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EVALUATION OF NEST FATE CLASSIFICATION ACCURACY, RESEARCH ACTIVITIES AND NESTING BEHAVIORS OF LEAST TERNS AND PIPING PLOVERS ON THE MISSOURI RIVER

by

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A Dissertation

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2018

This dissertation, submitted by Alicia Andes in partial fulfillment of the requirements for the Degree of Doctoral of Science from the University of North Dakota, has been read by the Faculty Advisory Committee under whom the work has been done and is hereby approved.

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July 24, 2018
Date

PERMISSION

Title	Evaluating Nest Fate Classification Accuracy, Research Activities and Nesting Behaviors of Least Terns and Piping Plovers on the Missouri River
Department	Biology
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Alicia Andes
August 1, 2018

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ABSTRACT

Federally protected interior Least Terns (*Sternula antillarum athalassos*) and Piping Plovers (*Charadrius melodus*) are small shorebirds that nest on un-vegetated sand habitat, such as temporary sandbars and permanent islands along inland river systems in the United States including the Missouri River, during the summer months. Extensive monitoring and research has been conducted on the Missouri River populations because they are an important component of recovery efforts for both species; therefore, two of my primary objectives included: 1) estimate rates of and determine factors that influence nest fate misclassifications and 2) evaluate the impacts of research activities on shorebird nesting behaviors and nest predation risk. The examination of possible effects that sand temperatures inflict on avian ground-nesting behavior will be critical to understand in order to adapt or develop recovery plans in response to climate change. My third objective was to assess the response of Least Tern and Piping Plover nesting behaviors in response to rising sand temperatures. As suitable breeding habitat continues to decline for both of these species, my final objective was to determine how the densities of these mixed-species colonies influenced their nesting behaviors.

With advancements in size reduction, increased quality and reduced costs of video cameras, it is possible to monitor multiple nests of a population throughout the reproductive season to capture nesting behaviors that are logistically impractical to document otherwise. During the 2013–2015 breeding seasons, I installed miniature surveillance cameras at 65 of 294 Least Tern and 89 of 551 Piping Plover nests under observation on the Missouri River in

North Dakota. For both species, there was no significant difference between the daily survival rate for nests monitored with cameras than without cameras (Piping Plovers: $\chi^2 = 3.28$, $P = 0.05$; Least Terns: $\chi^2 < 0.01$, $P = 0.98$). For a 7-day monitoring interval between visits, 45% of nests were partially and 27.5% were fully misclassified, but a more intensive (3-day) monitoring schedule decreased these rates to 20% and 8% respectively. Researchers were also less likely to correctly classify nest fates for Least Terns than for Piping Plovers and as clutch age as well as monitoring interval increased for both species. Factors that influenced misclassification of nest fates included clutch age, monitoring interval, species breeding attributes, and termination date. Furthermore, causes of failure (e.g., predators, weather) as determined from field evidence versus video disagreed for 53.5% of nests. Nest predators identified from video observation included: American Crow (*Corvus brachyrhynchos*), Black-billed Magpie (*Pica hudsonia*), Coyotes (*Canis latrans)*, Raccoon (*Procyon lotor*), Great Horned Owl (*Bubo virginianus*), Striped Skunk (*Mephitis mephitis)*, Bald Eagle (*Haliaeetus leucocephalus*) and Red Fox (*Vulpes vulpes*).

Adults of both species spent more time absent from the nest (Least Tern=39.7% ± 0.023 se, Piping Plover=26.5% ± 0.019 se) when researchers were present at the nest or in the surrounding area compared to one hour directly before (Least Tern=13.0% ± 0.013 se, Piping Plover=10.1% ± 0.01 se) and after (Least Tern=13.0% ± 0.013 se, Piping Plover=12.2% ± 0.012 se) the research activity time period ($n = 70$ nests, total number pre, during, post research activity time periods = 1,569). Additionally, daily nest attendance was lower on days with research activities (Least Terns=90.7% ± 0.017 se, Piping Plover=90.8% ± 0.012 se) compared to ones with no occurrence (Least Tern=93.2% ± 0.017 se, Piping Plover=91.7% ± 0.013 se). I found predation risk was 4.995 times more likely for a nest with one research activity/day compared to one without exposure to activities (long-term effect). There were little short-term observer effects on the risk of nest predation.

I installed thermocouples in the sand near all 52 Least Tern and 55 Piping Plover camera nests in 2014 and 2015. Nest attendance decreased 1.2 minutes per degree increase in maximum sand temperature. On average, daily nest attendance was greater for Least Terns (97% ± 13.9 se) compared to Piping Plovers (94% ± 14.4 se). The frequency and duration of shading behaviors increased by 0.21 and 0.31 minutes per day per degree increase in maximum sand temperature. Piping Plovers exhibited more and longer shading behaviors (number of daily shades=5.83 ± 3.16 se, duration of daily shades=4.13 minutes ± 2.69 se) compared to Least Terns (number of daily shades=0.46 ± 0.26 se, duration of daily shades=0.33 minutes ± 0.23 se). Sand temperature had less of an influence on the frequency of nest exchanges because these behaviors are also associated with the need of adults to leave the nest to forage throughout the day.

Both species nest in mixed-species colonies and the more aggressive nest defense behaviors of Least Terns may influence the nesting behaviors of Piping Plovers. Therefore, my objective was to evaluate the impact of colonial dynamics on the nest attendance of both species. I used generalized linear mixed models to evaluate the relationship between daily nest attendance and measures of colonial dynamics, including Least Tern and Piping Plover nest densities as well as the distance to the nearest nest of both species. Julian date, clutch age and species were also included as covariates to account for additional factors that influence nest attendance. Least Tern and Piping Plover nest densities as well as distance to the nearest Least Tern nest were the measures of colonial dynamics included in the top four models (along with species, clutch age and Julian date), which accounted for 45.3 % of the model weight (w_i). As Least Tern and Piping Plover nest densities increased by each additional nest/hectare, there was a corresponding rise in the daily nest attendance of both species by 0.55 and 0.88 minutes/day respectively. Adults of both species increased their daily nest attendance by 0.031 minutes/day as distance to the nearest Least Tern nest increased by one meter. The influence of Least Tern and Piping Plover heterospecific colonies on the nesting behaviors of both species may have important implications for potential future management decisions, especially as habitat quantity and quality continues to decline. In other words, the predator protection benefits to Piping Plovers nesting in close proximity to Least Tern nests or within colonies may become more important to manage. Therefore, it will be advantageous to determine which species provides a positive or negative influence within the colony.

CHAPTER I

LITERATURE REVIEW: LEAST TERN AND PIPING PLOVER ECOLOGY AND HISTORY OF NEST CAMERAS

Background Problem and Study Objectives

Both species are protected by The Endangered Species Act as endangered (Least Terns, *Sternula antillarum athalassos,* hereafter "Terns") and threatened (Piping Plovers, *Charadrius melodus*, hereafter "Plovers"). Damming the Missouri River to control water flow has disrupted the natural flood process that created habitat favorable for Terns and Plovers to successfully create nests, hatch chicks and fledge juveniles (Catlin 2009). The decline of suitable breeding habitat is the primary cause for the decrease in population size for Terns and Plovers (Stucker *et al.* 2013).

The Missouri River system supports nesting populations and is an important component of recovery efforts for both species. Suitable nesting habitat for Terns and Plovers is generated by the seasonal erosion, transportation and redistribution of sand in a naturally functioning river system. In particular, the succession of vegetation, which reduces suitable habitat, is constrained on sandbars, islands and beaches by the spring pulses from snow melts. However, the establishment of dams on the Missouri River assuaged peak spring flows, resulting in the deterioration of quality and quantity un-vegetated nesting areas for both species (Catlin 2009). In 2011, a historic flood overwhelmed the Missouri River Basin from an unanticipated, extraordinary amount of rainfall and snowmelt (USACE 2012). It was estimated by the Army Corps of Engineers (USACE) that 49 million acre feet of water runoff entered the river, which resulted in record releases from all of the main stem dams, including 150,000 cubic feet per second at Garrison, on the Missouri River in North Dakota (USACE 2012). Subsequently, this regulated river experienced conditions that mimicked the natural water flows of the past, which induced extensive habitat modification and augmented appropriate nesting habitat available for both species.

The circumstances engineered by the 2011 flood offered an unprecedented opportunity to understand how both species exploit and respond to the more natural habitat conditions on the Missouri River. Prior to the flood, there were several studies that estimated Plover and Tern population demographic parameters, at high densities that diminished reproduction, when habitat quality and quantity were degraded and diminished (Catlin 2009, Catlin *et al.* 2011, Sherfy *et al.* 2012, Shaffer *et al.* 2013). A comparison between pre and post flood data will allow investigation to determine if quality habitat availability, as well as causative mechanisms such as predation and food limitation, will substantially influence the population dynamics of both species. Furthermore, the results from this crucial opportunity may improve recovery plans for both species as well as refine river management.

Another aspect to improve recovery plans for Plovers and Terns involves the evaluation of nest monitoring techniques because methods that produce inaccurate demographic estimates may result in challenges to understand population dynamics and encumber management actions. Since recovery plans for imperiled bird species are developed from productivity estimates, such as nest survival, reproduction is often the primary focus of monitoring programs. However, past research identified, as a potential cause of inaccurate productivity estimates, incorrect conclusions about nest fate and causes of failure from classifying remains in the field (Larivière 1999, Pietz & Granfors 2000). To minimize researcher impacts to survival and behavior, nest checks often occur within one to three day time intervals. However, time between checks permit the occurrence of other events, like weather or scavenger visits, to modify evidence left at the nest and consequently increase the probability of fate misclassification (Staller *et al.* 2005).

Advancements in size reduction, increased quality and reduced costs of video cameras increased their popularity in wildlife research, especially in nest monitoring protocols. Video cameras allow the investigation of a variety of questions (while reducing the number of visits by researchers at the nest) including nest fate classification, researcher disturbance effects, predator identification, parental behavior, fledgling rates and weather influences. Many of these questions, which are highly relevant to management plan development, would be otherwise logistically impossible to collect with only field personnel (Cox *et al.* 2012, Ellis-Felege & Carroll 2012). The incorporation of cameras provides the opportunity to monitor nests and evaluate the accuracy of nest fate and failure cause determination by field evidence interpretation. It is possible to continuously monitor with video multiple nests of a population throughout the reproductive season to increase the accurate identification of predators and fates as well as document all nesting activity.

