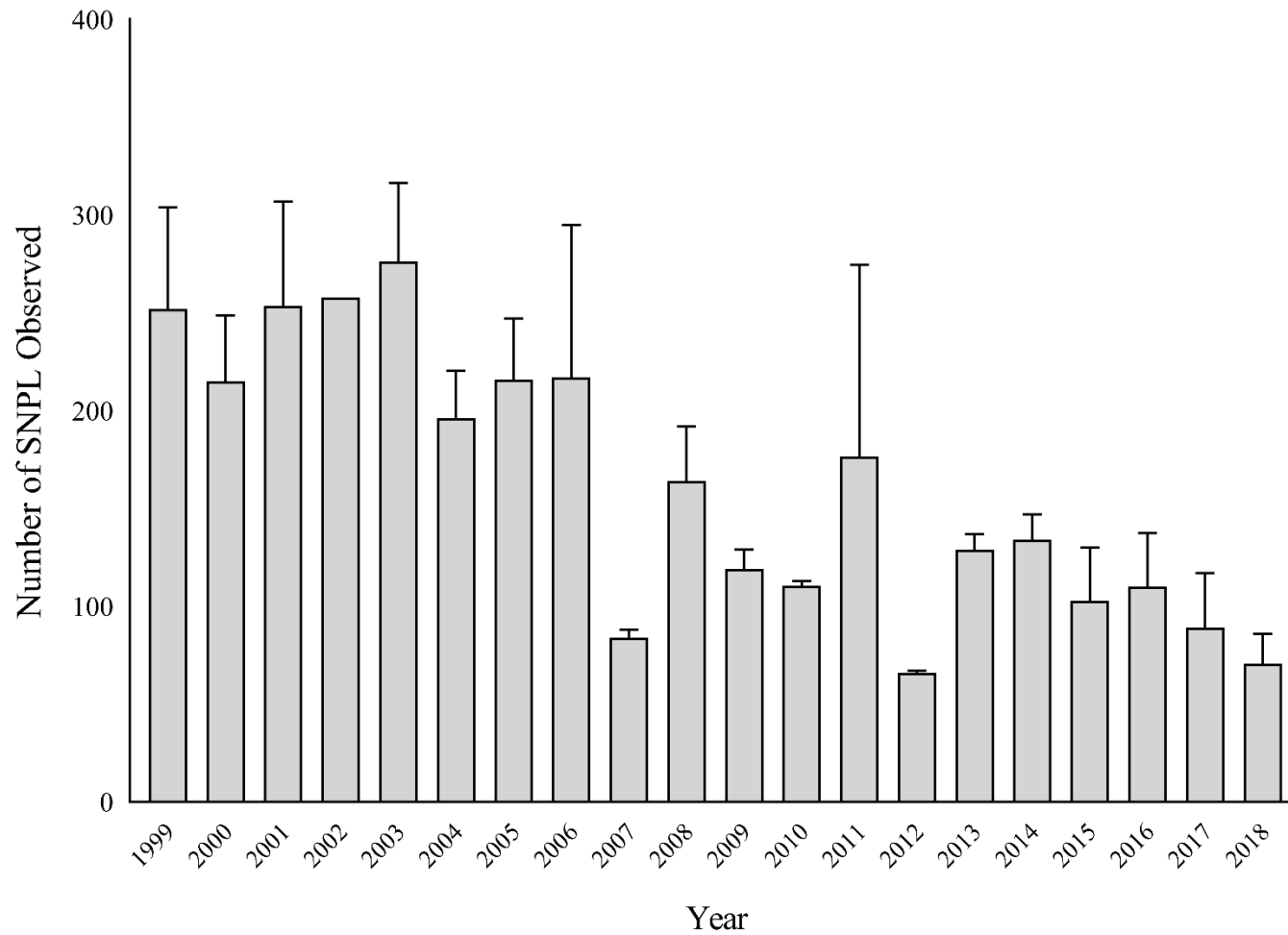
Figure 1.18. Number of snowy plovers (SNPL) observed during biweekly surveys in June at Bitter Lake National Wildlife Refuge from 1999-2018. Bars indicate standard error (SE).
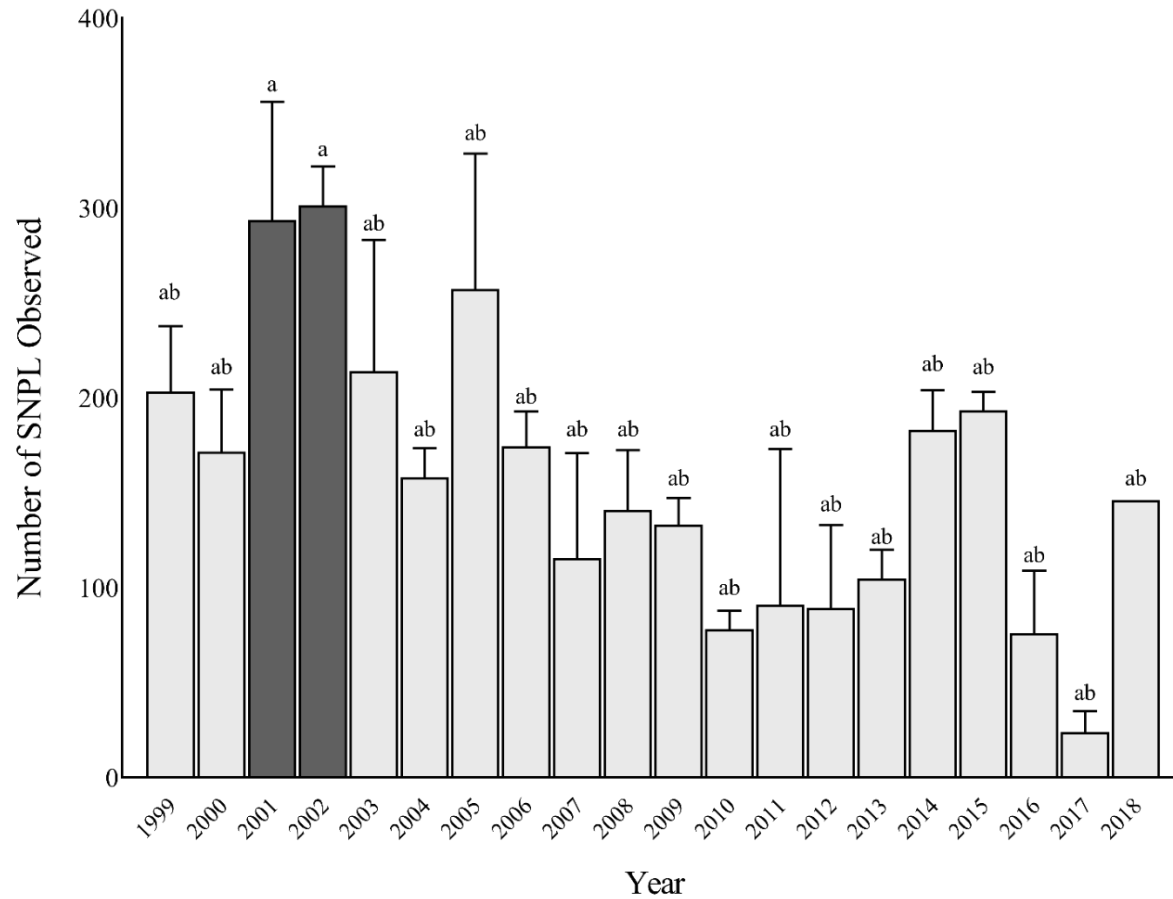
Figure 1.19. Number of snowy plovers (SNPL) observed during biweekly surveys in July at Bitter Lake National Wildlife Refuge from 1999-2018. Bars with the same letter/color are not different ($P > 0.05$) using Tukey post-hoc comparisons.
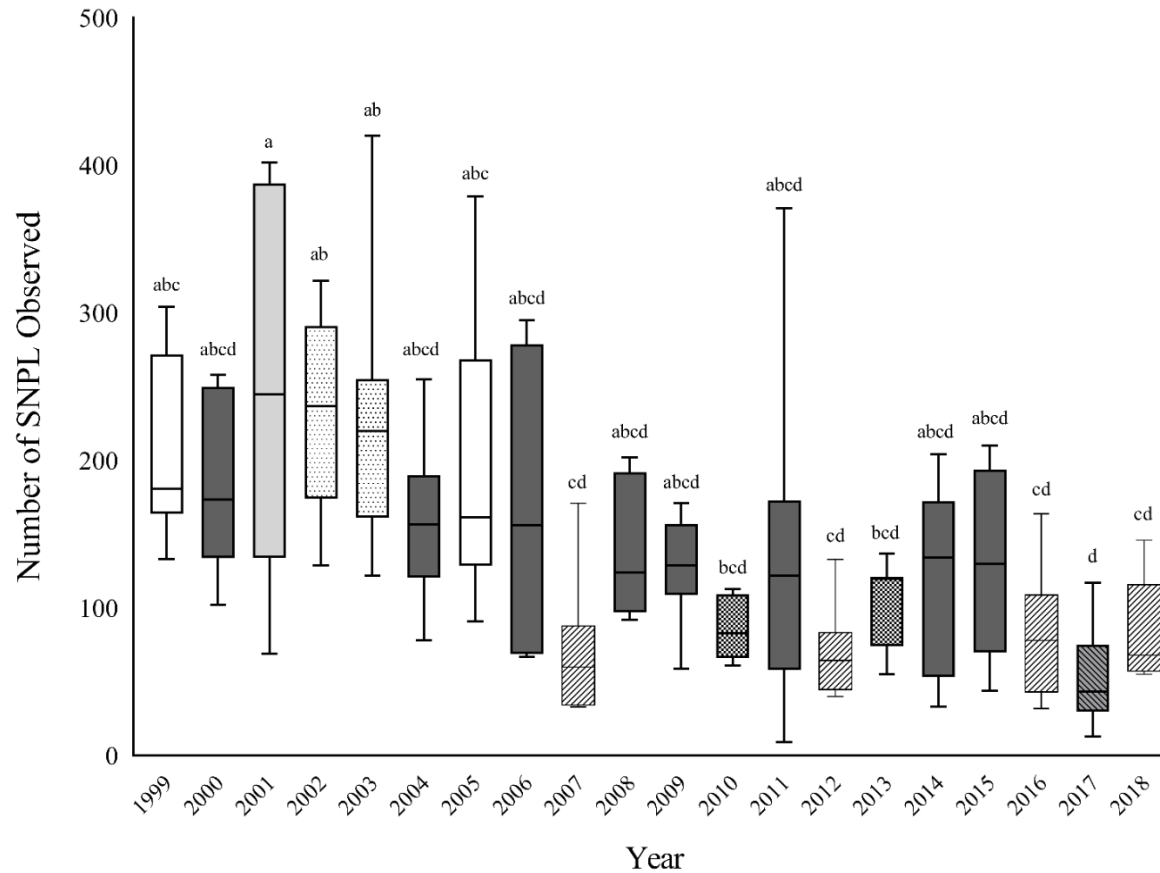
Figure 1.20 Number of snowy plovers (SNPL) observed during biweekly surveys in May-July at Bitter Lake National Wildlife Refuge from 1999-2018. Bars indicate maximum and minimum observations. Bars with the same letter/color are not different ($P > 0.05$) using Tukey post-hoc comparisons.
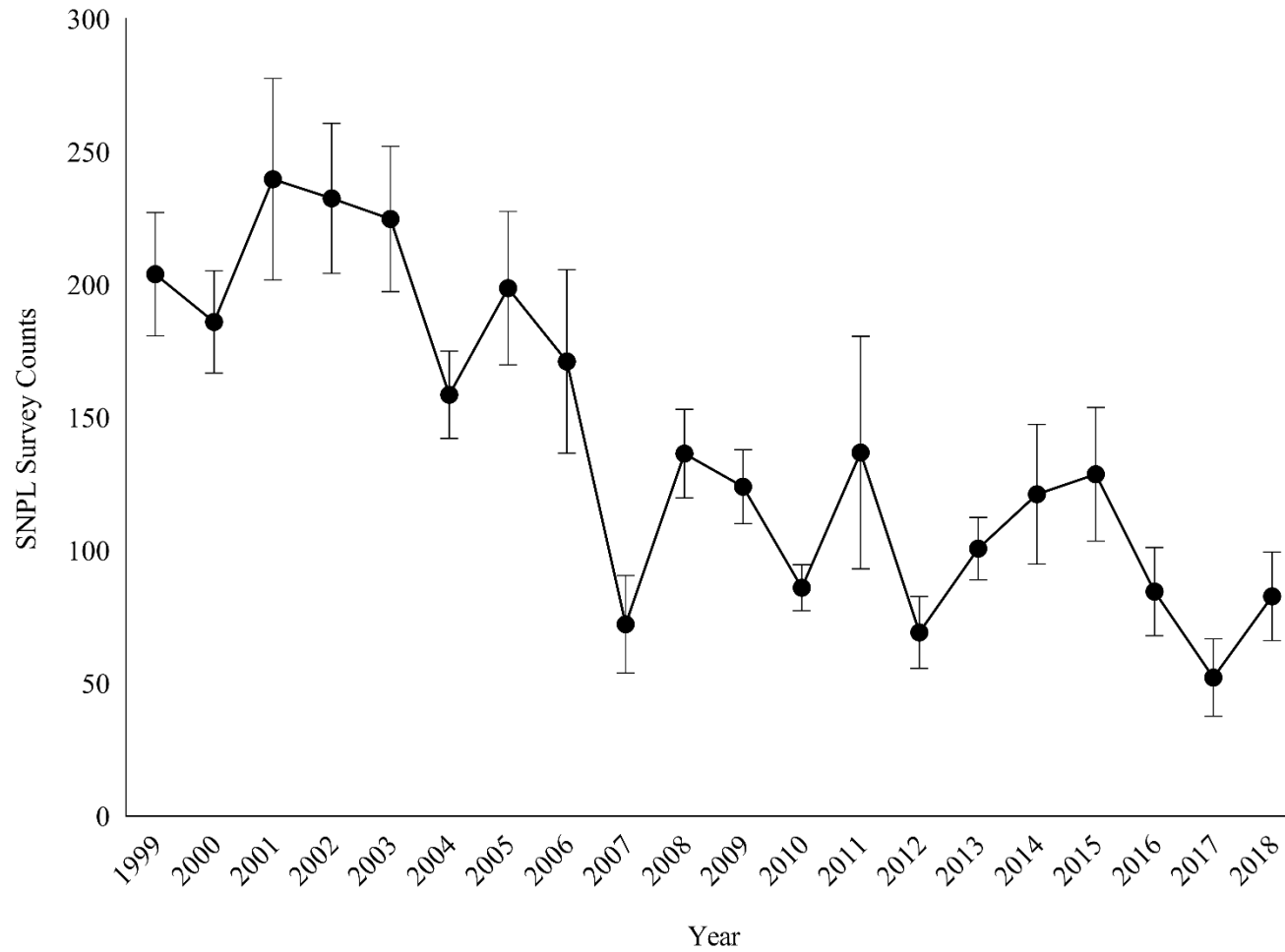
Figure 1.21 Mean number of snowy plovers (SNPL) observed during biweekly surveys in May-July at Bitter Lake National Wildlife Refuge from 1999-2018; bars indicate standard error (SE).
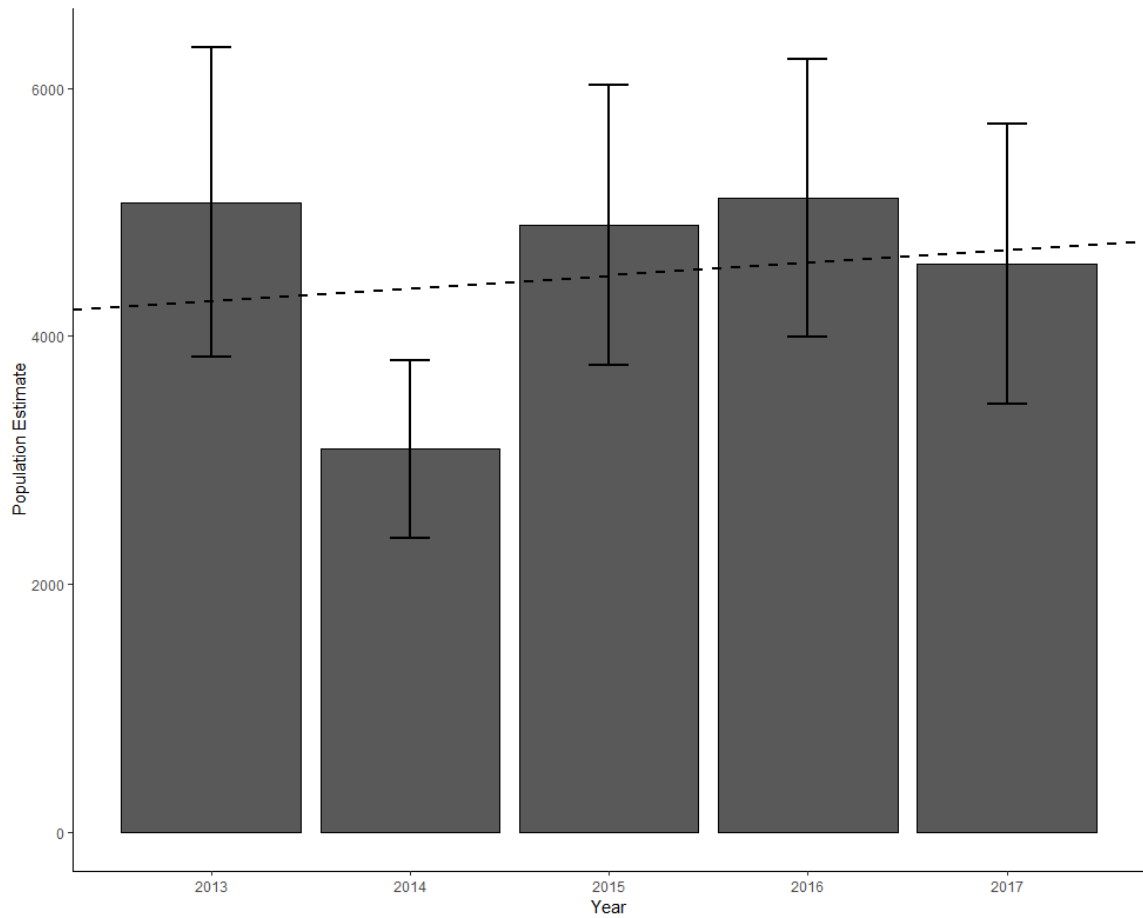
Figure 1.22. Snowy plover population estimates (with 95% confidence intervals) from annual surveys performed in May at Salt Plains National Wildlife Refuge from 2013-2017, with simple linear regression line indicating population stability ($R^2 = 0.04$, $F_{1, 3} = 0.12$, $P = 0.756$).
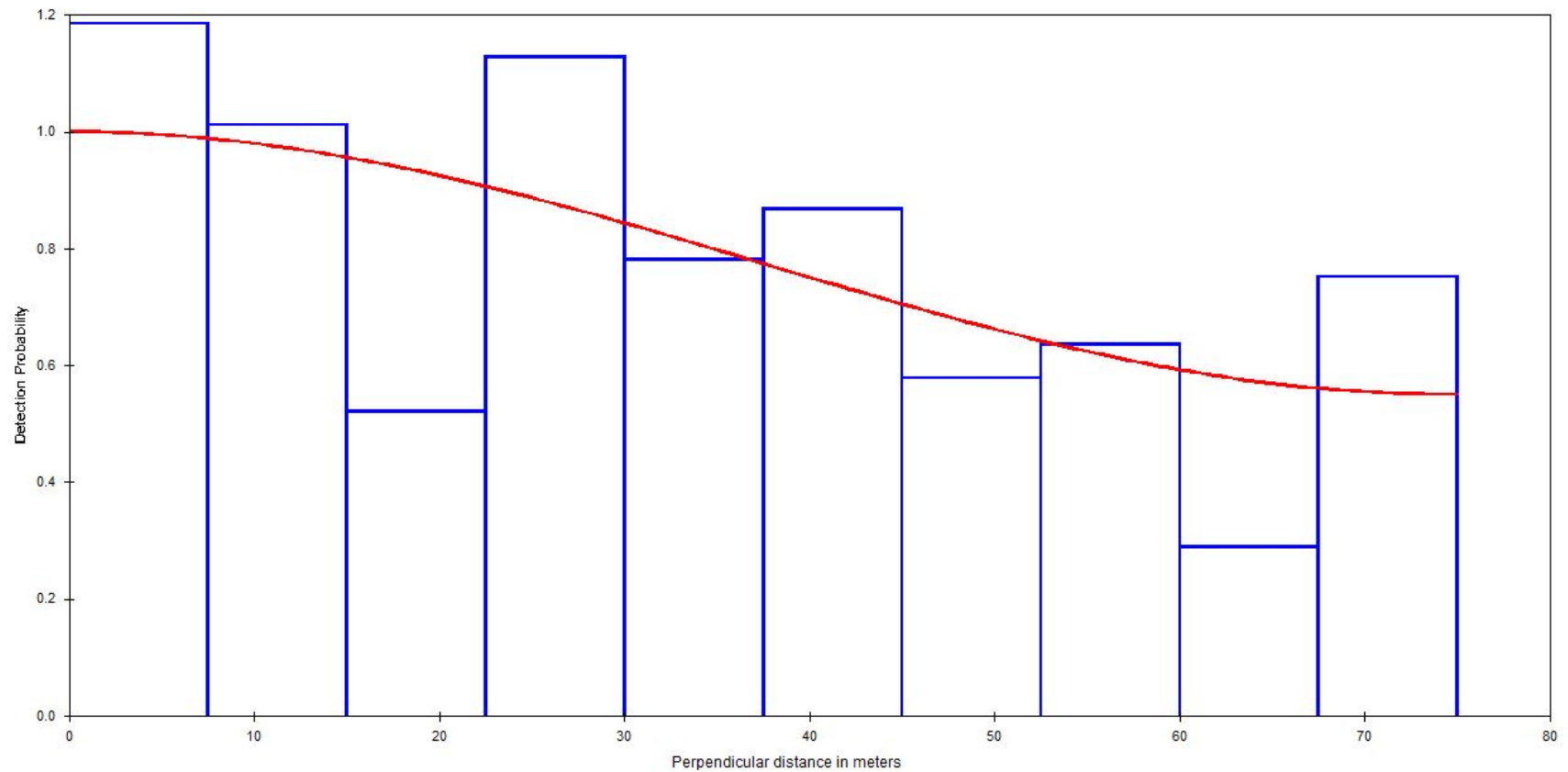
Figure 1.23. Detection probability function for snowy plovers calculated during summer surveys using distance sampling protocols at Salt Plains National Wildlife Refuge from 2017-2018; red line indicates the detection curve.