The USACE is responsible for the management of Plovers and Terns that nest on the Missouri River. To successfully implement management plans, the USACE collaborated with the United States Geological Survey (USGS) to conduct research that improves our understanding about the relationship between the current conditions of the breeding areas available to both species and their population dynamics. The standard protocols implemented by the USGS to locate and monitor nests have been used for over 9 years (Shaffer *et al.* 2013). However, the accuracy of researchers using these nest monitoring techniques to determine nest fate as well as any potential research activity impacts on nesting behaviors remains unknown. Cameras allow an unbiased assessment of current protocol efficiency to monitor and measure Plover and Tern productivity. Therefore, I utilized a camera system to evaluate the success of the current monitoring techniques with the intent to address the following objectives:

1) Estimate misclassification rates as well as identify factors contributing to incorrect identifications of nest fate using field evidence in and around the nest.
2) Assess the immediate and long-term impacts of various research activities on nesting behaviors and nest predation risk
3) Document and evaluate the nesting behavior plasticity of both species in response to sand temperatures
4) Investigate the effects of heterospecific colony characteristics on nesting behaviors

Least Tern Ecology

Terns belong to the family Charadriiformes with other shorebirds, gulls and skimmers (Thompson *et al.* 1997). More specifically, they are the smallest member of the Terns, classified in the Laridae family, in North America with a length of 21-23 cm and a wingspan of 48-53 cm (Thompson *et al.* 1997). Adults usually weigh 30 to 45 grams (Thompson *et al*. 1997). Sexes are alike in plumage throughout the year. Permanent adult plumage consists of a gray back, rump and upper wings with outer 2-3 black primaries, white underparts and a deeply forked white tail

(Thompson *et al.* 1997). During the breeding season, adults exhibit a black cap, white triangle on their forehead, white stripe through the eye, a yellow black tipped bill and yellow to orange legs (Thompson *et al.* 1997). The black cap reduces to a wide black stripe that connects both eyes and extends to the back, upper part of the head and forehead white with black specks and the beak turns black for the winter adult plumage (Thompson *et al.* 1997). Juveniles are distinguished by U-shaped patterns of gray to yellowish brown on their back and resemble adults in winter plumage (Thompson *et al.* 1997).

Terns have a wide breeding range that encompasses both the North American Pacific and Atlantic coasts as well as along interior rivers, bays, lakes and alkali wetlands (Thompson *et al.* 1997). Terns migrate south and spend the fall and winter seasons on coastal areas of the Gulf of Mexico, Florida, Central and South America (Thompson *et al*. 1997).

Terns build nests on the ground in sparsely vegetated sand, gravel and mud habitat on shorelines, sandbars, islands and wetlands (Sherfy *et al.* 2012, Stucker *et al.* 2013). Recently, Terns were recorded building nests on flat gravel rooftops in areas where there was a decrease in suitable natural habitat (Jackson & Jackson 1985). Nest bowl construction consists of a shallow depression or scrape in the substrate, usually adjacent to various sizes of woody debris (Thompson *et al.* 1997). In some cases, adults will lay eggs in depressions caused by human or mammal footprints. Adults will occasionally decorate the nest bowl edges with small pebbles and shells (Wolk 1974, Burger & Gochfeld 1990). Since ground-nesting birds are more susceptible to mammalian and avian predators as well as damage from human recreation and livestock presence, Terns nest in colonies for additional defense against predation and destruction. Terns often compete with other birds such as Plovers, Snowy Plovers (*C. nivosis*), Black Skimmers (*Rynchops niger*), Killdeers (*C. vociferous*) and Spotted Sandpipers (*Actitis macularius*) that nest in the same areas and habitats (Burger 1987).

Tern adults, juveniles and chicks feed primarily on small fish, shrimp and occasionally invertebrates (Atwood & Kelly 1984). Adults forage in various shallow water habitats (Stucker *et al.* 2013). Foraging behavior consists of searching for prey by flying and hovering over water until the adult dives into the surface to grasp fish with their beak (Thompson *et al.* 1997). The adults will rise from the water and shake off excessive wetness before either swallowing the fish in flight or carrying it to an incubating mate or chicks (Wilson *et al.* 1993). Adults sometimes catch invertebrates in flight and shrimp while standing in shallow water off sandbars, shorelines, islands and wetlands (Wilson *et al*. 1993). Since chicks are semi-precocial and are unable to forage by themselves until capable of flight, adults call to them in flight and they are fed on the ground (Atwood & Kelly 1984).

Terns are monogamous and form nesting colonies with various sizes that range from 2 to more than 2,000 pairs; however, the average colony size is less than 25 pairs (Massey 1974, Jackson & Jackson 1985, Thompson *et al.* 1997). Terns form pair bonds shortly before or at arrival to the breeding grounds. Courtship behavior consists of 2 stages: 1) aerial calling during flights and glides usually with an associated fish and 2) ground feeding, posturing and copulation with an exchange of fish between mates (Thompson *et al.* 1997).

Both parents are involved in nest-site selection and scrape formation (Thompson *et al.* 1997). Several scrapes are formed before the female ultimately selects the final nest site. Females lay 2-3 eggs in a clutch, one every day, that are oval, beige in color and speckled to camouflage against the nest substrate (Kirsch 1996, Thompson *et al.* 1997). Incubation begins at the start of the egg laying stage and lasts approximately 19-25 days (Thompson *et al.* 1997). Unless the nest is depredated or destroyed, pairs only breed once a season (Thompson *et al.* 1997). Both adults share parental responsibilities; however, the female parent contributes the most time to incubation and chick-rearing duties (Keane 1987).

Tern chicks are born semi-precocial, wet, covered with beige, spotted down and well camouflaged to blend into the ground substrate; after a few hours they are mobile but unable to feed themselves (Thompson *et al.* 1997). All chicks hatch within a few days, leave the nest permanently and are brooded by both parents until thermoregulation is achieved sometime before fledgling age at 20 days (Thompson *et al.* 1997).

Various types of predators were reported to depredate adults, chicks and nest such as the American Crow (*Corvus brachyrhynchos*), Great Horned Owl (*Bubo virginianus*), gulls (*Larus* spp.), Great Blue Heron (*Ardea Herodias*), Coyote (*Canus latrans*), Raccoon (*Procyon lotor*) and Striped Skunk (*Mephitis mephitis*) (Fisk 1972, Jenks-Jay 1980, Minsky 1980, Burger 1989, Jackson & Key 1992, Smith & Renken 1993, Wilson *et al.* 1993, Kirsch 1996, Devault *et al.* 2005). Adults utilize a variety of defensive behaviors to protect nests and chicks against predators, humans and livestock such as alarm calls, aerial dive bombing, aerial defecation (Burger 1989, Thompson *et al.* 1997). The dive bomb behavior consists of adults flying above the threat, dropping into a sharp dive at the head, in many cases defecating or striking and finally flying up overhead again to repeat the process until the predator, human or competing shorebird vacates the area (Burger 1989, Thompson *et al.* 1997).

The interior subspecies of Terns was federally listed as endangered on May 28, 1985 (U.S. Fish and Wildife Service 1985a). Under the Endangered Species Act, Tern adults, nests, eggs and chicks are protected from collection, removal, destruction or any type of damage by human activities. States where the interior population is protected include Arkansas, Colorado, Iowa, Illinois, Indiana, Kansas, Kentucky, Louisiana, Mississippi, Missouri, Montana, North Dakota, Nebraska, New Mexico, Oklahoma, South Dakota, Tennessee and Texas (U.S. Fish and Wildlife Service 1985a).

Management efforts to increase Tern population numbers focus on protecting, improving or maintaining nesting habitat (Thompson *et al.* 1997). The use of signs and fences to exclude human activity near nesting areas is a popular management practice (Burger 1989, Koenen *et al.* 1996). Habitat construction is a management practice utilized on the Missouri River with success to increase Tern productivity (Sherfy *et al.* 2012, Stucker *et al.* 2013). For the interior populations that nest on and along rivers, the most effective management practice to increase the amount of suitable nesting habitat includes restoring the natural flooding process that annually removes vegetation from islands, sandbars and shorelines (Catlin et al. 2011, Sherfy et al. 2012).

Piping Plover Ecology

Plovers also belong to the order Charadriiformes and are members of the family Charadriidae with other plovers, dotterels and lapwings (Elliott-Smith & Haig 2004). Plovers are characterized by their small body size (17-18 cm long), weight (43-63 g), orange legs, light upper feathers and a single black neck band during their breeding plumage (Elliott-Smith & Haig 2004). Similar species that overlap in their geographic range include Snowy Plovers, Semipalmated Plovers (*C. semipalmatus*), Wilson's Plovers (*C. wilsonia*) and Killdeer. There is limited information about their winter range outside of North America. However, Plovers are often sighted along the Atlantic Coast from North Carolina south and all of the Gulf Coast in the United States (Elliott-Smith & Haig 2004, Haig *et al.* 2005). Their summer range includes the Atlantic Coast and the Great Lakes north of their wintering areas plus inland alkali wetlands, rivers, lakes and reservoirs from the northern Canadian Provinces south to Nebraska (Ferland & Haig 2002, Elliot-Smith & Haig 2004, Haig *et al.* 2005).

Plovers use beaches, shorelines, sandbars, engineered islands and mudflats with minimal vegetation to build nests on the ground (Haig 1986, Schwalbach 1988b, Sidle & Kirsch 1993, Elliott-Smith & Haig 2004, Catlin *et al.* 2011). More specifically, Plovers select nest habitat with the following characteristics: open, elevated, small patches of vegetation and prevalence of sand, gravel, pebbles or shells (Cairns 1982, Weseloh & Weseloh 1983, Whyte 1985, Prindiville 1986, Burger 1987, Powell & Cuthbert 1992, Schwalbach 1988, Strauss 1990, Elliott-Smith & Haig 2004 Cohen *et al.* 2008). Males arrive first at the breeding grounds to establish a territory; therefore, Plovers do not exhibit the same colonial nesting behavior observed in Terns. Males scrape multiple depressions in the sand as part of courtship until copulation and the female selects a single bowl to become the nest (Cairns 1982). After the pair bond is established, both adults decorate inside and around the nest bowl with pebbles and shells (Cairns 1982). Plovers are primarily monogamous; however, there are reported occurrences of serial polyandry and polygyny (Haig & Oring 1988b).

Unless the nest is a failure, there is only one nest attempt per year. First attempt clutches typically contain four eggs, laid every other day, that are oval, sand colored with evenly distributed spots that camouflage into the ground substrate (Cairns 1982, Elliott-Smith & Haig 2004). Multiple re-nests are possible if the previous attempts are depredated or destroyed in any way; however, clutch size for re-nests decrease with attempts (Bottitta *et al.* 1997, Elliott-Smith & Haig 2004). Full incubation begins after the last egg is laid. There are reported instances when short incubation periods were observed during the egg-laying period (Cairns 1977, Whyte 1985). Both sexes incubate the nest, which lasts around 25 to 28 days (Wilcox 1959, Cairns 1977, Whyte 1985, Haig & Oring 1988a).

Plover chicks are born wet, downy and precocial with the ability to walk and feed themselves within a few hours of hatch. Down is white with a black speckled upper back and head areas in order to camouflage the chick into the surrounding sand substrate for protection (Elliott-Smith & Haig 2004). Broods and parents leave the nest permanently after all the chicks hatch. Chicks are brooded by both adults, but female desertion after 5-17 days was observed in the Great Lakes and on the Atlantic Coast (Wilcox 1959, Cairns 1977, Whyte 1985, Haig & Oring 1988a, Maxson & Haws 2000). Chicks are capable of flight three weeks after hatching.

Freshwater and marine invertebrates, such as marine worms, crustaceans, mollusks and insects, are the primary food source for Plover adults and chicks (Bent 1929, Nicholls 1989). Individuals forage alone or in groups along the water with a combination of rapid pecks and running sprints. In addition, Plovers are known to dislodge invertebrates from below the sand and bring them to the surface by shaking their feet (Cairns 1977). Since chicks are precocial, they begin to feed themselves shortly after hatch. However, parents and broods may feed at higher elevations or areas with less water movement until chicks are unable to be threatened by waves (Loegering & Fraser 1995, Elias *et al.* 2000).

Predators of Plovers are similar to the previous ones listed for Terns but also include Mink (*Mustela vison*), Short-tailed Weasel (*M. erminea*), Red Fox (*Vulpes vulpes*), Domestic

Cats (*Felis catus*), Ghost Crabs (*Ocypode quadrata*), beetles, snakes and Thirteen-lined Ground Squirrels (*Spermophilus tridecemlineatus*) (Loegering *et al.* 1995, Mabee & Estelle 2000, Elliott-Smith & Haig 2004, Ivan & Murphy 2005). Plovers use a variety of defense behaviors toward a perceived threat. For example, Plovers will attack other similar shorebirds that intrude into their territory. A distraction display, involving the repeated flapping of wings on the ground, is used when the intruder is a predator. Adults will feign an injury in order to lead the predator away from the nest (Cairns 1982).

The interior populations of Plovers were federally listed as threatened on December 11, 1985 (U.S. Fish and Wildlife Service 1985b). In addition, Plovers are listed as endangered in the Great Lakes region including Illinois, Indiana, Michigan, Minnesota, Mississippi, New York, Ohio, Pennsylvania and Wisconsin (U.S. Fish and Wildlife Service 1985b). All Plover adults, nests, chicks, and juveniles are protected from harm, destruction and collection by humans according to the Endangered Species Act. There are several local (signs, fencing, enclosures, predator control, and habitat management) and large scale efforts (International Piping Plover Recovery Group that surveys winter and breeding grounds across country and state borders) focused on conservation and management of Plovers across their geographic range (Elliott-Smith & Haig 2004). Management efforts described previously for Terns, such as engineered sandbars on the Missouri River, also increase available nesting habitat for Plovers. However, since nesting habitat extends beyond river and lake systems for interior Plover populations, management and conservation extends to shallow alkaline wetlands within grasslands in the Prairie Pothole Region, located in the northern Great Plains including Alberta, Saskatchewan, Manitoba, Montana, North and South Dakota, Minnesota and Iowa.

History of Cameras

Since the first mention of "photographs" in the literature (Gysel & Davis 1956, Royama 1959) during the 1950s, the frequency of cameras in wildlife research has increased. However, it was not until Pietz and Granfors (2000) designed and implemented a camera system to investigate predators, nest fates and the nesting dynamics of grassland birds in North Dakota that video became a widely used tool (Cox *et al.* 2012). Technological advancements that reduced equipment size and cost, while increasing video quality and storage capabilities, were also factors that contributed to their popularity in research (Cox *et al.* 2012). By 2000, the number of publications that mentioned the use of video technology was more than 20 per year (Cox *et al.* 2012). The technological advancements and adaptations of video cameras allow the examination of a multitude of questions pertaining to avian nesting ecology.

Before the introduction of video cameras, there were certain questions about avian nesting ecology that were logistically challenging to answer. For example, it is difficult to identify nest fates and predators from eggshell evidence (Larivière 1999, Pietz & Granfors 2000). In addition, past research that examined aspects of parental or fledgling behavior at the nest were limited to small sample sizes of abbreviated observations from a distance (Downs & Ward 1997, Eichholz & Sedinger 1998, Ward 1990, Brown & Downs 2003, Amat & Masero 2004). The addition of video cameras to study designs as a tool to monitor nests rectified many of the logistical problems from past research.

The use of video cameras is not limited to nest fate and predator identification. Additionally, it can be used to address parent and fledgling behavioral questions. Cox *et al.* (2012) conducted a literature review to determine the number and types of studies conducted with video cameras: 114 nest predator identification, 103 feeding ecology, 81 adult behavior, 32 camera technique introduction, 23 nest contents identification, 19 nestling behavior, 15 camera or technique evaluation, 13 intruder behavior and 7 other. Additional questions investigated by the use of cameras include: researcher visitation and weather effects on nest success and parental behavior (Keedwell & Sanders 2002, Fisher *et al.* 2010, Ibáñez-Álamo *et al.* 2012, Clauser *et al.* 2016). The future of camera systems relies on the modification of equipment to broaden their use to more species of birds and mammals.

Video cameras have advanced the study of avian ecology to new investigative levels; however, there are caveats to its use like any other tool used in research. It is essential that the system does not affect nest success or normal parental activities that may bias the data (Fair *et al.* 2010). Nest abandonment from camera presence was observed by Pietz and Granfors (2000), Renfrew and Ribic (2003) as well as Stake and Cimprich (2003). Predator behavior and distribution may also be affected by the presence of cameras (Richardson *et al.* 2009). Depending on the type, some predators may be enticed or deterred by the presence of cameras (Pietz & Granfors 2000). The distribution of cameras in an area is another factor that may alter normal predator distribution and behavior. If camera distribution is clustered in a single location, a predator with a large territory may learn to associate them with nests, which will unnaturally reduce nest survival (Picozzi 1975, Reynolds 1985, Cox *et al.* 2012). The final caveat from video camera use involves data analysis. Even with technological advances in video quality, it may be difficult to identify between individuals of the same species if they are not sexually dimorphic or have additional auxiliary markers such as band combinations. Advanced technology allows the rapid accumulation of large sample sizes of data; however, filtering through all of the video requires substantial personnel hours (Ellis-Felege *et al*. 2014). As long as the caveats included with video camera use are recognized, their continued inclusion in wildlife research will further our knowledge about avian nesting ecology.

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CHAPTER II

ACCURACY OF NEST FATE CLASSIFICATION AND PREDATOR IDENTIFICATION FROM EVIDENCE AT NESTS OF LEAST TERNS AND PIPING PLOVERS

Abstract

For federally listed species, such as Least Terns (*Sternula antillarum*) and Piping Plovers (*Charadrius melodus*), correct determination of nest fates and causes of nest failure is crucial for understanding population dynamics and improving monitoring programs. I used video cameras to evaluate nest fate misclassification rate and to identify factors that may cause researchers monitoring nests at different intervals to incorrectly classify Least Tern and Piping Plover nest fates. During the 2013–2015 breeding seasons, I installed miniature surveillance cameras at 65 of 294 Least Tern and 89 of 551 Piping Plover nests under observation on the Missouri River in North Dakota. Nest fates were assigned in the field from remains found at the nest site and then again by an independent researcher who reviewed camera footage. I used ordinal logistic regressions to examine whether monitoring interval, clutch age or temporal factors influenced a correct, partially misclassified (probable successful in the field vs successful by camera), or misclassified nest fate classification. For a 7-day monitoring interval between visits, 45% of nests were partially and 27.5% were fully misclassified. The percent of partially (20%) and fully (8.0%) misclassified nests decreased with a more intensive (3-day) monitoring schedule. Researchers were also less likely to correctly classify nest fates for Least Terns than for Piping

Plovers, and as clutch age and monitoring interval increased for both species. Furthermore, causes of failure (e.g., predators, weather) as determined from field evidence versus video disagreed for 53.5% of nests. The ability to accurately identify nest fate and cause of nest failure will facilitate a better understanding of factors that limit productivity and will lead to better informed management decisions for improving nest survival.

Keywords: misclassification rate, nest monitoring intensity, video cameras, shorebirds, nest predation

Introduction

Nest survival is a crucial demographic parameter used to understand the underlying factors that influence population size and viability over time. Additionally, in many circumstances nest survival is more straightforward to measure than most other significant traits of life history; therefore, it is often more feasible for research and management than many of the other vital rates that are important to productivity (Johnson 2007). It is no surprise that the issue of estimating nest survival has received considerable attention in the past and present, suggesting that there are still unresolved problems with the methodologies used for estimation (Johnson 2007). The challenges with estimating nest survival arose from the methods used to monitor nests, a problem first presented by Mayfield (1961). Nests are discovered after their initiation, at various stages of incubation, and then can either be monitored daily or on an interval of multiple days, depending on logistical constraints that are usually unique to each situation (Martin & Geupel 1993). Therefore, traditional nest monitoring methods measure survival in discrete time periods (usually in days with multiple checks) as either survived or failed; however, survival of nests is a continuous process, because nest failure can happen anytime during the monitoring interval (Manolis *et al.* 2000, Shaffer 2004, Heisey *et al.* 2007). If nest failure occurs between visits and monitoring is periodic, then the exact failure date is unknown and crucial evidence of the outcome may be lost, leading to a potential misclassification of nest fate and the cause of failure.