Table 1.1. Results from ranked negative binomial regression models for snowy plover survey counts at Texas lakes A and B from 1998-2000, 2008-2010 and 2017-2018.

Model	Parameters	ΔAIC[a]	wAIC[b]
Julian Date + Lake	2	0.00	0.51
Julian Date	1	0.00	0.49
Lake	1	13.80	0.00

[a]The difference in Akaike Information Criterion (AIC) values.

[b]Model weight, or the relative likelihood of the model.

Table 1.2. Snowy plover survey data (mean; standard error [SE]) during the breeding season (May, June, and July) at Lake C (in Texas) from 2008-2010; and 2018.

Year	May			June			July			Combined		
	n[a]	mean	SE	n	mean	SE	n	mean	SE	n	mean	SE
2008	4	31.0	7.1	4	22.3	5.4	2	6.5	2.50	10	22.6	4.4
2009	4	22.0	2.6	3	17.0	5.3	2	19.0	16.0	9	19.7	3.4
2010	1	22.0	na[b]	1	34.0	na	na	na	na	2	28.0	6.0
2018	2	19.0	4.0	3	20.3	3.3	3	14.7	1.76	8	17.9	1.7

[a] Number of surveys

[b] Not applicable (based on sample size of 1)

Table 1.3. Snowy plover survey data (mean; standard error [SE]) during the breeding season (May, June, and July) at Lake A (in Texas) within and among months from1998-2000, 2008-2010; and 2017-2018.

Year	May			June			July			Combined		
	n[a]	mean	SE	n	mean	SE	n	mean	SE	n	mean	SE
1998	5	129.6	21.9	4	60.5	19.4	2	19.0	2.0	11	84.4	17.9
1999	10	65.8	5.7	10	81.5	10.1	8	79.4	14.5	26	76.0	6.1
2000	11	49.0	11.1	8	72.4	13.7	3	85.0	13.6	16	67.4	8.4
2008	5	20.2	3.1	4	5.8	3.0	2	1.0	0.0	11	11.5	3.1
2009	3	31.7	3.3	4	26.3	8.9	2	22.0	21.0	9	27.1	5.3
2010	2	32.0	na[b]	1	45.0	Na	na	na	Na	2	38.5	6.5
2017	1	48.0	na	4	54.3	6.7	4	69.5	13.4	9	60.3	6.8
2018	2	20.0	7.0	4	27.3	2.5	3	22.7	6.4	9	24.1	2.6

[a] Number of surveys

[b] Not applicable (based on sample size of 1)

Table 1.4. Snowy plover survey data (mean, standard error [SE]) during the breeding season (May, June, and July) at Lake B (in Texas) within and among months from1998-2000, 2008-2010 and 2017-2018.

Year	May			June			July			Combined		
	n[a]	mean	SE	n	mean	SE	n	mean	SE	n	mean	SE
1998	3	122.0	36.1	4	73.2	23.31	4	34.8	11.3	11	72.6	16.2
1999	6	29.5	6.7	5	38.4	10.68	4	21.3	9.7	13	30.4	5.4
2000	4	42.2	11.7	4	71.8	13.83	1	36.0	na[b]	9	54.7	9.2
2008	4	36.5	4.9	3	43.7	9.26	4	40.3	3.0	11	39.8	3.0
2009	3	27.3	1.3	4	44.8	2.87	1	59.0	na	8	40.0	4.3
2010	2	58.0	na	1	56.0	na	na	na	na	2	57.0	1.0
2017	1	44.0	na	4	38.5	4.09	4	11.0	2.5	9	26.9	5.4
2018	2	25.0	7.0	4	23.3	0.85	4	24.8	2.2	10	24.2	1.4

[a] Number of surveys

[b] Not applicable (based on sample size of 1)

Table 1.5. Results from ranked negative binomial regression models for snowy plover survey counts at Bitter Lake National Wildlife Refuge from 1999-2018.

Model	No. parameters	ΔAIC[a]	wAIC[b]
Month + Julian Date	5	0	0.58
Julian Date*Month	4	0.6	0.42
Julian Date	5	17.8	0
Month	5	60.3	0

[a]The difference in Akaike Information Criterion (AIC) values.

[b] Model weight, or the relative likelihood of the model.

Table 1.6. Bi-weekly snowy plover survey count data (mean; SE) during the breeding season (May, June, and July) at Bitter Lake National Wildlife Refuge within and among months from1999-2018.

Year	n[a]	May mean	SE	n	June mean	SE	n	July mean	SE	n	Combined mean	SE
1999	2	157.0	24.0	3	258.7	30.8	2	169.0	5.0	7	204.0	23.3
2000	3	176.0	41.5	3	215.0	33.6	4	171.8	32.6	10	186.0	19.3
2001	3	110.3	21.0	5	303.8	49.2	3	290.3	56.2	11	239.7	37.9
2002	2	176.0	30.0	2	215.0	32.0	1	281.0	na[b]	6	232.5	28.2
2003	4	157.0	16.9	3	258.7	47.9	3	169.0	12.8	11	224.7	27.3
2004	3	157.0	21.4	4	258.7	24.2	3	169.0	15.7	10	158.6	16.4
2005	2	138.0	19.0	4	271.3	43.5	3	167.0	47.5	10	198.7	28.9
2006	2	174.0	105.0	3	196.7	49.4	2	102.5	90.5	7	171.1	34.5
2007	2	33.5	23.7	2	84.0	59.4	2	115.5	81.7	7	72.3	18.4
2008	2	102.0	10.0	3	176.7	20.5	2	110.5	13.5	7	136.4	16.7
2009	2	115.0	56.0	3	124.0	7.6	2	133.0	24.0	7	124.0	13.9
2010	2	69.5	8.5	3	103.0	7.6	2	43.0	25.0	6	86.0	8.6
2011	2	123.0	1.0	3	215.0	80.7	2	11.0	2.0	7	136.9	43.7
2012	1	40.0	na	2	66.0	1.0	2	89.5	43.5	6	69.2	13.6
2013	1	55.0	na	3	110.7	18.9	2	120.0	0.0	7	100.7	11.7
2014	2	46.5	13.5	2	134.0	13.0	2	183.0	21.0	6	121.2	26.3
2015	1	70.0	na	2	103.0	3.8	3	194	9.53	7	128.7	25.2
2016	2	55	23.00	3	110	27.50	2	76	33.00	7	84.6	16.62
2017	2	43.5	8.50	2	89	28.00	2	24	11.00	6	52.2	14.61
2018	2	63.5	4.50	2	70.5	15.50	1	146	na	5	82.8	16.68

[a] Number of surveys

[b] Not applicable (based on sample size of 1)

Table 1.7. Top performing distance models predicting density (D) and detection probability (P) of snowy plovers at Salt Plains NWR in 2017 and 2018.

Model ID	dAIC[a]	Param	D[b]	D			P[c]	P		GOF Chi-p
				LCL	UCL	CV		LCL	UCL	
1	0.00	1	0.54	0.37	0.78	0.16	0.78	0.68	0.88	0.019
2	1.43	2	0.54	0.37	0.79	0.17	0.77	0.66	0.90	0.015
3	2.17	1	0.51	0.35	0.74	0.16	0.82	0.73	0.92	0.009
4	3.33	2	0.52	0.35	0.77	0.18	0.80	0.65	0.98	0.009

[a] The difference in Akaike Information Criterion (AIC) values.

[b] Density (individuals/ha)

[c] Detection probability

Table 1.8. Density (D) and population (N) estimates of snowy plovers (*Charadrius nivosus*) for 3 regions at Salt Plains National Wildlife Refuge in Oklahoma from 2017-2018.

Region	Parameter	Estimate	SE[a]	95% CI	
North	D[b]	0.55	0.07	0.43	0.71
	N[c]	372	45	287	481
Middle	D	0.62	0.23	0.24	1.61
	N	422	153	163	1090
South	D	0.43	0.07	0.30	0.62
	N	292	47	203	418
Pooled[d]	D	0.54		0.37	0.78
	N	1085		744	1581

[a]Standard error (SE)

[b] Density (individuals/ha)

[c] Population estimate

[d] Combined for all 3 regions

CHAPTER 2
POPULATION CONNECTIVITY OF SNOWY PLOVERS ON THE SOUTHERN
GREAT PLAINS

Introduction

There have been recent calls for monitoring annual connectivity of avian populations (Marra et al. 2015, Taylor et al. 2017). Some have also argued that within-season movement events are too rarely studied, and further investigation is required to offer a more accurate spatiotemporal understanding of population connectivity for the purposes of conservation (Haig et al. 1998). Haig et al. (1998) defines these within breeding-season movements as movement among sites prior to breeding, movement to new locales to renest after nest failure, territory switching, use of foraging areas away from nest sites, use of brood-rearing habitat away from nest sites, molt migration, and post-breeding movements of young/adults to staging areas (or other age- or sex-specific resources). Understanding which movements are made and what corresponding reproductive benefits may be conferred, or lost, is a critical piece of puzzling together species conservation strategies. Furthermore, the study of an individual's movements can also reveal features of a species' biology and contribute to researchers' understanding of how abiotic change (e.g., climate change or the addition of human infrastructure such as wind turbines and communication towers) affects a population.

Snowy plovers are a small *Charadrius* shorebird that is widely dispersed across the Western Hemisphere with three recognized subspecies (Page et al. 2009). North American snowy plover (*C. n. nivosus*) breeding and wintering habitat consists of saline lake shorelines, alkaline flats, riparian sandbars and sandy coastal beaches (Page et al. 2009). Their range encompasses the Pacific coast, inland as far east as Kansas and the

Southern Great Plains (SGP) of Texas and south along the Gulf coast from Mexico to

Florida (Sibley 2001, Page et al. 2009). Throughout their geographic range, there are

subpopulations that coexist during the breeding season, but have consistently different

migration and movement strategies during other portions of the year. For example, snowy

plover populations along the Pacific and Gulf coasts are an amalgam of resident and

migratory individuals (Page et al. 2009, Eberhart-Phillips and Colwell 2014). In addition;

some individuals within a single population on the Pacific coast have demonstrated some

annual plasticity in migratory status (Stenzel et al.1994, Eberhart-Phillips and Colwell

2014). Midcontinental snowy plovers on the SGP are typically considered migratory,

although a paucity of data exists on specific migratory movements for these snowy

plovers (Paton 1995, Page et al. 2009). For example, winter resightings of SGP banded

snowy plovers have occurred from the west coast of Florida and along the Gulf coast to

Mexico, although confirmed winter resightings are rare (Conway pers. comm.).

Beyond these pre- and post-breeding season migratory movements, within-

breeding season movements > 800 km have been documented for snowy plover adults on

the Pacific coast; the longest movement for a re-nesting attempt was 660 km by a female

(Stenzel et al. 1994). Another study reports much lower—but still substantial—within-

breeding season movements of 10-100 km at Great Salt Lake (Paton and Edwards 1996).

However, to date, within-breeding season movements have not been described in SGP

snowy plovers. The landscape on which inland snowy plovers are found presents its own

set of challenges to studying their movements, in addition to those common to coastal

population dynamics studies (e.g., low detection probability, alteration of behavior,

predictability, and closely-linked habitat locales) (Haig et al. 1998). Among the inland

snowy plover population, long distances among discontinuous breeding habitat patches make monitoring movements logistically problematic (see Chapter I). In such regions, efforts to adequately monitor within-breeding season connectivity by applying widely used, traditional capture-mark-resight/recapture (CMR) techniques can be limited by excessive logistical efforts and complications as well as localized plover density, and unreliable occupancy of some breeding habitat patches (see Chapter I; Ashbaugh et al. 2018). However, the limited distribution and arrangement of saline lakes on the SGP landscape (see Hall 2001 for figure of SGP saline lakes) may obviate some of these challenges. For example, the isolated nature of these breeding habitats would eliminate the need for survey or capture efforts in the unsuitable landscape between these saline lakes, and provide opportunities to just focus upon known-to-be-occupied saline lakes, and those that might be potentially occupied in some years. This limited potential number of sites used has made previous studies possible (Haig and Oring 1988; Stenzel et al. 1994; Paton and Edwards 1996; Conway et al. 2005; Saalfeld et al. 2011; 2012a; 2012b; 2013a; 2013b). The potential SGP search areas for snowy plovers is narrow and this, coupled with advances in telemetry technology, may allow researchers to effectively monitor only specific areas.

There are numerous environmental and population-level factors that may influence the likelihood and degree to which an individual makes a movement (Greenwood 1980, Haig and Oring 1988, Stenzel et al. 1994, Clarke et al. 1997, Pearson and Colwell 2014). Given high nest failure rates (Saalfeld et al. 2011), spatially disjunct habitat distribution and weather stochasticity coinciding with a marginally male-biased sex ratio (Saalfeld 2013b), within-breeding season movements by SGP snowy plovers to

new locales for re-nesting is likely. Likewise, female snowy plovers may move farther and more frequently than males during the breeding season (Greenwood 1980, Stenzel et al. 1994, Paton and Edwards. 1996, Colwell et al. 2007), especially after nest failure. Although direct linkages between nest success or failure and post-breeding movements have not been found (Stenzel et al. 1994, Colwell et al. 2007), characterizing breeding connectivity of metapopulations, particularly those that may be population sinks, are critical to better define their current status and inform and develop appropriate recovery objectives (Eberhart-Phillips and Colwell 2014). It is also crucial to understand individual-level drivers for population viability, such as adult sex ratio, and their ramifications on survival and population growth when considering conservation strategies (Saalfeld et al. 2013, Eberhart-Phillips et al. 2017).

Certain abiotic conditions such as weather and photoperiod have been shown to affect the timing of an individual's departure from breeding grounds in various avian species (Dawson et al. 2001, Coppack and Pulido 2004, Deppe et al. 2015). Snowy plover movement and migration phenology have been studied on the Pacific coast and inland at Great Salt Lake (Stenzel et al. 1994, 2007, Paton 1995, Page et al. 2009), but relatively little is known about the SGP metapopulation, particularly at saline lakes in Texas and at Bitter Lake NWR, where migration behavior such as departure timing, sociality, and flight speed is unknown altogether. Determining migration phenology, and the factors affecting departures, may help researchers better understand the effects of climate change on snowy plover movements and their ramifications on regional persistence.

Methods for tracking individual bird movements are varied and differ in feasibility, cost and effectiveness for examining population connectivity. Although dramatic advances in transmitter technology have provided opportunities for examining movements of small migratory birds, snowy plovers remain on the margins of potential candidates for newer satellite transmitters (Barron et al. 2010). Additionally, CMR methods, while minimally invasive, are not always effective at marking enough individuals to obtain enough resighting or recapture data (Haig et al. 1998). The Motus network, however, has reduced transmitter mass and improved radio-tracking technology to make monitoring snowy plover movements possible (Taylor et al. 2017), particularly in the disjointed habitat distribution of the SGP, for which there is very little information relative to within-breeding season, or post-breeding movements.

Filling these information gaps can contribute to a suite of conservation management tools and objectives (eg., population dynamics/persistence models) as well as create a more robust understanding of snowy plover biology in the midcontinental U.S. Additionally, parameters gleaned from SGP snowy plover connectivity and population dynamics may help build population viability models. To address this, the Motus network was used at 6 sites on the SGP to track snowy plover individuals among breeding sites on the SGP and wintering sites on the Gulf coast. These data were combined with more traditional CMR techniques to monitor the spatial and temporal aspects of within- and outside of breeding season movements.

Methods

Study Sites

The SGP ecoregion encompasses > 96 million ha of semi-arid short- and mixed-grass prairie stretching north through Nebraska and includes the Southern High Plains (SHP) of Texas and New Mexico (Assal et al. 2015). This research was conducted at 6 saline lakes/alkali flats interspersed across the SGP of Texas, New Mexico and Oklahoma. Study sites included 3 privately owned saline lakes (designated as Lakes A, B and C) and Muleshoe National Wildlife Refuge (NWR) on the SGP of Texas; Bitter Lake NWR in eastern New Mexico; and Salt Plains NWR in north-central Oklahoma (Figure 1.1). Surface temperatures at SGP breeding habitats range from 7-54°C (Saalfeld et al. 2012b), with 73% of annual precipitation occurring from April through September, with 450-550 mm occurring on a west-east gradient (Haukos and Smith 1994, Heintzman et al. 2017, NOAA National Weather Service: http://www.srh.noaa.gov/). The landscape has strong, consistent winds and high evapotranspiration rates of > 200 cm/year (Reeves and Temple 1986, Rosen et al. 2013, Ashbaugh et al. 2018).

Texas

Approximately 40 saline lakes existed in the Texas SGP, historically fed by artesian freshwater springs (Brune 1981). The landscape is dominated by row-crop agriculture, with rangeland and mineral mining (caliche) activities occurring throughout the region (Brune 1981, Conway et al. 2005, Rosen et al. 2013). Most of the artesian springs in regional saline lakes have dried up due to mining of the Ogallala Aquifer for rowcrop irrigation, and currently < 10 lakes have actively flowing springs (Brune 1981, Rosen et al. 2013, Heintzman et al. 2017). The Ogallala Aquifer replenishes via

precipitation filtered through ephemeral wetlands (playas) in the region, and current recharge rates (estimated to be 0.25-25.0 mm/yr on irrigated cropland; Gurdak and Roe 2009) are far outpaced by depletion rates (Brune 1981, Haukos and Smith 1994). Thus, existing saline lakes now rely principally on precipitation runoff for surface water (Rosen et al. 2013, Heintzman et al. 2017). The lakes that remain are increasingly saline, and water levels fluctuate stochastically with precipitation within and among years (Andrei et al. 2008, Rosen et al. 2013, Heintzman et al. 2017, Ashbaughet al. 2018). Further, recent studies identify declining water quality as a consequence of increased salinity, elevated levels of total dissolved solids (TDS) and concentrations of Arsenic (As), Selenium (Se), Fluoride (Fl), sulfates, and perchlorates (Reeves and Temple 1986; Hudak 2009, 2010; Ashbaugh et al. 2018). Some of these naturally occur in the Ogallala Aquifer (Hudak 2010), although some may be of anthropogenic origin. For example, Hudak (2010) determined that the presence of As in 173 irrigation wells in the nearby Pecos Valley Aquifer was due to pesticide remnants from agricultural activity in the early to mid-20th century. During spring and fall avian migration, these saline lakes serve as stopover sites for shorebirds and waterfowl and provide winter habitat for sandhill cranes (*Antigone canadensis*) and, rarely, endangered whooping cranes (*Grus americana*, Conway et al. 2005, Andrei et al. 2008). During the breeding seasons, prominent nesting shorebirds include snowy plovers, American avocets (*Recurvirostra americana*), black-necked stilts (*Himantopus mexicanus*), and killdeer (*Charadrius vociferous*).

<div align="center">New Mexico</div>

The Bitter Lake NWR encompasses ~10,000 ha in eastern New Mexico and consists of managed wetland units, streams, sinkhole ponds, cropland, one saline lake and

desert uplands (MacRae et al. 2001, Roesler 2016). Bitter Lake is a shallow saline lake surrounded by salt flats and some salt marsh and is recharged via Salt Creek, Bitter Creek, artesian freshwater springs and precipitation runoff (Peterson and David 1998, MacRae et al. 2001). It provides habitat to several species of endemic plants and arthropods, some threatened and endangered (MacRae et al. 2001, Roesler 2016), and the refuge is year-round and stopover habitat for ~350 species of birds, as well as breeding habitat for snowy plovers, endangered interior least terns (*Sterna antillarum athalassos*), American avocets and others (U.S. Fish and Wildlife Service 2003). Wetland units are flooded seasonally to provide habitat for waterfowl and waterbirds (MacRae et al. 2001).

Oklahoma

The Salt Plains NWR was established in 1930 and currently encompasses ~12,900 ha (U.S. Fish and Wildlife Service 2002, Bonner 2008), including salt flats, salt marsh, ephemeral streams, some agriculture, a 4,000 ha reservoir and the Salt Fork of the Arkansas River (U.S. Fish and Wildlife Service 2002, Bonner 2008). The nearly 5,000 ha salt flats provide critical regional nesting habitat for snowy plovers, American avocets and interior least terns (U.S. Fish and Wildlife Service 2006). The Great Salt Plains Reservoir, created in 1941 with a dam of the Salt Fork of the Arkansas River, is shallow (average depth of 1.2 m) and is slowly filling with sediment from the Salt Fork (U.S. Fish and Wildlife Service 2002). It is expected to fill by 2050 (U.S. Fish and Wildlife Service 2002, Bonner 2008). Located on the eastern portion of the Central Flyway, Salt Plains NWR is a critical stopover site for migrating shorebirds and waterfowl and is breeding habitat for the second largest population of snowy plovers (~5000) in North America, second only to Great Salt Lake in Utah (Thomas et al. 2012). The Salt Plains NWR is

arguably the most important habitat for interior snowy plovers throughout the Great Plains.

Automated Telemetry Array

Prior to, and during, the 2017 snowy plover breeding season, 6 automated VHF telemetry towers, or Motus receiver stations (hereafter referred to as "SNPL towers"), were erected at study sites (Figure 1.1). As of 2017, there were $\geq$ 15 Motus towers on the Texas coast and > 300 stations across the Western Hemisphere (Taylor et al. 2017). The Motus towers on the Gulf coast provided migration connectivity data of snowy plovers on the SGP, contingent upon the birds' proximity to the coastal towers. Besides detecting snowy plovers, all towers were capable of detecting and recording the proximity of any Lotek nanotag in the network and were capable of contributing data to other Motus projects (see www.motus.org for tower locations).

Each receiver station in this study was ~30 m tall, fitted with three 9-element or 5-element Yagi antennae (Figure 2.1). The 9-element antennae system was considered to have a greater detection radius and was originally used at larger sites (Lake B, Salt Plains NWR). However, poor detection rates (of individual plovers known to be in close proximity to towers) in 2017 led to the replacement of all but two 9-element Yagi antennae at Salt Plains NWR by 5-element antennae. These modifications were made in consultation with Lotek engineers (see below), who reported the transmitters used on snowy plovers work better with 5-element antennae, which have a greater depth of detection and detect birds on the ground at a much greater rate than do the 9-element systems. Specifically, 1 9-element antenna at Salt Plains was removed and was replaced by 2 5-element antennae. On the tower at Lake A, all 3 9-element antennae were replaced

by 3 5-element antennae. All of these modifications were completed prior to the beginning of the 2018 breeding season.

At the base of each tower were a data-logger and a solar-powered battery (Renogy 100-Watt, 12 Volts Monocrystalline Solar Panel; AMG 12 Volt battery). Each "Sensorgnome" (SG; https://sensorgnome.org/) data-logger was placed in a weather-proof tub with the battery (Figure 2.2). Each SG was comprised of 3-4 radio receivers (Funcube Dongles), a computer (Beaglebone Black, or RaspberryPi model), a 32 GB micro SD card and a GPS that provided a tower location and precise timestamps for each detection (Figure 2.3). The receivers were connected by ~12 m of RG-58 coaxial cables to the Yagi antennae, each of which had an individual coaxial cable connection. The solar panel, battery and data-logger were all wired through a charge-controller (SunSaver 6L), which opened and closed the circuit to the data-logger in the event of a low battery. This prevented the SG from shutting down completely and not turning back on, particularly during long periods of low sunlight (Figure 2.2). The radio receivers detected VHF signals from each nanotag transmitter (Model ANTC-M-3 or NTQB-4-2S, www.lotek.com) attached to adult snowy plovers within range (≤ 20 km; Taylor et al. 2017). The SG-computer recorded these detections on the 32 GB SD card.

Capture

Nest searching occurred during surveys and dedicated search times to locate snowy plover nests on all study sites. Once nests were discovered, they were marked using a GPS unit, and clutch size and age were recorded. Eggs were aged using an egg floatation chart created for Kentish plovers (Székely et al. 2008; see Chapter I). After the maximum clutch size had been laid, bownets (Conway and Smith 2000, Duffie 2017,

Ashbaugh et al. 2018) were used to capture both male and female adult snowy plovers.