With increased picture quality and reduced size and cost, the use of video cameras has increased in wildlife research, especially for nest monitoring applications. Video cameras eliminate the uncertainty inherent in traditional nest survival estimates because they provide continuous monitoring of a continuous-time process (Pietz & Granfors 2000). Uncertain or misclassified nest fates as well as misidentification of predators can potentially introduce bias in demographic models and causal analyses of nest survival that underpin management plans (Manolis *et al.* 2000). Misclassification rates of nest fates, which ranged from 15-40% for passerines in West Virginia, Minnesota, North Dakota and western Canada, were estimated by the incorporation of video cameras into observational study designs (Manolis *et al.* 2000, Pietz & Granfors 2000, Williams & Wood 2002, Ball & Bayne 2012). Additionally, several investigators reported that video monitoring was more successful in identifying predators of passerine nests compared to field observations (Thompson *et al.* 1999, Pietz & Granfors 2000, Stake & Cimprich 2003, Stake *et al.* 2004, Bolton *et al.* 2007, Benson *et al.* 2010, Conkling *et al.* 2012). The major concern for utilizing cameras to monitor nests of various avian species is the potential to influence nest survival. However, numerous studies that utilized camera systems to identify predators of gamebird, passerine and shorebird nests revealed, on average, a slight positive to no effect on overall success (Thompson *et al.* 1999, Pietz & Granfors 2000, DeVault *et al.* 2005, Ivan & Murphy 2005, Staller *et al.* 2005, Sabine *et al.* 2006, Coates *et al.* 2008, McKinnon & Bêty 2009, Richardson *et al.* 2009, Herring *et al.* 2011).

Traditional methods of assigning nest fates and identifying predators often rely on the interpretation of evidence left after chicks hatch or eggs are depredated; however, weather events, scavenging predators and the parents themselves will often alter remaining evidence (Mabee 1997, Sargeant *et al.* 1998, Larivière 1999, Pietz & Granfors 2000, Williams & Wood 2002, Mabee *et al.* 2006, Ball & Bayne 2012). Many predators, including the American Crow (*Corvus brachyrhynchos*), Raccoon (*Procyon lotor*), Red Fox (*Vulpes vulpes*) and gulls (*Larus* spp.), were reported to remove entire eggs from nests and leave no evidence behind, leading to nest fate misclassifications (Sargeant *et al.* 1998, Larivière 1999, Pietz & Granfors 2000, Sabine *et al.* 2006). Additionally, nest fate misclassification was often influenced by the dependence of researchers on projected hatch date to classify nest fates, nest fate itself, fledgling age, predator type and the range of evidence left in the surrounding area (Sargeant *et al.* 1998, Pietz & Granfors 2000, Thompson & Burhans 2003, Ball & Bayne 2012). Productivity was overestimated when researchers reported using projected hatch dates to classify empty nest bowls with no evidence of hatching as successful nests (Pietz & Granfors 2000, Ball & Bayne 2012). Successful nests were 12.2 times more likely than failed nests to be classified correctly for boreal songbirds nesting in northern Canada, leading to a positive bias of nest productivity by 35% and ultimately an overestimate of population growth by 6% (Ball & Bayne 2012).

Predator identification from nest remains is complicated by intra- and inter-specific similarities of depredations for various bird and mammal species, parental alterations of evidence after nest failure and multiple predation events by different predators at the same nest site

(Sargeant *et al.* 1998, Pietz & Granfors 2000). Additionally, longer intervals between visits to nests allowed additional events to alter or eradicate evidence left by the original predators (Larivière 1999). Predator class (avian, mammalian, snake) was incorrectly determined from field evidence at the nest site for 12 of 21 (57%) depredated Wood Thrush (*Hylocichla mustelina*) nests (Williams & Wood 2002). White *et al.* (2010), relying on field evidence, misclassified two Piping Plover (*Charadrius melodus*; hereafter Plover) nests as destroyed by Cattle (*Bos taurus*) when Coyote (*Canis latrans*) predation was the actual cause. In addition, Plover parents returned to the nests after depredation events and further obscured fate evidence by scraping the empty nest bowl and removing pebbles (White *et al.* 2010).

The majority of past research that examined nest fate misclassification and predator misidentification concentrated chiefly on passerines, waterfowl and gallinaceous birds, with nests that were somewhat sheltered from weather and visually isolated from predators. Conclusions gained from this past research may not be applicable to other avian species, especially shorebirds that nest on the ground and prefer open, sparsely vegetated sand habitats exposed to frequent wind and precipitation, which may quickly destroy evidence of nest fate. Furthermore, unlike altricial passerine chicks that remain in the nest until fledging, providing a window of several days for determining nest fate, shorebird chicks are semi- to fully-precocial and vacate the nest within hours after hatching. Researchers are left with a short amount of time (several hours to 1-2 days) to determine nest fate before the brood departs the area and weather-related events alter or remove evidence in and around the nest bowl. Factors that influence accurate interpretation of field evidence for the purpose of assigning nest fates of shorebirds are poorly understood.

This study had four primary objectives: (1) evaluate if and how frequently nest fate and causes of nest failure were misclassified by researchers based on evidence in and around the nest, (2) identify factors that contributed to nest fate misclassification, (3) identify the nest predators and their predatory behaviors in our system and (4) determine the agents leading to misidentification of nest failures causes, especially predators, from nest remains. I was particularly interested in the effect of nest monitoring interval (days between nest visits) on misclassification rates of nest fates because weather and precocial behavior of chicks shorten the time that field evidence is available. The breeding grounds for Plovers and Interior Least Terns (*Sternula antillarum athalassos*; hereafter Terns*)* on the Missouri River in North Dakota provided a unique opportunity to evaluate our objectives. Both species are federally protected by The Endangered Species Act as endangered (Terns) or threatened (Plovers) (U.S. Fish and Wildlife Service 1985a, U.S. Fish and Wildlife Service 1985b). Two federal agencies, with different monitoring intervals, conducted productivity research and monitoring at the same sites during the same time period, allowing us to assess the effect of nest monitoring schedules on fate misclassification. Finally, the debate about whether predators can be identified from nest remains has yet to be addressed in our system, in which ground-nesting shorebirds use sparsely vegetated sand and gravel habitat, such as temporary sandbars and permanent islands exposed to frequent weather events that may alter evidence of nest fate (Shaffer *et al.* 2013).

Methods

Field Methods

This study was conducted on the Garrison Reach of the Missouri River in North Dakota, from the dam at Riverdale south to Bismarck, previously described by Shaffer *et al.* (2013), during May through August from 2013 to 2015. Field crews from two federal agencies simultaneously conducted research and monitoring all Tern and Plover nests found throughout the study area (refer to Shaffer *et al.* (2013) for a detailed description of the monitoring methodologies). The average clutch size for Terns is 3 eggs (1st attempt), incubated for 18-25 days (Thompson 1982, Kirsch 1996), while Plovers incubate 4 eggs/clutch (1st attempt) for 25 days (Cairns 1982, Whyte 1985, Haig & Oring 1988). Clutch age was calculated by egg floatation at the initial nest visit (Mabee *et al.* 2006, Shaffer *et al.* 2013). Egg floatation allowed researchers to estimate hatching date for nests of both species (assuming 18- and 25-day incubation periods for Terns and Plovers (Shaffer *et al.* 2013)). Fundamental differences between the two agencies included objectives, the number and size of crews, proportion of time spent using various nest searching methods and differences in how evidence was interpreted to determine nest fates (Table 1). One agency searched for and monitored nests as part of a focused research project on Tern and Plover productivity and use of available habitat. For this research project, crews searched for nests twice a week with additional nest visits for adult trapping and banding as well as checks for hatched chicks (hereafter referred to as 3-day monitoring). The primary objective of the second agency was compliance monitoring, which consisted of searching and monitoring suitable habitat for birds and nests once a week (hereafter referred to as 7-day monitoring).

Camera System Setup

To ensure a uniform sample distribution that encompassed the entire study area, cameras were installed at a subset of monitored nests, with the consideration that they were interspersed with non-camera nests and not spatially clumped within a segment of the river. However, due to the colonial nature of Terns, several cameras were active at once within a given nesting colony. The camera systems were installed at nests of both species after incubation reached a minimum of two days. A camera system was not removed until the nest was assigned a fate in the field by 3-day monitoring researchers.

Camera systems were designed to blend into the sand substrate associated with suitable Plover and Tern nesting habitat and included miniature infrared surveillance cameras (hereafter camera) equipped with 24 LEDs and 4.3-mm lenses (Jet Security USA, Buena Park, CA), sunshields, cushion clamps, bolts, screws, washers, 1.27 cm dowel rods, 25-30 m coaxial cables, weatherproof plastic cases (hereafter "DVR boxes"; SEAHORSE Protective Equipment Cases, Fuertes Cases, La Mesa, CA) silicate packets, digital video recorders (DVR) boards (Advanced Security, Bellevue, IL), 32-GB SD cards and 12 V, 35 Amp-hour batteries. Sunshields were cut on both sides to accommodate the cushion clamps, bolts and screws that anchored the cameras to the dowel rods. Holes were drilled on one side of the DVR boxes and were fitted with waterproof seals to allow coaxial cables to connect the DVR boards to the cameras and a power cable to the battery. All exposed connections between the camera and DVR board were wrapped in electrical tape to avoid exposure to water and sand that may disrupt the recording of video. DVR boards were equipped with 32-GB SD cards to record video and were housed in the DVR boxes with silicate packets to avoid moisture accumulation. The DVR box, battery (located 25-30 m from the nest) and coaxial cable were all buried in the sand. The camera was installed ≥ 1 m away from the nests at a height of 15 – 25 cm.

Nest Fate Classification and Predator Identification

Four nest fate categories were used by both agencies monitoring Plover and Tern nests: (1) successful—determined by at least one chick in the nest bowl, (2) probable successful—determined by estimated hatch date and secondary evidence left in and around the nest bowl by chicks (eggshells, pipping fragments, chick droppings/tracks, chicks near nest bowl or "on site"), (3) failed—determined primarily from estimated hatching date, eggshell evidence, status of the nest bowl and secondary signs left by predators and (4) unknown (3-day)—determined by the absence of eggs but no evidence observed or detected in or around the nest bowl or undetermined (7-day —reflecting incubation sufficient that eggs could have hatched but, evidence at the nest bowl to determine fate of either hatched or failed was lacking. Both programs used similar methods and cues in the field to fate nests based on evidence in and around the nest bowl. Once the brood vacated a nest, the fate was classified by both programs as probable successful if eggshells, pipping fragments, droppings, tracks or appropriately aged chicks "on site" (all considered secondary evidence) were observed in or around the nest bowl (Mabee 1997, Mabee *et al.* 2006). A nest was classified as failed if the eggs were under water (caused by water level rise), abandoned (the eggs were cold, embedded in sand, had condensation after three nest visits), infertile (determined by egg floatation), depredated or destroyed by livestock (eggs damaged, destroyed, displaced from the bowl or missing) or weather (hail, wind, erosion). If the eggs were missing, the nest was classified as failed if they could not have hatched based on the previously estimated incubation stage and projected hatching date (determined by egg floatation on the initial visit). If there was no evidence left in or around the nest bowl, the cause of nest failure was designated as no evidence by researchers.

A second independent fate was assigned to each nest based on video observation by a different individual from the personnel who assigned fates in the field. The presence of ≥ 1 chick in the nest bowl, observed on video, was interpreted as a successful nest. A nest was classified as failed if no chicks were observed hatching on video. If a predator was observed consuming or removing eggs on video, failure was attributed to depredation. We quantified which class (avian or mammalian) and species of predators were most common causes of nest failure. When the adults ceased incubation for > 24 hours on video, the fate was classified as abandoned. A nest was considered destroyed by livestock if cows or horses were captured on video walking around and interacting with the nest (e.g., feeding on eggs, crushing nest contents). A weather event was considered the cause of nest failure if the nest was destroyed (buried in sand or the eggs destroyed or displaced from the nest bowl) by wind or hail.

Data Analysis

I evaluated the accuracy of researchers using both monitoring intervals to correctly classify nest fates by comparing misclassification rates (number of nest fates misclassified based on field evidence / total number of nest fates verified by video observation). I used Program MARK (White & Burnham 1999) to estimate daily nest survival rates (DSR) for both species, based on the 3-day monitoring and videoed fates, to determine if there were any influences of cameras on nest survival. I used Wald tests to compare DSR between nests with and without cameras as well as nests located in areas with and without cameras. To assess the influence of informative censoring on nest survival estimates, I compared DSR for nests monitored by both cameras and the 7-day researchers. All fates for the camera nests were either successful or failed; whereas, the fates for nests monitored by 7-day researchers included successful, failed and unknown. All unknown nest fates classified in the field by researchers using both monitoring intervals were right-censored at the end of the last known survival interval (Manolis *et al.* 2000). Exposure days for nests monitored with cameras were calculated based on the actual date of fate recorded on video.

I was concerned that nest fate classifications may exhibit spatial autocorrelation or a lack of independence; therefore, I used SAM v4.0 (Rangel *et al.* 2010) to conduct a spatial analysis of nests fates to determine whether their distribution across the study area was random, clumped or evenly dispersed. Nest locations were grouped by similar distances into bins and a Moran's I, a measure of spatial autocorrelation, was estimated for each bin. If the nest fates located in each bin were distributed randomly, then the Moran's I = 0 and there is no spatial autocorrelation.

An ordinal logistic regression analysis in R version 3.4.3 (R Development Core Team 2017) was used to model nest fate, as the response variable, with three levels of classification: (1) misclassified, (2) partially misclassified and (3) correct. I defined a correct classification between field and video evidence if both nest fates were classified as successful or failed. A partial misclassification consisted of a nest fate classified as probable successful in the field and successful based on video observation. A probable successful fate is partially correct for a successful nest but, it represents an inherent uncertainty because secondary evidence was used to determine the presence of chicks rather than by direct observation. There were several different scenarios that led to an incorrect nest fate classification: (1) probable successful or unknown/undetermined by field evidence and failed by camera and (2) failed or unknown/undetermined by field evidence and successful by camera. Clutch age (CA), nest termination date (TD), time between visits (TBV), and species (Spp) were used as predictor variables in the regression analyses because previous research determined that they may influence nest fate classification (Williams & Wood 2002, Ball & Bayne 2012). I evaluated the accuracy of researchers from both agencies to estimate clutch age by using a paired *t*-test to analyze the difference between the actual (determined by video) and the estimated hatching date. Only successful nests that were found and monitored by both agencies and video were included in the clutch age analysis. The termination date was the actual day the nest was successful (first chick hatched) or failed (day the last egg was destroyed/removed or parents incubated) as determined from our video observation. Time between visits was calculated as the number of days between the penultimate and last visit to the nest, used as a measure of monitoring intensity. I implemented an information-theoretic approach using R package *MuMIn* (Barton 2018) and compared the differences between Akaike's Information Criterion corrected for small sample size (ΔAIC_c), Akaike model weight (w_i) and the residual deviances to select the models that best explained the variation in correct classification of nest fates (Burnham & Anderson 2002). Models that best described the data had the lowest ΔAIC_c scores, the largest model weights and a residual deviance that was lower compared to the null (Burnham & Anderson 2002).

I determined misclassification of nest failure causes by comparing 3-day monitoring fates determined from field evidence to ones from video observation. Causes of failed nest fates determined from field evidence were categorized as avian and mammalian depredation, livestock and weather destruction, abandonment and unknown, which included nest fates that were classified by researchers as "no evidence" or "unspecified predator". I defined five categories of nest failure causes based on video observations: (1) avian depredations, (2) mammalian depredations, (3) destruction by livestock, (4) destruction by weather and (5) abandonment. Predatory behaviours observed on camera were also described and compared to determine inter- and intra-specific similarities between species, which may lead to misidentification of nest failure causes.

Results

I installed cameras at 154 nests (65 of 294 Tern and 89 of 551 Plover) under observation as part of the 3-day monitoring effort. Only nests for which fate was determined by 3-day monitoring researchers from both field evidence and video recordings were used in the analyses (138 camera nests: 57 Tern and 81 Plover). I excluded 16 camera nests from our analyses for the following reasons: the camera was prematurely removed from one Plover nest to avoid destruction by horses present in the area and 15 nest fates were not recorded on video due to camera malfunction. Because the 7-day monitoring researchers were unaware of camera nest locations, they only found and monitored 109 camera nests (48 Tern and 61 Plover). On average, nests were found, before camera installation, at a clutch age of < 1 day ± 1.92 sd (min = 0 days, max = 14 days, median = 0 days) compared to 9 days ± 7.38 sd (min = 0 days, max = 23 days, median = 8 days) using the 3- and 7-day monitoring intervals. The estimated hatching dates were statistically different ($t = 3.2$, $df = 34$, $P = 0.0033$) and more accurate for the 3-day ($\bar{x} = 1.9$ days ± 1.7 sd, min = 0 days, max = 6 days, med = 2 days) compared to the 7-day monitoring program ($\bar{x} = 3.4$ days ± 2.5 sd, min = 0 days, max = 10 days, med = 3 days). For both species, there was no significant difference between the DSR for nests monitored with cameras than without cameras (Plovers: $\chi^2 = 3.28$, $P = 0.05$; Terns: $\chi^2 < 0.01$, $P = 0.98$; Fig. 1a). I also found no significant difference for nests located on sandbars and islands with cameras compared to nesting areas with no camera monitoring (Plovers: $\chi^2 = 3.28$, $P = 0.07$; Terns: $\chi^2 = 0.10$, $P = 0.76$; Fig. 1b). There was no large-scale spatial correlation between nest fate classifications across the entire study area (average Moran's I = -0.008 $n = 40$ distance classes). I found that there was a small positive spatial correlation for nests located at shorter distances from each other (the first bin had a distance of 124 m with Moran's I = 0.181 ± 0.062 se, $P = 0.003$)).

Nest Fate Accuracy

I determined by video observation that 90 of 138 total camera nests were successful (the remaining 48 failed) for the 3-day monitoring effort (actual time between last and penultimate visits $\bar{x} = 3.42$ days ± 2.8 sd, min=1 day, max = 23 days, median = 3 days). Compared to video observation, researchers using the 3-day monitoring interval correctly classified 99 nest fates (56 successful and 43 failed), for a 72% correct classification rate (Table 2). Eleven nest fates were misclassified (8%) by the 3-day monitoring researchers in the field: nine unknown (five successful and four failed), one as probable successful (failed) and one as failed (successful). Video reviewed by researchers revealed that the misclassified probable successful nest was destroyed by weather and that all eggs hatched in the successful nest misclassified as failed. Video also revealed that 28 nest fates were partially misclassified (20%), in that they were classified as probable successful from field evidence (correct but researchers were not 100% certain because a chick was not observed in the nest bowl, introducing uncertainty into the nest fate) but, were actually successful.