Nestlings were captured by hand (Conway et al. 2004). Once captured, a USGS

aluminum band (size 1P) and a unique combination of color bands were attached to each

plover following established protocols (Saalfeld et al. 2011, Duffie 2017¸ Ashbaugh et al.

2018). After banding, the following data were collected: mass (g), wing chord (mm for

all other linear measures), tarsus length, tail length, culmen length, forehead patch width,

parasite load (defined as None, Low, Medium or High) and molt (location – head, body,

primaries or tail—and feather designation, if a primary or rectrix). All snowy plovers

were captured and handled according to approved institutional animal care and use

protocols (Texas Tech University IACUC 15035-05; 18049-06 and T18049), state

scientific permits (Texas Parks and Wildlife Department SPR-0413-039; New Mexico

Department of Game and Fish 3558; Oklahoma Department of Wildlife Conservation

7104 and 7411), and the USGS Bird Banding Laboratory Master Banding Permit

(Number 23393).

Avian Nanotags

The Lotek nanotag transmitters (NTQB-4-2S, ANTC-3-M) were set to a 24-h, 10

sec burst rate designed to last an estimated 124-344 days once activated (depending on

nanotag model, burst rate and on/off programming; longer-lasting tags were used later in

the season to increase chance of return spring detections). Each Lotek nanotag

transmitted the same frequency (166.380 MHz) and could be detected on any VHF Motus

telemetry tower, and each nanotag had a uniquely coded identifier that was recorded and

registered with the network before deployment. Tags were attached using a leg-loop

harness method (Rappole and Tipton 1991, Sanzenbacher et al. 2000, Streby et al. 2015).

Harnesses were made of flexible beading thread and sewn into a figure-eight shape, where at the intersection of the strands, the (inactivated) transmitters were glued with super glue gel (Figure 2.4). Transmitters were activated just prior to attachment using a Lotek infrared activator (Figure 2.5), which can turn the tag on or off repeatedly as desired. Each harness was approximately 50-51 mm long from (flattened) loop tip to tip, and was designed to have 1-2 mm space between it and the bird, with slight movement felt if moving the transmitter from side-to-side. If the harness was too tight, it was promptly removed and the bird released, however this was a very rare occurrence.

Data Analysis

Tower detection data were downloaded on-site to a laptop computer at least monthly during the breeding season, bi-monthly pre- and post-breeding seasons, and once from October-February. These data were downloaded by either connecting directly via a USB cable, turning off the Sensorgnome, removing the microSD chip and inserting the chip into the laptop, or via a Wi-Fi server connection (RaspberryPi models only). Data were later uploaded to the Motus network database for processing. Processed data were downloaded using program R (package *motus* version 1.0.0) and cleaned/organized using package *tidyverse* (version 1.2.1) and code from *Motus R Book* (version 1.0; Crew et al. 2018).

All Motus detections were filtered using a run length ≥ 3, where "runLen" was the number of times that a tagged snowy plover was continuously and sequentially detected on a tower. For detections at study-site specific SNPL towers, a runLen of 2 was conditionally accepted. False detections (very rarely occurring at a runLen > 2) on the Motus Wildlife Tracking Network are common, particularly at "noisy" towers, which

tend to occur in areas of high electromagnetic activity where filtering software was more likely to falsely identify a tag's signal where it did not exist (Taylor et al 2017). Additionally, "noisy" tags are more likely to be falsely detected than normal tags at any tower (including, and most tellingly, at towers where snowy plovers do not occur), perhaps because their signal was more commonly misidentified by detection software. False detections were common, and all detections were filtered on a case-by-case basis using runLen, whether a tag was detected on a noisy tower or whether an individual tag was noisy. Some final screening of detections was also based on natural distribution (i.e., detections in areas where snowy plovers are rare or do not occur were omitted if runLen was < 2) and flight speed of snowy plovers. All detections were filtered using recommended Motus protocols (Crewe et al. 2018), and a conservative approach was employed, where any questionable detection was omitted from analysis to maintain data quality.

Once all Motus detections were screened and identified as "positive" (not false, as described above) individual bird identifiers, location and date of detection were compiled for each bird. Using these detection data, "departure date" (DD), defined as the ordinal date (number of days since 1 Jan) that a tagged snowy plover was last detected in a given year on a SNPL tower, was determined to provide insight relative to the initiation of fall migration. As all plovers marked during this research were captured and affixed with a nanotag during the breeding season, the first germane element of connectivity was focused upon this post-breeding, fall migration departure date. As such, DD was modeled using a zero-inflated Poisson distribution (R package *pscl* 1.5.2; Yau et al. 2003). Model fit was verified using a Chi-square Goodness of Fit Test (R package *MASS* 7.3-50). To

confirm that a zero-inflated Poisson distribution was a superior model to a Poisson distribution, a Vuong Non-nested Hypothesis Test was used (R package *pscl*1.5.2).

For analysis of DD, birds whose tag was detected only 1-2 times were removed from the model to ensure the bird was being sufficiently and continually detected to accurately estimate DD. The following suite of potentially relevant abiotic covariates that might influence DD were included in these models: temperature (T), 24-Hour % temperature change, or the percent change in temperature between the previous day and the day of departure (TC), relative humidity (RH), dew point (DP), wind speed (WS), and photoperiod (P). Weather data were obtained from the National Weather Service (NWS) Automated Surface Observing Systems (ASOS) data via the Iowa State University Environmental Mesonet (https://mesonet.agron.iastate.edu/request/download.phtml) and were averaged over 24-hour units and correlated to the day of departure. These weather covariate data were extracted from the closest airport to the departure site study areas – Lubbock International Airport (LBB) for Texas saline lakes, Roswell Industrial Air Center (ROW) for Bitter Lake NWR and Vance Air Force Base (END) for Salt Plains NWR. All weather data were constrained to 11 May – 30 Sept to exclude environmental conditions that would not affect departure decisions of snowy plovers. These dates were chosen using the estimated date of termination of the first observed nesting attempt (11 May) and the date of last detection by a snowy plover within what was deemed a reasonable outer-range for migration (30 September). These covariates were examined for multicollinearity, where RH and DP had Variance Inflation Factors (VIF) of >5. As RH has been used as a predictor variable in other studies (Deppe et al. 2015), DP was removed from subsequent models (R 1.0.143 package *mctest* 1.2; Sheather 2009).

A two-way analysis of variance (ANOVA) was used to examine differences in DD between sexes and among sites (OK, TX and NM). Simple linear regression was used to examine DsFate and DD, where DsFate was defined as the time interval (in days) between the termination of a breeding attempt and DD (breeding/nesting attempts may terminate due to nest success or failure). DsFate was estimated using one of the following methods, depending on a combination of criteria for each nest associated with a tagged snowy plover: (1) hatch date, which was calculated by floating eggs and assuming an average 26 days of incubation (Kosztolanyi et al. 2007) or (2) nest failure date. Nests were checked as often as possible but always > 3 days apart to minimize disturbance, and spaced out temporally to provide a more precise estimate of nest fate (success or failure). Nests at Bitter Lake NWR were visited less frequently than other sites due to logistical issues, so those nests were often only checked once after discovery.

Departure times (DT, or the hour of last detection on DD) were defined as the beginning of the last flight detected, which can be identified as follows: when a marked bird flies by a tower, transmitter signal begins as "weak", becomes stronger, and then weakens again, creating a signal arc (Figure 2.6). Using this signal strength plot, the time when a bird began its last flight, or at the beginning of this arc, is when the bird was deemed to have begun its last detected flight. As with DD, birds were excluded if they were only detected 1-2 times on a tower. Because time are circular data, departure times were analyzed using directional statistics (R package *circular* 0.4-93). A Rayleigh Test of Uniformity was used to examine if there was significant unimodal directionality, or if DTs were randomly distributed over 24 hours (Fisher 1995). A Watson Two-Sample Test

of Homogeneity was used to determine if two samples significantly differed (Watson and Williams 1956). Differences in DT by site (TX, NM and OK) and sex were examined.

Results

Among all study areas, 38 male and 178 female adult snowy plovers were captured in 2017 and 2018. Of these 216 adults, 119 nanotag transmitters were deployed on 99 females and 20 males (Table 2.1). All but 11 tagged snowy plovers were detected at least once (of these 11, all were from Salt Plains NWR; 2 of these undetected snowy plovers were, however, resighted at Salt Plains NWR after marking there; Table 2.2). Of all snowy plovers that were tagged, 9% were never detected on a tower, 38% were detected <10 times, 42% were detected ≥10 times, and 11% >1000 times. There were ~46,000 detections of 108 tagged snowy plovers in total.

Within-breeding Season Movements

During this study, 21 individual snowy plovers (3 males and 19 females) made at least 1 within-breeding season movement between 2 towers (a SNPL or non-SNPL/coastal tower), and 2 untagged birds made a similar among/between study area movement, detected by resighting those individuals using color band combinations (Table 2.3, Figure 2.7). Within-breeding season movements were made to and from Lakes A, B, C and Bitter Lake NWR (Figure 2.7). No individuals were known to make a movement to Salt Plains NWR or to Muleshoe NWR from other study areas (Figure 2.8). The Muleshoe NWR tower was erected in September 2017 and experienced a blackout period from mid-July 2018 to mid-August 2018 that may have precluded detections. However, very few individual snowy plovers have been observed at Muleshoe NWR during the last several years of monitoring (Duffie 2017, Ashbaugh et al. 2018). Of the 19

females that made movements, 14 made 34 detected movements between SNPL towers during the breeding season, but there was no confirmed "renesting" for any of these individuals at a different study site locale. Despite an increase in the female movement sex ratio from 0.82 to 0.91, females did not make more movements (breeding season or migration) than expected given the sex ratio of tagged snowy plovers ($\chi^2 = 0.59$, df = 1, *P* = 0.442; Figure 2.9). The average within-breeding distance flown by a female was 39 km (range:13-218 km; Table 2.4). In contrast, 3 males made 6 within-breeding season movements between Texas lakes, with an average distance of 13 km (range:13-26 km; Table 2.4). Of note, a single adult female, marked at Bitter Lake NWR, made the longest within-breeding season movement, after or near the terminus of a breeding attempt on 9 July 2018, from Bitter Lake NWR to Lake B and back (436 km) within the span of 7 hours (~62 km/hour, given the bird flew from tower-to-tower; Figure 2.7). No known re-nesting attempts at different lakes within the same breeding season were verified for any male or female. However, it is possible that an attempt may have occurred without our knowledge due to the time intervals between site visits. Likewise, no snowy plover was found re-nesting at another lake other than their natal site or where they were first captured. Furthermore, all tagged snowy plovers that were detected on a SNPL tower or resighted in the season following their initial capture returned to their site of capture. The only exception was a breeding female captured (while incubating) at Salt Plains NWR in 2014 that was resighted in 2018 nesting on Mustang Island on the Texas coast.

Non-breeding season movements

Outside of the breeding season, 5 female and 2 male snowy plovers made movements from Salt Plains NWR to 6 Texas coastal towers and 1 Louisiana coastal

tower between 8 July and 13 October. Also, one male banded on 24 May 2018 at Salt Plains NWR was detected briefly on 8 July 2018 at Lake A, presumably during migration. In one instance, a male from Salt Plains NWR engaged in a direct flight 871 km to San Bernard NWR in 14 hours on 31 July 2018, again approximately 62 km/hour (tower-to-tower). A female, also captured at Salt Plains NWR, flew to Matagorda Bay in 37 hours from 23-24 July 2018, ~25 km/hour. In total, including resighted birds, 7 snowy plovers were detected on the 270 km stretch between Aransas NWR, Texas to Holly Beach in southern Louisiana (Figure 2.7). No snowy plovers from Bitter Lake NWR or the Texas saline lakes were detected on any of the 6 towers erected for this project (i.e., no known migration movement was detected).

Overall, Motus telemetry towers were successful at detecting snowy plover movements among known towers on breeding season locations on the SGP, although there were some differences in how individual towers detected marked plovers during this study. Specifically, detections were strongly dependent upon the proximity of tagged snowy plovers to the tower, the antenna type used and the terrain of the surrounding area. For example, towers equipped with 5-element antennae instead of 9-element antennae increased snowy plover detections within close range (within 500 m) of the tower. For example, at Salt Plains NWR, the 9-element antennae were replaced with 5-element antennae and detection rates improved dramatically within the same day (Figure 2.10). Relative to the position of the tower on the landscape, the tower at Lake B appears to have been most ideally placed due to it being centrally in the saline lake and also being relatively close (< 1 km) from most snowy plover nesting activity (Figure 2.11). For example, 13 tagged snowy plovers were detected between 1,000-11,000 times, and all of

these detections occurred at Lake B. In total, 43,015 detections out of 45,959 occurred at

Lake B, roughly 94%, from 2017-2018. This is likely because this tower was ideally

situated on a berm between and among several active springs, nesting and foraging areas

of snowy plovers. This also positioned the tower within the "bowl" of the lake as opposed

to on a ridge surrounding the lake where all other towers except Salt Plains NWR were

placed (Figure 2.11). This was made possible by a caliche berm that extend toward the

center of the lake, which provided a solid foundation upon which to put the tower.

Additionally, this berm was easily accessible for set-up and maintenance. The number of

detections at Salt Plains NWR, Bitter Lake NWR, Lake A and Lake C ranged from 565-

986 in 2017 and 2018 for a total of ~3,000. There were no snowy plovers detected at

Muleshoe NWR, but it is important to note there were no snowy plovers tagged at

Muleshoe NWR, which likely impacted detection rates.

Formal Analyses

Photoperiod and wind speed influenced DD of snowy plovers at all sites between

11 May and 30 September 2017 and 2018 (Table 2.5). Greater wind speeds were

negatively correlated with the likelihood of a departure ($z_{1,284}$=-3.09, $P < 0.001$) whereas

longer photoperiods were positively associated with the probability of a departure ($z_{1,284}$

$= 2.50$, $P = 0.012$). The average calendar day of departure was 29 July for all sites but

ranged from 1 June and 20 November. Departure dates did not vary between sexes ($F_{1, 98}$

$= 0.11$, $P = 0.740$) nor sites ($F_{1, 98} = 1.97$, $P = 0.130$; Table 2.6). The DsFate, or days it

took a snowy plover to depart after a nest fate was known, ranged from 0-143 days, with

a mean of 57 days between nest fate and departure. DsFate and the ordinal date of nest

fate were weakly correlated ($t_{1,115} = -5.63$, $P < 0.001$, $R^2_{adj} = 0.21$; Figure 2.12),

showing that plovers were more likely to leave sooner after a nesting attempt later in the season.

The circular mean of DT (the hour of last detections) for tagged snowy plovers was ~21:00 and exhibited directionality (i.e., were not random in distribution; Figure 2.13). Birds departing the Bitter Lake area did not exhibit directionality ($z_{12} = 0.357$, $P = 0.220$), but there were unimodal distributions for Texas birds ($z_{32} = 0.617$, $P < 0.001$) and birds from Salt Plains NWR ($z_{26} = 0.362$, $P = 0.031$; Figure 2.14), and DTs were similar between Oklahoma and Texas birds ($U^2_{26, 32} = 0.140$, $P > 0.05$). The DTs of males were uniform in distribution ($z_{11} = 0.507$, $P = 0.056$), although female DTs showed a distinct unimodal distribution with a mean of ~21:00 hours ($z_{59} = 0.456$, $P < 0.001$). Male and female departure times were similar ($U^2 = 0.081$, $P > 0.05$; Figure 2.15).