I determined from video observations of 109 total nests that the 7-day monitoring effort (actual time between last and penultimate visits $\bar{x}$ = 8.1 days ± 1.7 sd, min=5 days, max = 14 days, median = 8 days) correctly fated 30 (16 successful and 14 failed, 27.5%), partially misclassified 49 (45%) and fully misclassified 30 nests (27.5%; Table 2). The 30 misclassified nests included: 1) two as probable successful when they failed, 2) three as failed when they were successful and 3) 25 as undetermined when 12 hatched and 13 failed. The 12 successful nests that were misclassified as undetermined consisted of nine Tern and three Plover nests. Likewise, the 13 failed nests that were misclassified as undetermined consisted of three Tern and 10 Plover nests. More successful and failed nests were misclassified for Terns and Plovers respectively. The DSR for the nests monitored by 7-day researchers (Tern DSR = 0.9895, 85% CI = 0.9834 – 0.9957, Plover DSR = 0.9896, 85% CI = 0.9846 – 0.9946) was greater compared to the estimate based on video (Tern DSR = 0.9889, 85% CI = 0.9839 – 0.9939, Plover DSR = 0.9876, 85% CI = 0.9835 – 0.9917). I determined that the correct classification rate for the 3-day monitoring (72%) was higher compared to the 7-day monitoring (27.5%). The 7-day monitoring effort had a higher percentage of partially misclassified nest fates (45%) compared to the 3-day monitoring effort (20%) for nests that were classified from field evidence as probable successful and successful from video observation. The researchers from the 3- and 7-day monitoring intervals misclassified 8% and 27.5% of nest fates respectively.

Ordinal Logistic Regression Models

For the ordinal logistic regression analyses, I pooled all of the data across the three study years due to small samples sizes. I found that CA (age in days of the nest when it failed or hatched) was the most important predictor of nest fate classification for the 3-day monitoring effort (included in all of the top models and accounting for 90.7% of the w_i) followed by Spp (two models), TBV (three top models) and TD (one model, Table 3). From the top six models, I considered 4-6 as noncompetitive due to the addition of an uninformative parameter (TD) that lowered the ΔAIC_c score but did not significantly improve model fit (residual deviance) or w_i. I concluded that the top two models explained the most variation in the 3-day monitoring nest fate classifications because they had similar AIC_c scores, w_i and residual deviances. However, I used parameter estimates from model two (CA+Spp+TBV) to calculate odds ratios (Table 4) because it better fit the data (smaller residual deviance = 188.0) and had a similar w_i compared to the top model (CA+Spp). Model three (CA+TBV) was also considered competitive because it was not nested within one of the top-ranking models (the same model but with additional parameters), it accounted for 11.5% of the w_i and reduced the residual deviance (191.5) compared to the null model (210.7). For each day that CA increased, 3-day monitoring researchers were 1.2 times less likely to correctly classify the nest fate of both species (Table 4). I found that the misclassification rate was 95 and 27 times greater for Plover and Tern nests that were near hatching (25- and 18-day clutch ages) compared to nests that were assigned a nest fate earlier in incubation (closer to the laying period). For Plover nests, 3-day researchers were 2.75 times more likely to correctly classify the nest fate. Three-day researchers were 1.1 times less likely to correctly classify a nest fate as the TBV (final visit – penultimate visit in days) increased per day. Under 3-day monitoring, researchers were 1.3 times less likely to correctly classify the nest fate if TBV was three days.

For the 7-day monitoring interval, TD (date nest was fated in the field) was the most important predictor of correct fate determination, with models including that parameter accounting for 99% of the model w_i. However, I only considered the top two and the fifth models as competitive because models 3-4 and 6-8 were nested models with the addition of uninformative parameter(s), which did not improve model fit or increase w_i. Nest fate classification for the 7-day monitoring effort was also influenced (on a lesser scale compared to termination date) by CA (included in two top models) and Spp (included only in the top model). I calculated odds ratios from model parameter estimates obtained from the top model (CA+TD+Spp) with the lowest $\mathrm{AIC_c}$ and the best model fit (residual deviance = 219.0). As TD increased by one day, researchers from the 7-day monitoring effort were 1.05 times more likely to correctly classify a nest fate. Nests terminated 30 days later in the nesting season were 4.32 times more likely to be correctly classified. If the nest was a Plover, 7-day monitoring researchers were 2.46 times more likely to correctly classify the nest fate. Seven-day researchers were 1.11 times less likely to correctly classify a nest fate as CA increased by one day. In other words, fate misclassification was 18.6 and 6.5 times more likely for Plover and Tern nests at later stages of incubation using a less intense (longer) monitoring interval.

Causes of Nest Failures

Types of Plover nest predators and number of depredation events captured on camera included: one Red Fox, ten American Crows, nine Black-billed Magpies (*Pica hudsonia*), one juvenile Bald Eagle (*Haliaeetus leucocephalus*), one Great Horned Owl (*Bubo virginianus*), one Raccoon and two Coyotes. Tern nest predators identified on camera included two Black-billed Magpies, two Raccoons, one Great Horned Owl and one Striped Skunk (*Mephitis mephitis*). All of the Magpies, seven Crows and one Red Fox recorded on video depredating nests removed the eggs individually over the span of several minutes to multiple days. I observed three Crows, all

Raccoons, Coyotes and one Skunk destroying and consuming the eggs at the site. No partial depredations resulted in abandonment; all adults returned to the nest and resumed incubation until the last egg was depredated. There were two unusual predators that were recorded on video depredating nests, including a juvenile Bald Eagle at a Plover nest and two Great Horned Owls at nests of both species (Fig. 2). The juvenile Bald Eagle broke and consumed the eggs at the Plover nest site while both Great Horned Owls consumed the eggs whole at the nests of both species.

I used 43 failed nests (13 Tern and 30 Plover) correctly classified by researchers using the 3-day monitoring interval to evaluate their accuracy to identify the cause of failure (Table 5). Video revealed that camera nest failures were caused by avian (46.5%) and mammalian (16.3%) depredations, livestock destruction (2.3%), weather (7.0%) and abandonment (27.9%). Using these video observations, I determined that the 3-day monitoring researchers incorrectly identified the causes of 23 failed nests (53.5% misclassification rate). Researchers were unable to identify the cause of 19 failed nests due to lack of evidence in the field, wherein the actual causes included: 1) avian predators (14), 2) mammalian predators (4) and 3) abandonment by adults (1). Two nests were classified as failed due to livestock destruction and researchers confirmed from video observation that one cause was correctly identified while the other was actually abandoned by the adults. Researchers using field evidence misidentified abandonment as the cause of a failed nest, when video observation revealed it was actually destroyed by weather. Four failed nests that were incorrectly identified as destroyed by weather and livestock and no evidence in the field were actually verified by researchers using cameras as abandoned (Table 5). Avian predators accounted for the nest failure cause that was misidentified the most by researchers (61%), followed by mammals and abandonment (each 17%) and weather (4%).

Discussion

I believe that this is the first large scale study to use video cameras to evaluate the accuracy of shorebird monitoring in fating nests from field evidence and to identify specific factors that influence misclassification. Both Terns and Plovers are federally protected, and therefore it was important that the camera systems did not negatively influence nest survival. I believe based on previously published literature that the slightly higher DSR of camera nests, although not statistically significant, for both species can be attributed to later stages of incubation (≥ 2 days) when cameras were installed (Pietz & Granfors 2000). It is widely documented that nests later in incubation have a higher probability of survival (Richardson *et al.* 2009). There were a number of nests, especially Plover nests, which did not have the opportunity for camera monitoring because they never reached two days of incubation before failure. I took special care to avoid clustering of cameras in nesting areas to prevent instances of predator attraction or avoidance to camera systems, which may have reduced learned predator behaviors toward our systems (Pietz & Granfors 2000). When clustering of cameras did occur due to the colonial nature of Terns as well as reduced available nesting habitat, I observed that both camera and non-camera nests in the same colonies were depredated equally by corvids, specifically American Crows and Black-billed Magpies. Based on the similar DSR between areas with and without camera nests, I concluded that the corvids were not drawn specifically to any of the cameras, a behavior that would decrease nest survival (which was not reflected in the DSR).

My primary objective was to estimate misclassification rates, as well as identify factors contributing to incorrect identifications, of nest fate using field evidence in and around the nest. Nest fate determination on the Missouri River is especially difficult because frequent weather events, such as high winds and precipitation, often altered or destroyed evidence of nest outcomes in a short amount of time. The rate of correct classification for both shorebird species by 3-day monitoring researchers was slightly lower than the rates of ≥ 80% reported for songbirds in mature mixed wood boreal forests of western Canada (Ball & Bayne 2012), grassland passerines in North Dakota (Pietz & Granfors 2000) and Wood Thrushes in West Virginia (Williams & Wood 2002). I attributed the lower rate of correct classification in our system to weather events that destroyed field evidence of nest fates in a very short period of time, the volume of suitable habitat needed to be searched (>1500 ha on the Missouri River alone from the Garrison Dam to Bismarck) and the increased number of nests resulting from more habitat. For example, one nest hatched on 27 June 2014 and blowing sand from a wind storm on 28 June 2014 destroyed all evidence of hatching as well as the original nest bowl before the researchers could visit, resulting in an unknown nest fate.

There has been considerable variation in the approaches to handle unknown nest fates in survival estimations but, if successful and failed nests do not have the same probability of exclusion, then estimates may be biased due to informative censoring (Manolis *et al.* 2000). For example, the ratio of successful/total nests determined from video observation (65%, 90/138) was similar to the proportion of successful/total unknown fates (55%, 5/9) classified from using a shorter monitoring interval (3-days). These similar proportions of successful nests may result ultimately in negligible bias due to informative censoring. In contrast, 73% (80/109) of nest fates classified by researchers using the 7-day monitoring interval were successful. However, the longer monitoring interval resulted in a much smaller proportion of successful to total unknown nest fates (44%, 11/25). The longer monitoring interval resulted in different proportions of known to unknown successful nests (73% true value determined by camera vs 44% classified as unknown based on field evidence), which resulted in positively biased survival estimates. Overall survival estimates, based on the nest fates determined from 7-day monitoring, were overestimated by 1% and 4% for Terns and Plovers. A shorter monitoring interval can significantly decrease the probability of unknown nest fates, thus reducing the need to right-censor fates for nest survival analyses and improve estimates.

Factors that influenced misclassification of nest fates included clutch age, monitoring interval, species breeding attributes, and termination date. Since both monitoring programs based many of their nest fate classifications on estimates of clutch age and projected hatch dates, it is crucial that these estimates be accurate. I found that the egg floatation method produced hatch date estimates that were closer to the actual date than the 2.1 ± 2 days reported by Mabee *et al.* (2006) when utilized in combination with experienced researchers conducting systematic nest searching with decreased monitoring intervals (regular nest searches and checks every 3 days). However, there were other fundamental differences, besides experienced researchers, systematic nest searching and decreased monitoring intervals, between the two monitoring programs that may have influenced the accuracy of clutch age estimates and therefore nest fate classifications. For all 3 years of this study, the 7-day monitoring researchers began regular nest searching and monitoring, on average, 10 days later than the other agency. Therefore, early-stage nests that failed before the start of the 7-day monitoring interval would be unknown to those researchers.

Additionally, the longer nest monitoring interval, fewer personnel with less experience and more area to search resulted in nests that were found later in clutch age, resulting in a less accurate estimated hatch date and more difficult nest fate determination. The fact that termination date influenced nest fate misclassification indicates that 7-day monitoring researchers were more likely to correctly fate nests later in the season. This result may indicate that researchers improved their skills at nest fate classification or that their ability to locate nests earlier in incubation improved, leading to more accurate estimates of hatch date. Increased attention to training field technicians in order to increase accuracy of nest fate classification was a solution previously reported by Ball and Bayne (2012). To increase accuracy of clutch age estimates and reduce classification uncertainty, researchers should implement a more intensive monitoring program (approximately 3 days between nest searching with additional visits as estimated hatch data approaches) because it allows more nests to be found earlier in the nest-laying and incubation stages (Mabee 1997) as well as decreases the likelihood that external factors will alter evidence of fate in and around the nest bowl. This technique is currently the standard used to conduct research on shorebirds in the Arctic (pers comm. Paul Smith and Jeroen Reneerkens). There were several circumstances that prohibited the 7-day monitoring program from implementing a more frequent interval to monitor shorebird nests: (1) their primary objective was compliance monitoring for the Endangered Species Act, (2) the species was protected by federal laws, (3) a large study area and (4) too few personnel. All of these circumstances may influence shorebird monitoring in other areas as well. If a primary objective of monitoring is not nest predator identification, then nest visits can be kept at a minimum during early stages of incubation and more time should be spent nest searching. Researchers should also take into account breeding characteristics of the particular focal species during the development of nest monitoring schedules. For example, Plover nests that had larger clutch sizes and longer incubation periods were more likely to be correctly classified than Terns during this study. For species with short incubation periods, researchers should be aware that there is less amount of time that an early-stage nest can only be fated as failed, based on estimated hatching date. Likewise, smaller clutch sizes decrease the amount of time chicks are in the nest bowl, increasing the probability that researchers will misclassify nest fate. Care should be taken that nest monitoring does not negatively influence normal nesting behaviors and ultimately nest survival.

The ability to correctly identify causes of nest failure will increase understanding of the limiting factors, such as predation, and the predator community that influence the population dynamics of various orders of avian families as well as provide improved estimates of predation rates. I found that the predator community for Plovers and Terns on the Garrison Reach of the Missouri River was similar to others reported by studies conducted in the United States, except for gull and snake predation (DeVault *et al.* 2005, Ivan & Murphy 2005, Sabine *et al.* 2006, White *et al.* 2010). Accordingly, I was able to verify many of the reasons originally proposed by Larivière (1999) and Pietz and Granfors (2000) about why predators cannot accurately be determined from nest remains. Knowledge of the predator community and predatory behaviors may provide information that will improve habitat characteristics that will decrease nest vulnerability to predation (Pietz & Granfors 2000). Inter- and intra-specific predatory behaviors may mislead conclusions about the current predator community as well as potential management strategies to reduce nest predation. If predator identification is a primary objective, then nest visits can be scheduled more frequently throughout the nesting stages or the incorporation of cameras into the study design may be considered. During the development of nest monitoring programs, principal investigators can research the likely composition of the predator community present in their systems, determine all of the common predatory behaviors that may be observed during nest monitoring and consider the incorporation of cameras to assist in the interpretation of ambiguous or nonexistent evidence of predators left at nests.

The use of video cameras can be an expensive technique to incorporate into monitoring programs. For our study, I continuously deployed ≈ 35 camera systems, costing $700-800 each, on multiple nests throughout the summer for three years. I was able to monitor 51 nests of both Plovers and Terns on average per year. However, the camera systems failed to record fates for 10% of the videoed nests, primarily due to loss of battery power during increased temperatures later in the nesting season. Since increases in heat reduce battery life, exchanging batteries in the field more frequently may improve the reliability of video monitoring. Additionally Burr *et al.* (2017), using a similar camera system, monitored 163 Sharp-tailed Grouse (*Tympanuchus phasianellus*) nests across 185.9 km^2 divided between two study sites in one season. Williams and Wood (2002) monitored three Wood Thrush nests per camera system per season using only 9 total systems. Depending on the study area size or nest density, it may be unproductive and cost inefficient to monitor all nests with video cameras, rather a subsample should be selected based on study objectives, nest survival rates, incubation length, accessibility of nests and size of the study area (Williams & Wood 2002). Alternatively, temperature data loggers are a less expensive, intrusive and smaller option that have also been successfully utilized to accurately monitor nest survival rates and nesting behaviors (Hoover *et al.* 2004, Hartman & Oring 2006, Weidinger 2006, Schneider & McWilliams 2007, Moreau *et al.* 2018). However, disadvantages of data loggers are that predators as well as predatory and nest defense behaviors cannot be determined.

The use of video cameras in monitoring programs for avian populations allows the evaluation of nest monitoring techniques. Their use may also improve the accuracy of demographic estimates, which lead to a greater understanding of population dynamics and the effect of management actions. It is possible to continuously monitor multiple nests of a population throughout the reproductive season with video cameras to increase the accurate identification of predators and fates, as well as document all nesting activity. Recent technological advances increased the ease to adapt and incorporate digital camera systems into experimental design methods to study avian nesting ecology, especially for shorebirds. Camera systems reduce time and number of research visits to the nest, which may mitigate possible negative impacts to parental behavior. Video cameras allow the investigation of a variety of questions, while reducing the number of visits by researchers at the nest, including research activity effects, parental behavior adaptations, fledging rates and weather influences. Many of these questions, which are highly relevant to management plan development, would be otherwise logistically impossible to address with only field personnel (Cox *et al.* 2012, Ellis-Felege *et al.* 2012).

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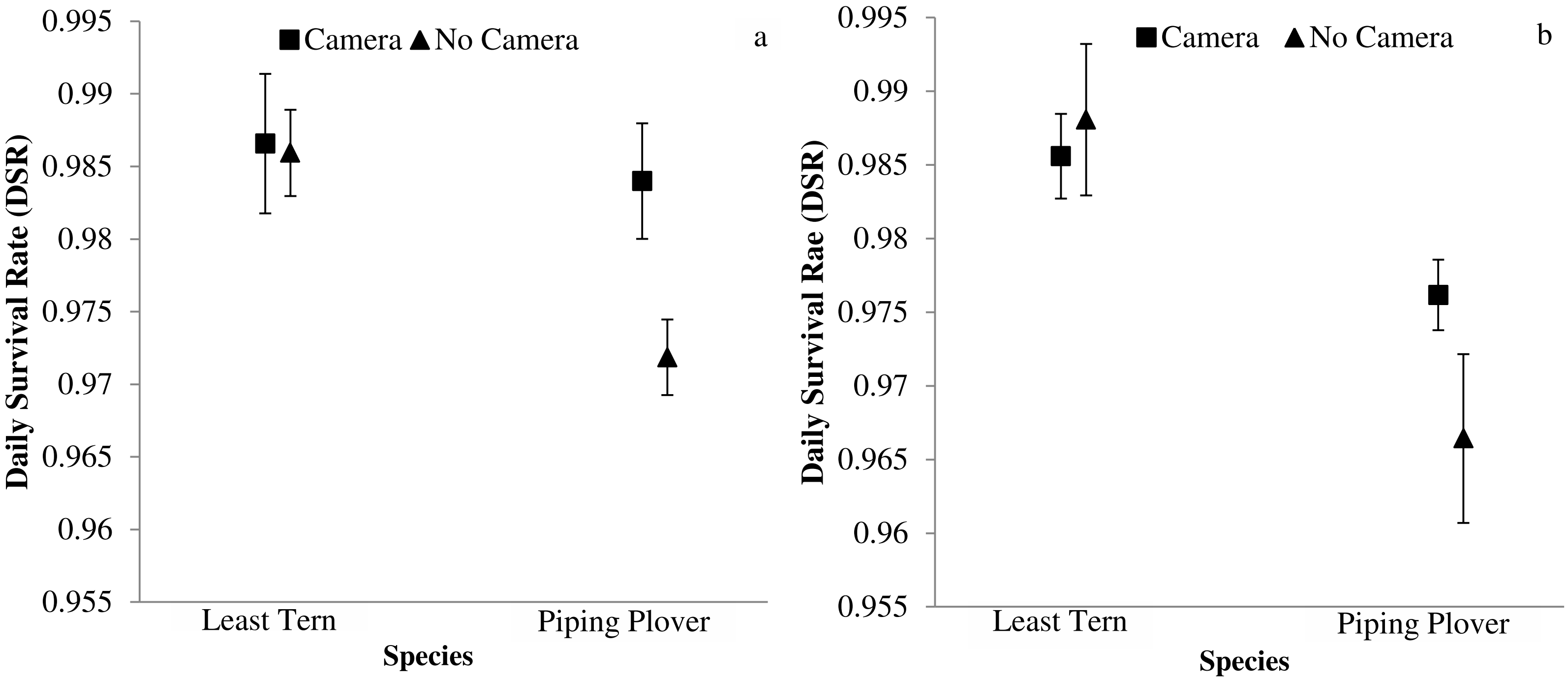

Figure 1. Daily nest survival rates with 85% confidence intervals (Arnold 2010) of Interior Least Tern (*Sternula antillarum athalassos)* and Piping Plover nests (*Charadrius melodus*) (a) with and without cameras and (b) at sites with cameras and sites with no cameras on the Missouri River in North Dakota from 2013-2015.