Discussion

Breeding Season Movements

Results from multiple snowy plover population dynamics and population genetics studies show high levels of population connectivity of snowy plovers (Stenzel et al. 1994, Funk et al. 2007, Küpper et al. 2009, D'Urban Jackson et al. 2017). Long-distance (>800 km) breeding movements of females have been documented in coastal snowy plovers (Stenzel et al. 1994), and multiple studies have analyzed microsatellites to conclude that North American snowy plovers are panmictic (Funk et al. 2007, Küpper et al. 2009), although a recent study proposes that Atlantic snowy plovers may be genetically isolated (D'Urban Jackson et al. 2017). Both polygamy and monogamy have been reported in snowy plovers, but it is generally agreed that long-distance breeding movements of females is likely a result of snowy plovers' breeding strategy of polygamy, or more

specifically, sequential polyandry (Stenzel et al. 1994, D'Urban Jackson et al. 2017, Eberhart-Phillips et al. 2017). Similar to Jackson et al (2017), results from this study on the SGP may indicate that North American snowy plover populations may be less panmictic than previously reported (Funk et al. 2007). However, these above referenced studies dramatically under-sampled (Funk et al. 2007 included only samples from Salt Plains NWR from the SGP region) or left out entirely (Kupper et al. 2009) snowy plover samples from the SGP.

It is clear from this research that there are instances of long-distance breeding movements by females captured in the SGP, but very limited connectivity (only one instance) among breeding snowy plovers in the SGP Texas and those in New Mexico. Also, it appears that Salt Plains NWR snowy plovers are not as linked to Texas and New Mexico as predicted based upon these aforementioned previous studies (Funk et al. 2007, Küpper et al. 2009). No snowy plovers flew to Salt Plains NWR from any of the Texas saline lakes or Bitter Lake NWR, and only one snowy plover from Salt Plains NWR flew briefly near Lake A, presumably on migration considering the time of year and brevity of detection (see Figure 2.8). Therefore, it is possible that breeding snowy plover subpopulations existing in the SGP are somewhat genetically divergent among the Texas, New Mexico and Oklahoma subpopulations, with Texas and New Mexico snowy plovers potentially comprising a quasi-isolated population (Figure 2.16). Clearly – this research provides the best evidence to date relative to regional (SGP) (dis)connectivity among breeding snowy plovers in the SGP of Texas and New Mexico, and those on Salt Plains NWR. However, these movement patterns (or lack thereof relative to Salt Plains NWR) provide a strong foundation to more closely examine finer scale population genetic

structuring among these SGP populations and its potential impacts upon SGP population dynamics and trends (see Chapter I). This is particularly germane in light of recent findings that indicate relatively high levels of genetic diversity exists in SGP (Texas) snowy plovers (Conway et al. unpublished data) which suggests high, not low, connectivity among those subpopulations in the past. This suggests this study's findings of apparent low connectivity may reflect recent isolation, and may be important when developing or building population models aimed at regional conservation.

Tangential to the study of population connectivity and long-distance breeding movements is snowy plovers' inclination for site fidelity. Snowy plovers are often described in the literature as strongly philopatric (Stenzel et al. 1994, Paton and Edwards 1996, Page et al. 2009), males more so than females (Stenzel et al. 1994, Paton 1995, Page et al. 2009). This behavioral trait appears to be supported on the SGP, where 26% (n = 10) of males banded in 2017 were resighted in the same location in 2018, compared to only 13% of females (n = 24), although this may reflect differences in survival rather than, or on combination with, philopatry. In contrast some individuals, particularly females, do have the ability or behavioral plasticity to nest in widely disparate locations. On the SGP, for instance, a breeding female captured at Salt Plains NWR in 2014 was resighted 4 years later nesting on Mustang Island on the coast of Texas, a distance of roughly 1000 km between known nesting sites for this individual female. The frequency in which this behavioral plasticity occurs remains unknown, but does indicate some level of connectivity between Salt Plains NWR and the Texas coast rather than Salt Plains NWR and breeding habitats on the SGP of Texas or New Mexico. Conversely, individual adult snowy plovers from SGP breeding habitats have been documented to nest mere

meters away from their natal nest site nearly 10 years later (Saalfeld et al. 2012a), and early efforts on snowy plovers in the SGP of Texas indicated tremendous inter-year philopatry, which seems to have decayed with parallel population declines (see Chapter I). For example, Conway (2001) documented 17 individual snowy plovers (8 females, 9 males verified by molecular sex determination; see Conway et al. 2004) out of 78 individuals that were banded on Lake A or Lake B as nestlings in 1999 and returned as nesting/incubating adults in 2000 to those same lakes. Similarly, during the same period, 72 individual adult snowy plovers (47 female; 25 male) out of 125 individuals that were banded as adults in 1999 were observed in 2000 at those same two Lake A and Lake B study sites (Conway 2001). Clearly, this research occurred when local populations were at the highest recorded in the last 20 years (see Chapter I), used resighting data rather than any automated telemetry system and the level of documented philopatry has either declined, over-winter survival has been poor and negatively impacted resighting probabilities (see Chapter I), or this philopatry has not been "captured" during the last several years of research (see Saalfeld et al. 2011, Duffie 2017, Ashbaugh et al. 2018).

This variety in philopatry, and documented disparity in within- and among-season movements suggests a wide range of strategies by snowy plovers, a phenomenon labeled "bimodal dispersal," where different individuals in a population vary in their tendency to move short or long distances, or one individual in a population varies in vagility year-to-year (Wiens 1976). Fittingly, Paton and Edwards (1996) found that snowy plovers nesting at Great Salt Lake exhibited 4 different patterns of within breeding season movements that ranged from high to low philopatry depending upon sex, the previous years' nest success, the previous years' nest density and available nesting habitat. Males

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were more likely to exhibit site fidelity than females, but Paton and Edwards (1996) also documented a wide range of within-breeding season movements, as did Stenzel et al. (1994). Haig and Oring (1988) found similar patterns of variable site fidelity in piping plovers (*Charadrius melodus*), although no difference between sexes, and only intra-annual movements were noted. Each strategy provides advantages to individual birds based upon different environmental conditions, where philopatric individuals benefit by taking advantage of known successful breeding grounds and vagile individuals benefit by following favorable habitat on a variable landscape (Wiens 1976). It makes sense for individuals within a population to employ different behaviors, as vagile individuals (in this case, likely snowy plover females) may facilitate gene flow and thus help prevent a population from extinction in times of extreme selection pressure or inbreeding. Snowy plovers likely use this same strategy to both take advantage of isolated habitat patches but cushion themselves from environmental stochasticity and potential extinction.

Tagged snowy plovers in this study moved between 15 km to > 200 km within the breeding season among isolated habitat patches. Causes of these movements remain unknown, and some of these movements may have been followed by another breeding attempt within the same season at the new locale, but this cannot be verified. These may also have been foraging expeditions designed to take best advantage of variable habitat quality if foraging opportunities decline after some breeding failures (Paton and Edwards 1996, Haig et al. 1998). Regardless, this confirmed connectivity and within-breeding season movement among breeding locales in the SGP is noteworthy. As mentioned before, it has been suggested that snowy plovers' vagility on the Pacific coast is due to a sequential polyandous breeding strategy and stochastic habitat conditions (Stenzel et al.

1994), a scenario that they are exploiting to potentially maximize breeding potential by finding and renesting at the highest-quality habitat available on a variable landscape. Habitat on the SGP is similarly characterized as changeable, so similar behavior seen in this study is not surprising. Males did not exhibit the same degree of movement as females in this study, further supporting the potential for sequential polyandry behavior strategy in SGP snowy plovers similar to those described on the Pacific coast (Stenzel et al. 1994, 2011; Page et al. 2009). Despite this, sequential polyandry has not been exclusively described in SGP subpopulations, and some monogamy has been documented (Boyd 1972; Conway pers. comm.). Moreover, Saalfeld et al. (2013b) revealed an offspring sex ratio of near parity, a parameter which would not necessarily favor a female-biased breeding strategy over monogamy. Thus, further investigation of SGP snowy plover breeding strategies and their subsequent effect on breeding-season movements and overall population connectivity is warranted.

Population Dynamics

Hanski (1999) states that the theory of metapopulations "is of the greatest value when applied to species living in physically patchy environments." Additionally, Haig (1998) stressed the importance of studying wetland connectivity, particularly for highly mobile species like shorebirds, due to the inherent disjunct distribution of wetlands and a lack of research on large-scale spatiotemporal movements among them. Snowy plover subpopulations on the SGP range in size from > 5,000 individuals to < 30, and exist in isolated breeding locales, 13 – 600 km apart. Demonstrated connectivity in this study, coincident with discrete habitat patches across a large region, suggests that given the population connectivity described herein, metapopulation dynamics likely exist for SGP

snowy plover populations and may be a major driver in regional persistence – particularly as related to the disconnectivity between Salt Plains NWR plovers, and those breeding in the SGP of Texas and New Mexico. Knowledge of these dynamics is key to creating spatially explicit models of the regional population dynamics that may help uncover, or describe persistence probabilities of inland snowy plovers as exemplified in other studies (Haig et al. 1998, Plissner and Haig 2000, Eberhart-Phillips and Colwell 2014).

In terms of habitat importance, Lake B appears to be regionally significant to SGP snowy plovers, as nearly half of breeding season movements detected during this study were made to Lake B from other locales (Figure 2.17). Regional saline lakes have been observed to annually fluctuate in water depth, often containing more water during winter when precipitation is generally low (Rosen et al. 2013, Heintzman et al. 2017). This suggests that water levels are not necessarily a result of precipitation, but correlate strongly with irrigation pumping for row-crop agriculture, the usage of which is greatest during summer (Rosen et al. 2013). These negative effects of irrigation pumping on water and salinity levels are likely exacerbated by high summer temperatures and evapotranspiration rates (Saalfeld et al. 2012*b*, Rosen et al. 2013, Heintzman et al. 2017, Ashbaugh et al. 2018). Springs at Lake B are primarily seeps and pools, and despite irrigation pumping in the area, remained flowing during both 2017 and 2018 breeding seasons. In contrast, some or all springs at Lakes A, C, Muleshoe NWR and Bitter Lake NWR diminished greatly or stopped flowing altogether in both years of this study and were entirely reliant upon precipitation for surface water. Lake B appears to maintain at least some water surface availability more reliably than surrounding saline lakes, which may drive snowy plover use and consistent occupancy. Paton and Edwards (1996) also

suggested that snowy plover chicks may have a reduced tolerance for highly saline water. Thus adults may select habitats with fresh water sources (artesian springs) over surface water created by precipitation runoff as better quality habitat to raise offspring – potentially driving occupancy at lakes such as Lake B. Spring flow is not a primary driver of population size, however. For example, Lake A saw much greater flows from 2017 to 2018 after a large area of saltcedar at the base of a flowing spring was sprayed with herbicide; but still suffered a 50% population decline between years (see Chapter I) and there were few movements to Lake A as compared to Lake B. Finally, Lake B may have attracted more movements due its location between Lakes A and B, although this does not explain why a female snowy plover from Bitter Lake NWR flew to Lake B and not Lake C which was closer.

Due to its consistent freshwater inflows via seeps and pools, Lake B may exist as higher quality habitat for regional breeding snowy plovers. This may also be a result of its location relative to other saline lakes. It is important to consider, however, that the tower at Lake B was responsible for nearly 93% of detections on all towers. Most of these were resident breeding birds captured at Lake B, in close proximity to the tower and almost continuously detected. It does raise the question, though, of whether or not the tower at Lake B had superior detectability and was thus better at detecting the movements of non-resident birds. This could, at least in part, explain why more birds were detected moving to Lake B than to other sites.

Migration

Shorebirds typically fly at high altitudes during both nocturnal and diurnal migrations (Kerlinger and Moore 1989, Mabee and Cooper 2004). Although this research

was not focused upon estimating the altitude of snowy plover migration flights, it is clear

that snowy plovers are nocturnal migrants departing ~21:00 hours local time and reaching

speeds of ≥ 60 km/hr (the consistency of 2 long-distance movement speeds, both 62

km/hour, may suggest this is a typical long-distance flight speed for snowy plovers).

Most avian species—and likely snowy plovers—that migrate at night do so at high

altitudes (≥ 500 m; Mabee and Cooper 2004, Kerlinger 2008). Furthermore, it appears

that SGP snowy plovers are more likely to depart sooner after a nesting attempt

failure/success as the season progresses, which is intuitive. As the breeding season

wanes, there are fewer opportunities to breed and the benefits of staying on breeding

grounds may no longer outweigh the costs of departing. Therefore it makes sense for a

plover to migrate if conditions are good rather than stick around without any chance to

breed.

Regarding migration initiation, snowy plover departure dates were widespread

across the mid-to-late breeding season, suggesting that adults on the SGP may not

migrate socially, at least not in large groups seen in other shorebird species such as the

red knot (*Calidris canutus*) or sanderling (*Calidris alba*). From what is known about

Charadrius migration sociality, it appears that plover species run the gamut of strategies,

from highly social like the semipalmated plover (*Charadrius semipalmatus*), which can

occur in flocks > 30,000 individuals at a staging site on southward migration, to less-

social migrants that move in small flocks (3-6 individuals), such as piping and snowy

plovers (Conklin 2019). Large staging flocks do not necessarily correlate with large

migrating flocks, and even members of large flocks at stopover sites migrate in in small

groups (5-60 individuals; Conklin 2019). One possible explanation for non-social

migration behavior is that shorebirds that migrate across inland North America tend to encounter more variable habitat (regardless of season), both in quality and location, than do coastal migrating shorebirds (Colwell 2010). As a result, inland shorebirds perhaps employ more variable or plastic migration strategies and behaviors, with opportunistic use of stopover sites, than do coastal migrant shorebirds that rely upon highly predictable food sources (see Andres et al. 2012). Unsurprisingly, it appears that SGP snowy plovers, subject to highly stochastic weather conditions and habitat quality at breeding and stopover sites, would likely benefit from more opportunistic, plastic migration patterns. Conklin (2019) in fact postulated that short-distance migrants (like snowy plovers) may not migrate with temporal or behavioral consistency from year-to-year and that coastal, in contrast to long-distance migrants that tend to aggregate at stopover locations in large flocks and migrate with temporal consistency.

Although this study did reveal new aspects of SGP snowy plover movements and migrations, nothing is known about the migration of Bitter Lake NWR snowy plovers and little of those in from the SGP of Texas. In light of recent and significant declines (see Chapter I) it is imperative that further research be done to fill this information gap. There is an increasing call for more complete, annual-cycle studies on avian species (Haig et al. 1997, Ådahl et al. 2006, Marra et al. 2015, Woodworth 2017) and the plight of Bitter Lake NWR and SGP Texas snowy plovers is a seminal example of why this is vital. Although declines may be linked to multiple factors including heavy metal contamination, decreased availability of surface water and increased predation rates to name a few, overwinter survival and locations of currently unknown winter grounds will exert important roles in regional snowy plover population persistence and structuring.

Overall, Motus tower technology was a valuable tool to discern the movements of snowy plovers across the SGP. Females moved farther and more often than males, a behavior attributed in other snowy plover populations to a breeding strategy of sequential polyandry (Stenzel et al. 1994, 2011). No re-nesting attempts were discovered after a movement event, though some may have gone undetected. Furthermore, new aspects of snowy plover biology were discovered. Snowy plovers, at least on the SGP, appear to favor nocturnal migrations. Also, straight flights of up to 62 km/hr to winter grounds were detected, although whether or not these sites were the terminus of their migration is unknown. Other snowy plovers appear to have traveled slower, possibly using wetland stopover sites on the way. Finally, weather conditions unsurprisingly influenced the departure times of migrating snowy plovers

Despite these advances in knowledge of SGP snowy plovers, a scarcity of data still exists. The advent of store-on-board and satellite technology are promising new paths, and with time should become the method to monitor these birds' movements. Automated telemetry is valuable when habitat patches are known, however in terms of unidentified migration pathways and winter habitat, they tell us little. Population declines in SGP snowy plovers highlight the need to discover these areas and hopefully discern both the causes and the solutions to these patterns of disappearance.

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Figure 2.1. Automated Motus telemetry tower with 9-element antennae and a 100 Watt solar panel.
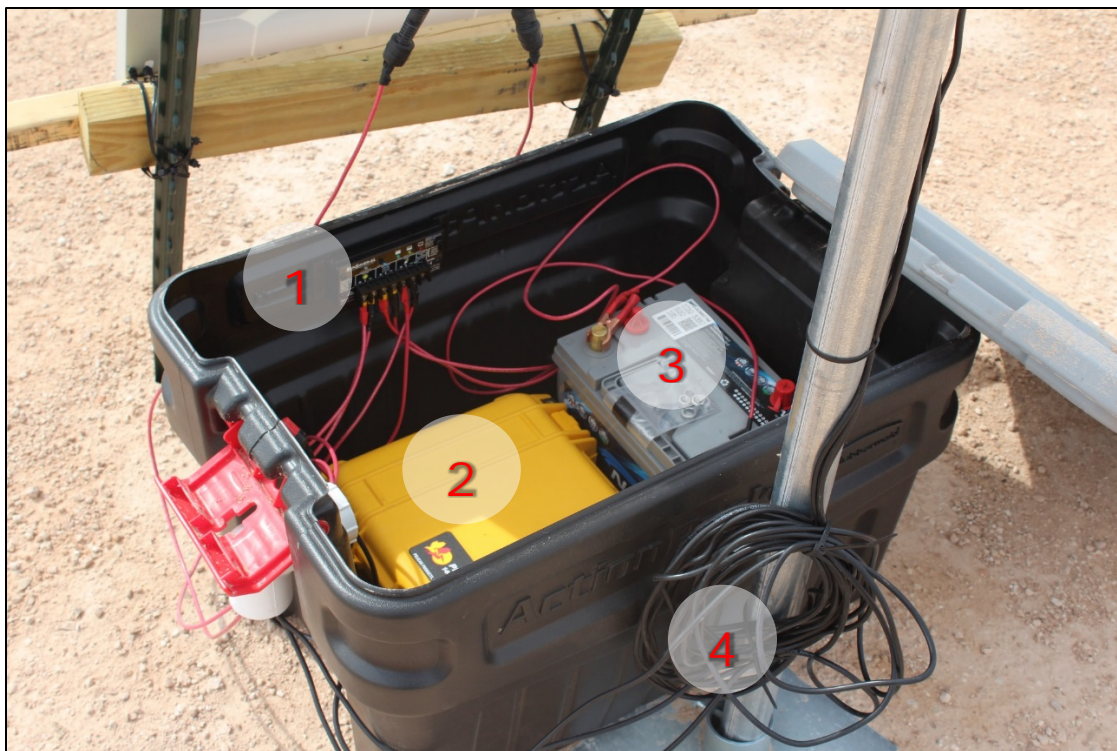
Figure 2.2. External components of a Motus tower: (1) Sunsaver Charge Controller for regulating power from the solar panel and battery to the computer components, (2) Pelican case containing the internal components of a Sensorgnome, (3) 12V battery attached to the charge controller and (4) the coaxial cables that connect the receivers inside the Sensorgnome pelican case to the antennae on top of the tower.
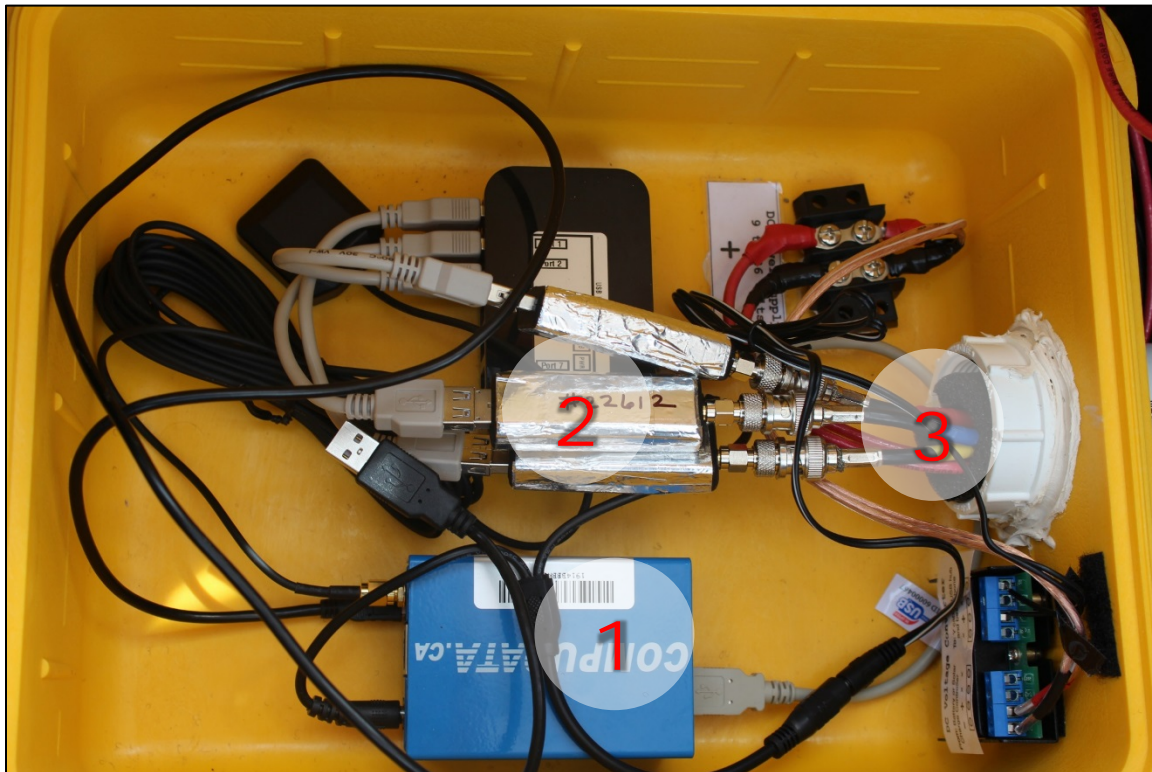
Figure 2.3. Internal computer and electronic components of a Sensorgnome: (1) Beaglebone or RaspberryPi computer with microSD chip, (2) 3xFuncube Dongle receivers and (3) 3xCoaxial cables that connect to antennae on top of the tower.

Figure 2.4. Leg-loop harnesses made of white elastic beading string, tied in a figure-eight by cotton sewing thread and glued to Lotek avian nanotag ANTC model transmitters with a small (4x4 mm) square of foam glued to the bottom to cushion the bird's back from the transmitter (top); snowy plover wearing a leg loop harness and an attached NTQB model transmitter (bottom).

Figure 2.5. Avian nanotag infrared activator that turns the transmitter signal on and off.
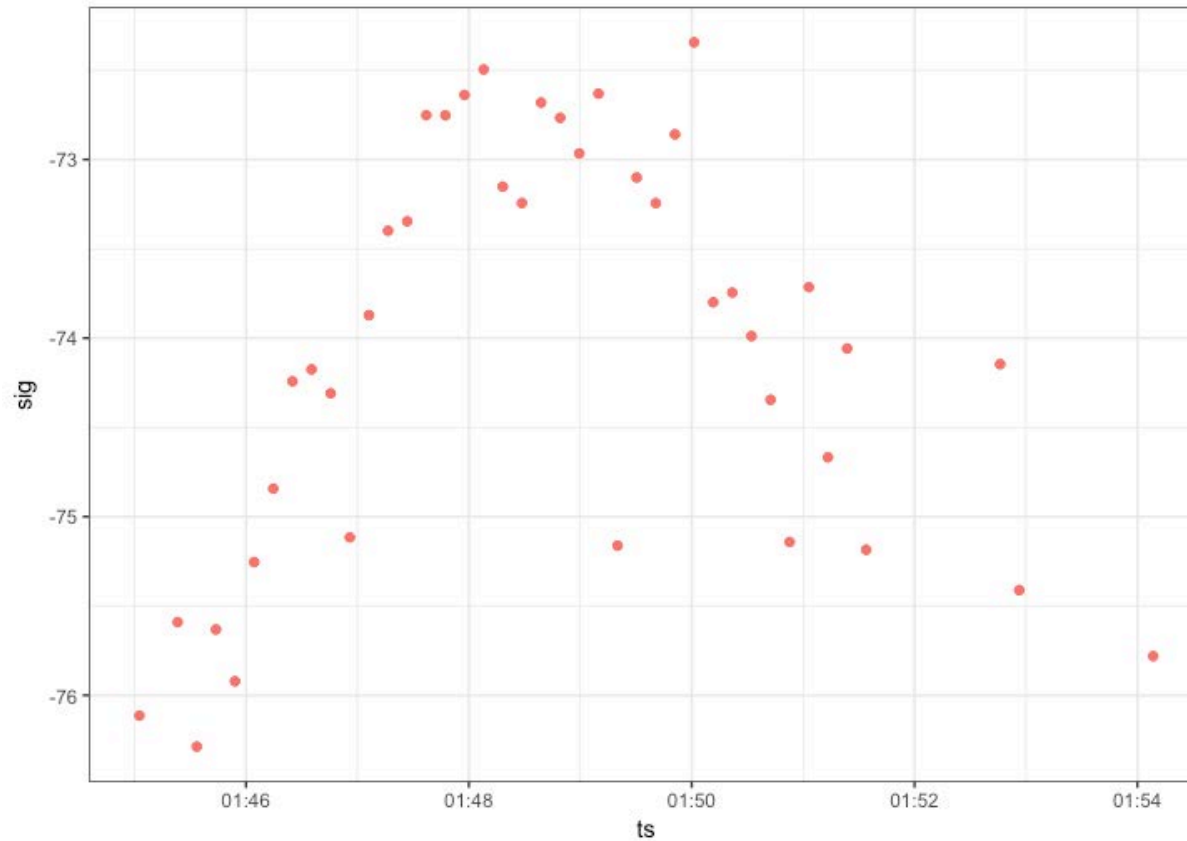
Figure 2.6. Detections of a departing tagged snowy plover represented as signal strength (sig) over time (ts); as the bird flies by the tower, the signal strength increases, then decreases as the bird flies away.
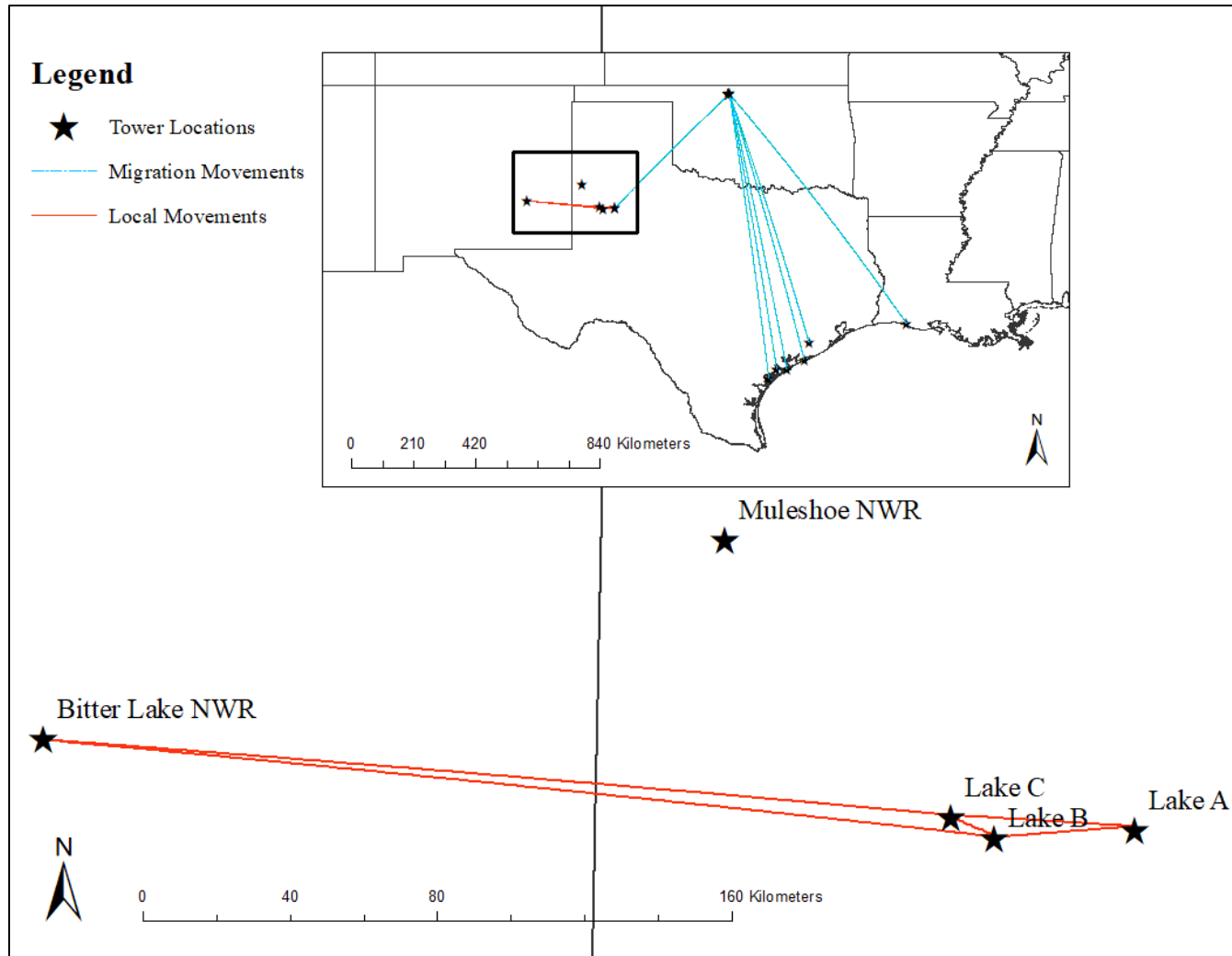
Figure 2.7. Map of local movement paths made by tagged snowy plovers in Texas, New Mexico and Oklahoma from 2017- 2018
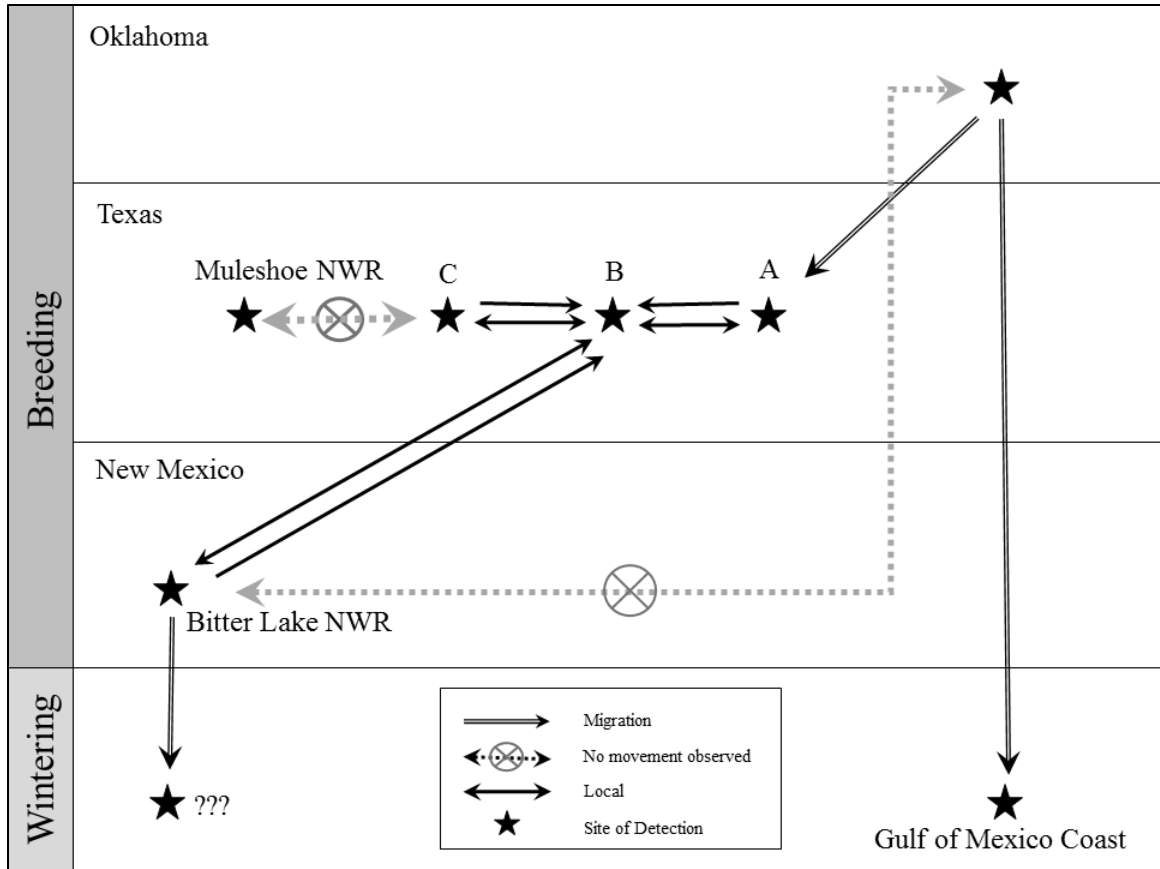
Figure 2.8. Representative figure (not to scale) of movements made by snowy plovers on the Southern Great Plains in Texas, New Mexico and Oklahoma from 2017-2018. This includes the type of movements made, direction of those movements and whether these movements were made during the breeding season or constituted a movement to a wintering ground.
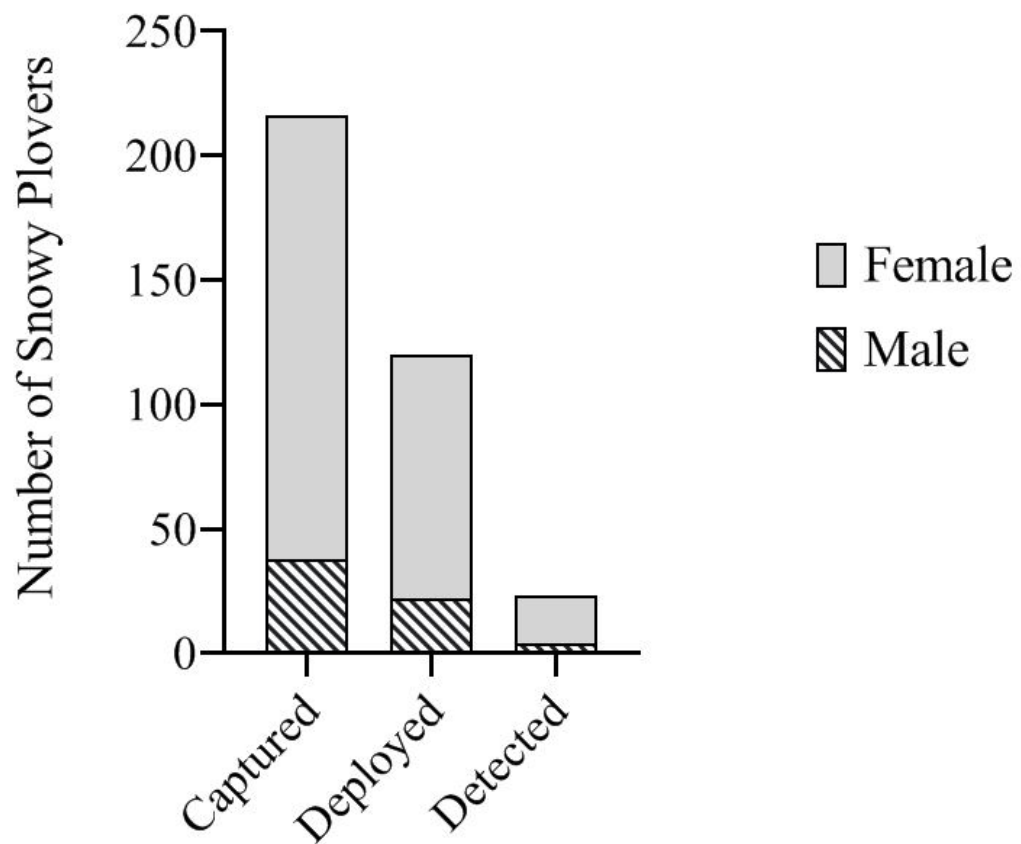
Figure 2.9. Distribution of captured adult snowy plovers, adults with deployed tags and adults that were detected on a Motus tower in 2017 and 2018 in Texas, New Mexico and Oklahoma.
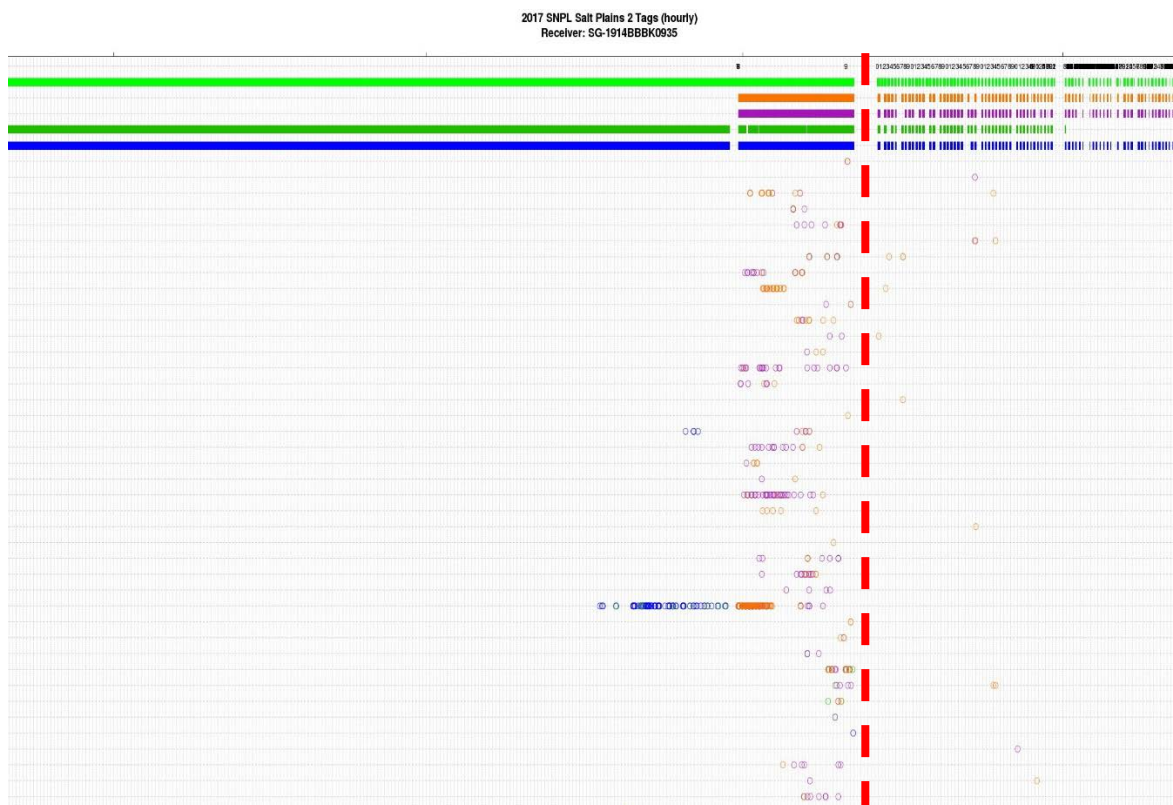
Figure 2.10. Hourly detections of multiple snowy plovers at Salt Plains NWR before and after adding 2 5-element antennae; detections on these antennae are represented in orange and purple. A large jump in birds being detected (each line of detections represents 1 tagged snowy plover) can be seen immediately after placement of the 2 antennae (red dotted line).

Figure 2.11. Location of the Motus tower (star) at Lake B inside the "bowl" of the lake (instead of on the edge, or ridgeline surrounding the lake) creating ideal conditions to detect nearby tagged snowy plovers.
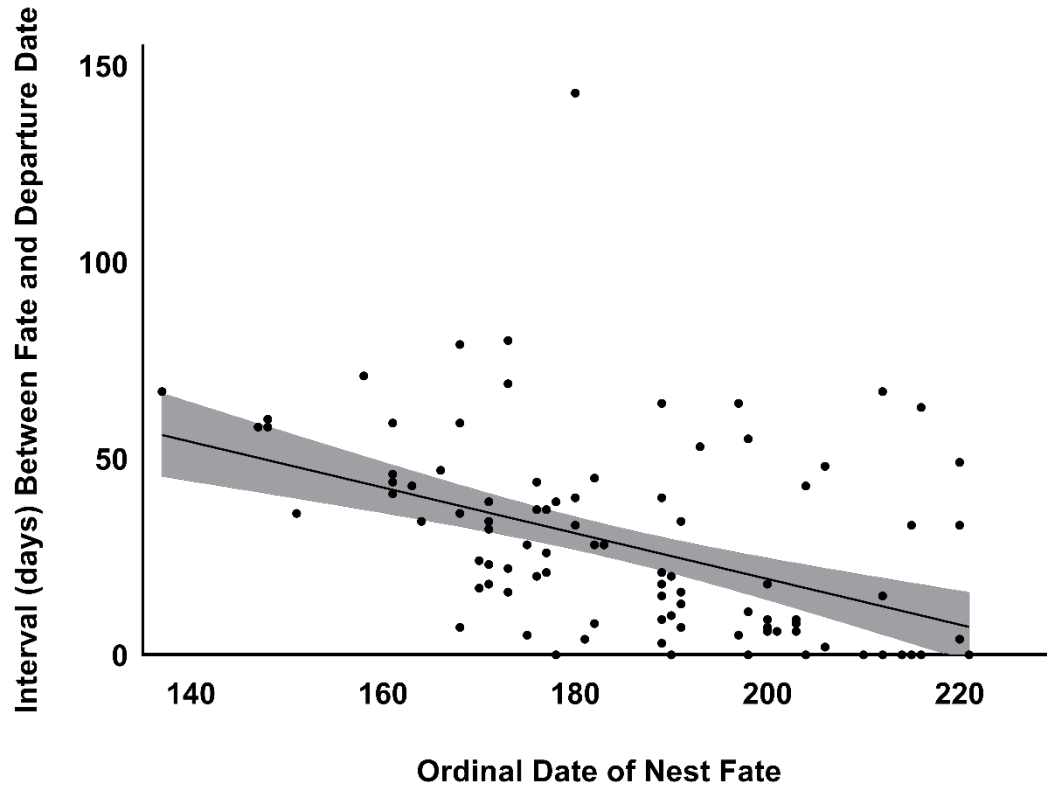
Figure 2.12. Linear regression model of the interval between date of fate and departure (DsFate) and the ordinal date of nest fate ($t_{1, 115} = -5.63$, $P < 0.001$, $R^2_{adj} = 0.21$)
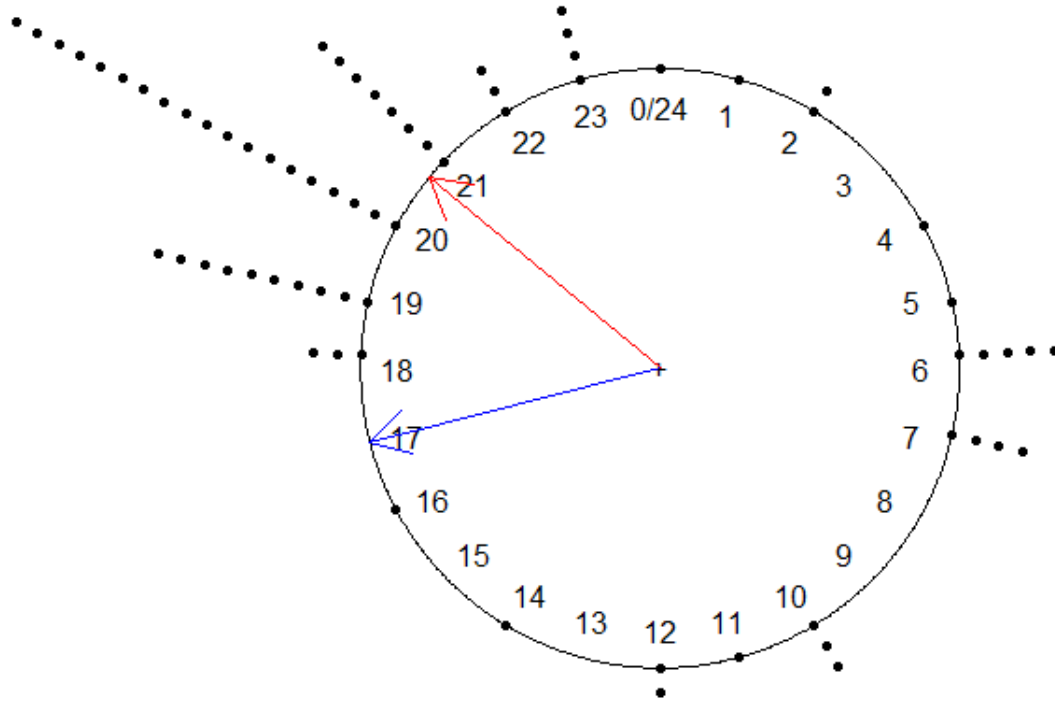
Figure 2.13. Circular departure times (hour of last detection) of tagged snowy plovers from sites in Texas, New Mexico and Oklahoma in 2017 and 2018 with arithmetic mean (blue arrow) and circular mean (red arrow).
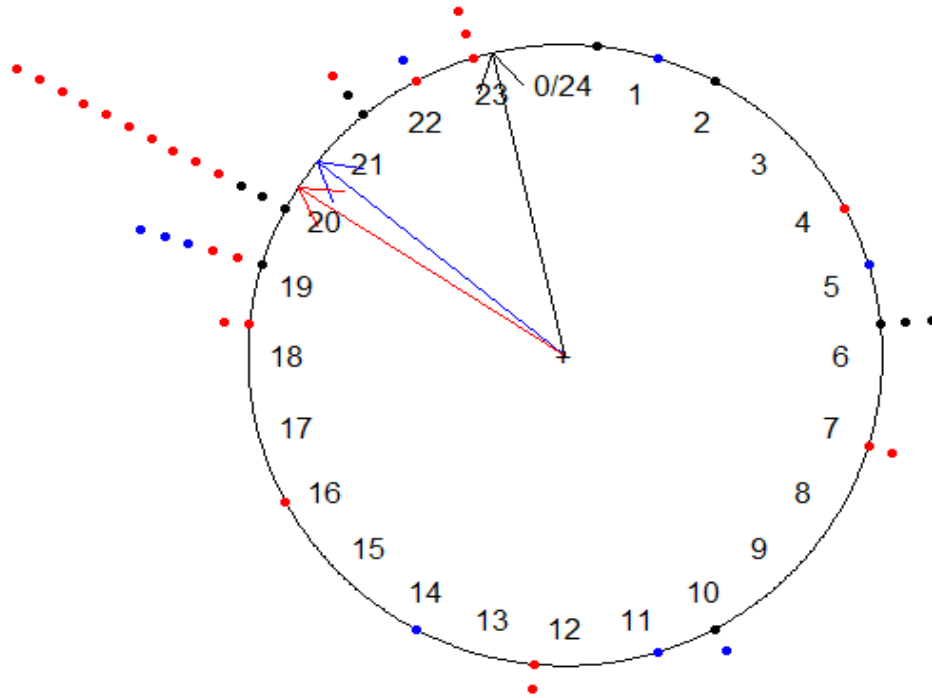
Figure 2.14. Circular departure times (hour of last detection) of tagged snowy plovers with circular means of sites in Texas (red), New Mexico (black) and Oklahoma (blue) in 2017 and 2018.
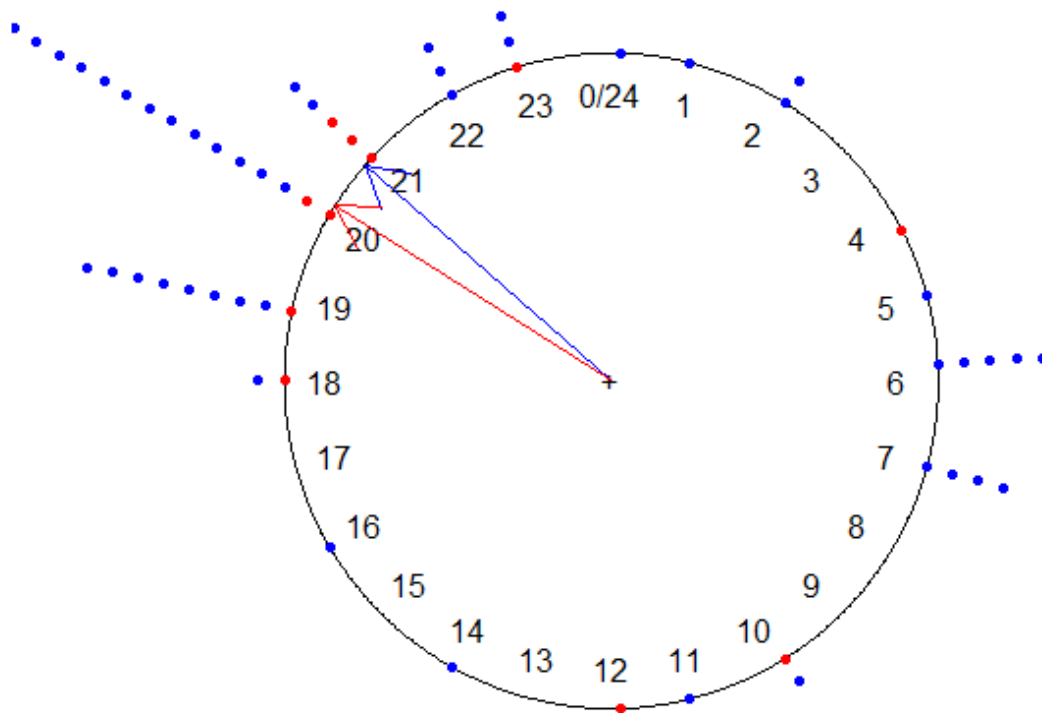
Figure 2.15. Circular departure times (hour of last detection) of tagged snowy plovers males (red) and females (blue) in Texas, New Mexico and Oklahoma from 2017-2018.
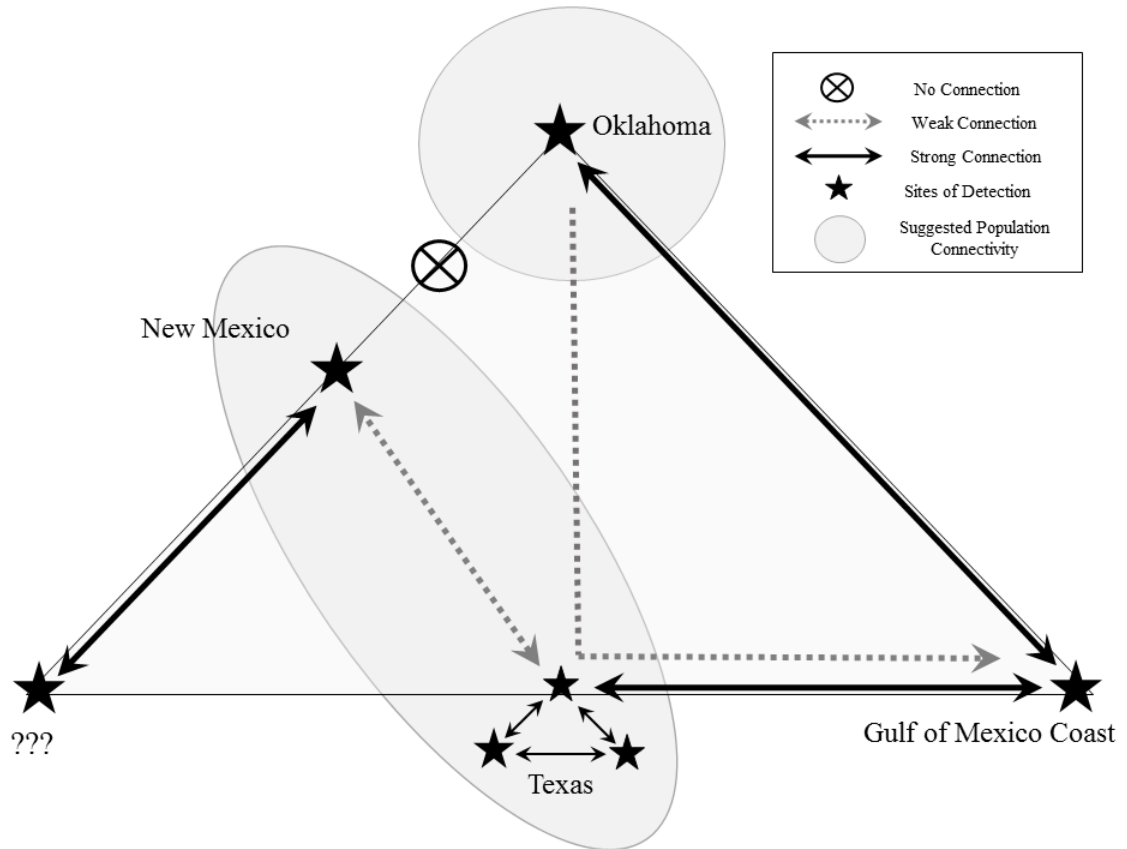
Figure 2.16. Theoretical population connectivity of snowy plovers on the Southern Great Plains of Texas, New Mexico and Oklahoma.
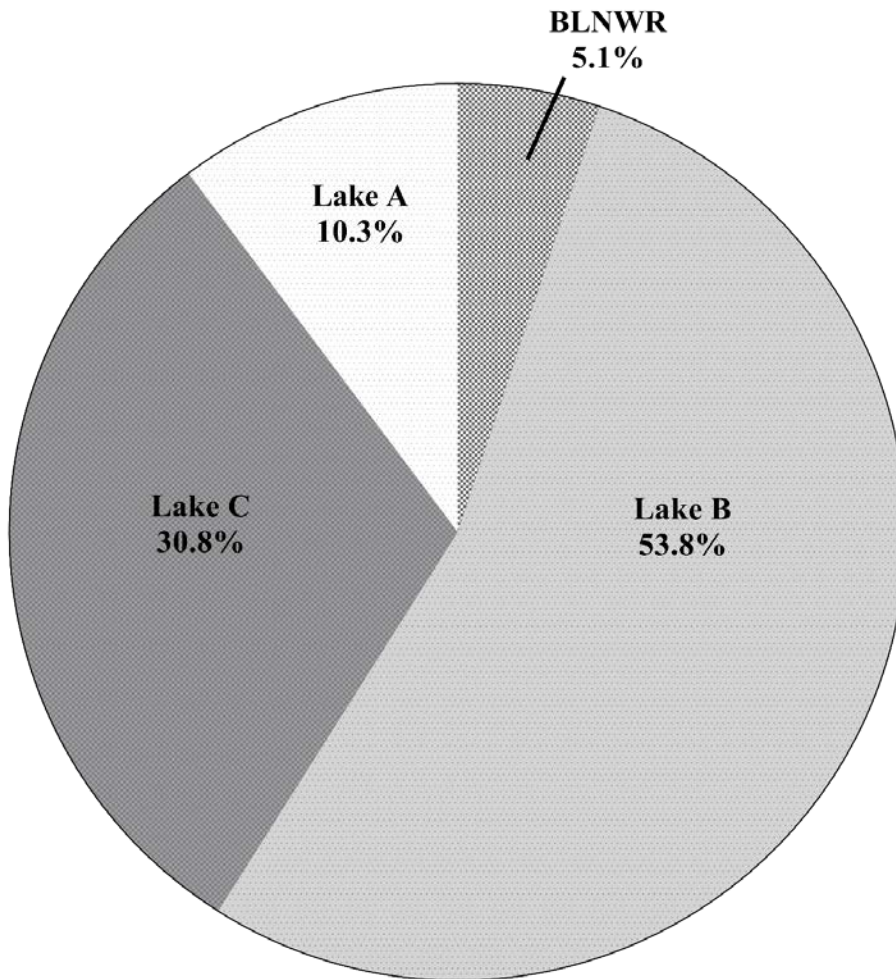
Figure 2.17. Proportion of the number of local (not including migratory) movements (n = 40) that tagged snowy plovers made to sites on the Southern Great Plains in 2017-2018. Note that no movements were made to Salt Plains NWR or Muleshoe NWR.

Table 2.1. Number and percentages of adult male and female snowy plovers that were captured, tagged with a nanotag (deployed), detected after deployment on a Motus tower, made at least 1 movement and made a migration movement in Texas, New Mexico and Oklahoma from 2017-2018; birds resighted only not included.

	Male		Female		
	n[a]	%	n	%	Total
Captured	38	18	178	82	216
Deployed	20	17	99	83	119
Detected	19	18	89	82	108
Movements[b]	1	9	20	91	21
Local	1	0	14	0	15
Migration	1	14	6	86	7

[a] Number of individuals

[b] Number of individuals that made at least one movement from one tower to another, including to non-SNPL (coastal) towers

Table 2.2. The number of banded and tagged adult snowy plovers by site that were detected, made at least one movement or were detected migrating from 2017-2018 in Texas, New Mexico and Oklahoma.

	Site[a]					
	Bitter Lake NWR	Lake A	Lake B	Lake C	Salt Plains NWR	Grand Total
	Adults Banded					
	20	16	34	14	133	217
	Tags Deployed					
Yes	19	7	18	8	67	119
No[b]	1	9	16	6	66	98
	Tags Detected					
Yes	19	7	18	8	56	108
No	0	0	0	0	11	11
	Tags Moved					
Yes	3	2	3	6	7	21
No	16	5	15	2	49	87
	Tags Migrated					
Yes	0	0	0	0	7	7
No	3	2	3	6	0	14

[a] Site where snowy plover was banded

[b] Snowy plovers that were banded but not tagged

Table 2.3. Detailed movements of tagged snowy plovers on the Southern Great Plains in 2017 and 2018. Movement type is within breeding season (B), or migratory (M).

Tag ID	Movement Type	Sex	Date of Movement	Bitter Lake NWR	Lake A	Lake B	Lake C	Matagorda Bay	Aransas NWR	Rockefeller NWR	Rockport Bay Education Center	San Bernard NWR	Total
								Movement To					
26143	B	F	?			1							1
11915[a]	B	F	6/27/2018				1						1
	B		7/11/2018			1							1
11925[a]	B	M	6/23/2018				1						1
26123	B	F	7/25/2018			1							1
26128	B	F	8/1/2017			1							1
26129	B	F	6/12/2018			1							1
	B		6/16/2018		1								1
	B		7/4/2018				1						1
	B		8/1/2018			1	1						2
26136	B	F	8/8/2018			1							1
	B		8/8/2018				1						1
	B		8/8/2018			1							1
26138	B	F	6/17/2018		1								1
	B		6/17/2018			1							1
	B		6/30/2018			1	1						2
	B		6/30/2018			1							1
	B		6/30/2018				1						1
26140	B	F	7/20/2018			1							1
	B		7/20/2018				1						1
	B		7/22/2018			1	1						2
	B		7/23/2018			1							1

Table 2.3. Continued

Tag ID	Movement Type	Sex	Date of Movement	Bitter Lake NWR	Lake A	Lake B	Lake C	Matagorda Bay	Aransas NWR	Rockefeller NWR	Rockport Bay Education Center	San Bernard NWR	Total
								Movement To					
29711	B	F	7/9/2018			1							1
	B		7/9/2018	1									1
29717	B	M	7/7/2018			1	1						2
	B		7/7/2018			1							1
29720	B	F	6/28/2018			1							1
29723	B	F	7/19/2018		1								1
29819	B		7/20/2018			1							1
29821	B	F	7/2/2018				1						1
	B		7/3/2018			1							1
29822	B	F	7/11/2018				1						1
	B		7/12/2018			1							1
26157	M	M	7/8/2018		1								1
26166	M	F	7/24/2018					1					1
26177	M	M	7/31/2018									1	1
26179	M	F	8/8/2017								1		1
26207	M	F	10/13/2018							1			1
29735	M	F	8/10/2018						1				1
29752	M	F	8/8/2018						1				1
			Total	2	4	21	12	1	2	1	1	1	44

[a] Individual was not tagged, but a resight was made indicating movement between sites

Table 2.4. Mean distance and number of movements made by snowy plovers on the Southern Great Plains in 2017 and 2018. Movement type is within-breeding season (B) or migratory (M).

Tag ID	Sex	Movement Type	Mean Distance[b]	Movement #
26143	F	B	13	1
11915[a]	F	B	13	1
26123	F	B	13	1
26128	F	B	13	1
26129	F	B	31	2
26136	F	B	13	6
26138	F	B	31	2
26140	F	B	13	9
29819	F	B	13	1
29821	F	B	110	2
29822	F	B	13	2
29711	F	B	218	2
29717	F	B	13	3
29723	F	B	31	1
29735	F	M	945	1
29752	F	M	945	1
26166	F	M	925	1
26179	F	M	974	1
26207	F	M	929	1
26177	M	M	871	1
26157	M	M	498	1
11925[a]	M	B	13	1
29720	M	B	13	1
			Total	43

[a] Individual was not tagged, but a resight was made indicating movement between sites

[b] Distance in kilometers (km)

Table 2.5 Results of a zero-inflated Poisson regression model of departure dates of tagged snowy plovers in Texas, New Mexico and Oklahoma from 2017-2018.

Variable[a]	Df[b]	Coefficient	SE[c]	*z*-value	Pr(>*z*)
Wind Speed	1	-0.18	0.05	-3.71	< 0.001
Photoperiod	1	0.62	0.04	2.50	0.012
Temperature	1	0.02	0.24	2.50	0.586
Relative Humidity	1	-0.01	0.01	-0.931	0.352
24-Hour % Temp Change	1	-3.94	2.96	-1.33	0.184

[a] Variables averaged over 24-hours.

[b] Degrees of freedom

[c] Standard error

Table 2.6. Ordinal departure dates (mean;SE) of tagged snowy plovers in Texas, New Mexico and Oklahoma from 2017-2018

Site	Female			Male			All		
	n[a]	mean	SE[b]	n	mean	SE	n	mean	SE
NM	16	202.8	2.32	4	216.5	15.71	20	205.6	3.57
OK	37	220.9	4.08	13	208.7	2.49	50	217.8	3.17
TX	42	207.5	3.77	5	219.0	9.03	47	208.7	3.52
All	95	212.0	2.44	22	212.5	3.61	117	212.1	2.09

[a] Number of individuals

[b] Standard error