Figure 2. Unusual avian predators of Interior Least Tern (*Sternula antillarum athalassos)* and Piping Plover (*Charadrius melodus*) nests on the Missouri River in North Dakota. Images were taken from miniature surveillance cameras installed at nests and depict (a) a Great Horned Owl (*Bubo virginianus*) swallowing whole eggs and (b) a juvenile Bald Eagle (*Haliaeetus leucocephalus*) destroying and consuming the eggs at a nest site.

Table 1. Comparison between the different components of a 3- and a 7-day monitoring interval for Interior Least Tern (*Sternula antillarum athalassos)* and Piping Plover (*Charadrius melodus*) nests on the Missouri River in North Dakota from 2013-2015.

Components	Nest Monitoring Intervals	
	3-Day	7-Day
Objective	• Evaluate the impacts of the 2011 flood on Interior Least Tern and Piping Plover productivity	• Monitor trends in Interior Least Tern and Piping Plover populations
Number of Crews	• 4	• 1
Size of Crews	• 4 people in 2013-2014 • 2 people in 2015	• 4-9 people in 2013-2015
Nest Search Methods	• ≈75% systematic grid and 25% opportunistic searching of habitat in 2013-2014 • 100% opportunistic searching of habitat in 2015	• ≈75% opportunistic and 25% systematic searching of habitat in 2013-2015
Nest Fate Categories	• Successful, Probable Successful, Failed, Unknown	• Successful, Probable Successful, Failed, Undetermined

Nest Fate Evidence	• Successful – chick(s) in nest bowl
	• Probable Successful
	  • Pipping fragments
	  • Chick tracks
	  • Chick droppings
	  • Eggshells
	  • Chicks observed near nest bowl[1]
		• Successful – chick(s) in nest bowl
		• Probable Successful
		  • Pipping fragments
		  • Chick tracks
		  • Chick droppings
		  • Eggshells
		  • Chicks on Site (Site is defined as the area that contains the nest were they hatched. Chicks must be of appropriate age to have hatched from suspected nest based on estimated hatch date)[2]

[1] Used only in combination with other evidence of a probable successful nest fate

[2] Chicks are observed on site. The chicks observed must be the appropriate age to have hatched from the nest. Can be used independently without other secondary evidence of chicks to fate a nest as probable successful

Table 2. The accuracy of nest fate classification by researchers using two different monitoring intervals (3- and 7-day) to classify fates of 57 Interior Least Tern (*Sternula antillarum athalassos*) and 81 Piping Plover (*Charadrius melodus*) nests on the Missouri River in North Dakota from 2013-2015. Fates were verified independently using video cameras installed at the nest of both species.

	Nest Fate Classification Rates						
	Correct		Partially Misclassified		Misclassified		Total
Monitoring Interval	N	%	n	%	n	%	n
3-day	99	72%	28	20%	11	8%	138
7-day	30	27.5%	49	45%	30	27.5%	109

Table 3. Model-selection results for ordinal logistic regression analyses of 3- and 7-day monitoring programs to correctly classify Interior Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius melodus*) nest fates on the Missouri River in North Dakota from 2013-2015. Accuracy was determined by comparing nest fate determination between traditional nest monitoring methods and methods based on video camera monitoring. The response variable, identification of nest fate, was an ordered multinomial with three outcomes: misclassified, partially misclassified and correct. Covariates include clutch age (age in days of a nest when it fails or hatches, CA), termination date of nest in days (TD), species (Spp) and time between nest visits (number of days between the final and penultimate nest visits) during the interval in which the nest hatched or failed (TBV).

	Model	**AIC_C[a]**	**ΔAIC_c[b]**	**w_i[c]**	**K[d]**	**RD[e]**
3-day	CA + Spp	198.2	0	0.248	4	189.9
	CA + Spp + TBV	198.4	0.2	0.224	5	188.0
	CA + TBV	199.8	1.54	0.115	4	191.5
	CA + Spp + TD[f]	199.8	1.59	0.112	5	189.3
	CA + Spp + TBV + TD[f]	199.9	1.74	0.104	6	187.3
	CA + TBV + TD[f]	200.0	1.75	0.104	5	189.5
	CA	201.6	3.38	0.046	3	195.4
	CA + TD	201.6	3.39	0.046	4	193.3
	Null	214.8	16.61	0	2	210.7
7-day	CA + TD + Spp	229.6	0	0.258	5	219.0
	CA + TD	230.2	0.58	0.193	4	221.8
	CA + TD + TBV[f]	231.1	1.50	0.121	5	220.5
	CA + TD + Spp + TBV[f]	231.2	1.66	0.112	6	218.4
	TD	231.3	1.69	0.111	3	225.1
	TD + TBV[f]	231.5	1.95	0.097	4	231.2
	TD + Spp[f]	233.4	3.84	0.038	4	233.0
	TD + Spp + TBV[f]	233.7	4.11	0.033	5	223.1
	Null	237.3	7.70	0.005	2	233.2

[a] Akaike's Information Criterion corrected for small sample sizes

[b] AIC_c distance of a model from the lowest AIC_c model

[c] w_i Weight of a model

[d] The number of parameters estimated in the model

[e] Estimate of model goodness of fit

[f] Model has minimal support (Burnham and Anderson 2002)

Table 4. Parameter estimates and odds ratios for 3- and 7-day nest monitoring intervals to correctly classify, misclassify or partially misclassify Interior Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius melodus*) nest fates using field evidence compared to video observation. Odds ratio is the likelihood of a correct nest fate classification given the associated covariate. Covariates include termination date of nest in days (TD), species (Spp_PIPL), clutch age in days (age in days of a nest when it fails or hatches, CA) and time between nest visits ((number of days between the final and penultimate nest visits) during the interval in which the nest hatched or failed, TBV).

Covariate	Estimate (± 85% CI)				se		Odds Ratio (± 85% CI)			
	3-Day	85% CI	7-Day	85% CI	3-Day	7-Day	3-Day	85% CI	7-Day	85% CI
Intercept(Inc|Part)[a]	-7.13	-	5.16	-	1.30	2.49	-	-	-	-
Intercept(Part|Cor)[b]	-5.42	-	7.30	-	1.23	2.55	-	-	-	-
CA	-0.173	-0.252– -0.105	-0.101	-0.162– -0.042	0.051	0.041	0.841	0.777–0.900	0.904	0.850–0.959
Spp_PIPL[c]	1.01	0.227–1.87	0.90	0.122–1.69	0.566	0.544	2.75	1.25–6.49	2.46	1.13–5.42
TBV	-0.094	-0.200–0.003	-	-	0.069	-	0.910	0.819–1.00	-	
TD	-	-	0.048	0.02–0.068	-	0.014	-	-	1.05	1.03–1.07

[a] Incorrect|Partial

[b] Partial|Correct

[c] Piping Plover nest fates compared to Least Terns

Table 5. Comparison of 3-day monitoring in the field (estimated) and video camera (actual) monitoring to determine the fate causes of 13 Interior Least Tern (*Sternula antillarum athalassos)* and 30 Piping Plover nests (*Charadrius melodus*) that failed on the Missouri River in North Dakota from 2013-2015. Causes of nest fates determined by video observation were classified into 5 categories: avian, mammalian, livestock, weather and abandonment. If the predator could not be determined or there was no evidence of the nest fate cause, it was classified as unknown.

Actual Fate	Estimated Fate					
	Avian	Mammalian	Livestock	Weather	Abandoned	No Evidence
Avian	6	0	0	0	0	14
Mammalian	0	3	0	0	0	4
Livestock	0	0	1	0	0	0
Weather	0	0	0	2	1	0
Abandoned	0	0	1	2	8	1

CHAPTER III

SHOREBIRD NESTING BEHAVIORS AND NEST PREDATION RISK IN RESPONSE TO RESEARCH ACTIVITIES

Abstract

Most, if not all, avian reproductive research requires repeated visitation to monitor nests. However, research activities at and around the nest may alter normal adult nesting behaviors, which ultimately may negatively influence nest survival. I used video cameras installed at the nests of Least Terns and Piping Plovers on the Missouri River in North Dakota to evaluate the influence of various research activities on three temporal scales: 1) an immediate impact on nest attendance, 2) an effect on daily nest attendance and 3) an overall observer effect impacting nest predation risk. Adults of both species spent more time absent from the nest (Least Tern=39.7% ± 0.023 se, Piping Plover=26.5% ± 0.019 se) when researchers were present at the nest or in the surrounding area compared to 1 hour directly pre (Least Tern=13.0% ± 0.013 se, Piping Plover=10.1% ± 0.01 se) and post (Least Tern=13.0% ± 0.013 se, Piping Plover=12.2% ± 0.012 se) the research activity time period (n = 70 nests, total number pre, during, post research activity time periods = 1,569). Similar attendance patterns pre and post research activities suggests the adults recover normal nesting behaviors quickly after the researchers vacate the nesting area. Additionally, daily nest attendance was lower on days with research activities (Least Terns=90.7% ± 0.017 se, Piping Plover=90.8% ± 0.012 se) compared to ones with no occurrence (Least Tern=93.2% ± 0.017 se, Piping Plover=91.7% ± 0.013 se). I found predation risk was

4.995 times more likely for a nest with one research activity/day compared to one without exposure to activities. A more realistic monitoring scenario is a predation risk 1.7 times greater (85 % CI=1.612 –1.793) for a nest visited on a 3-day monitoring schedule (0.33 daily research activity rate) compared to a nest subjected to no daily research activities. Based on the results of this study, I suggest that research and monitoring protocols be designed to minimize activities at and around shorebird nests to reduce disturbance to nesting behaviors and predation risk.

Keywords: Least Tern, Piping Plover, research activities, observer effect, nest predation risk, nesting behaviors, Cox proportional hazards model, *Sterna antillarum athalassos*, *Charadrius melodus*

Introduction

Repeated research activities at and around avian nests are necessary to determine important rates that influence population dynamics such as nest success, fledgling recruitment and adult survival. However, observer effects from repeated research activities may alter parental nesting behaviors (Sandvik & Barrett 2001, Verboven *et al.* 2001, Stien & Ims 2016) and may bias breeding estimates that are vital to management and conservation of avian populations (Rotella *et al.* 2000, Weidinger 2008, Stien & Ims 2016). There is evidence that nests left unattended at a higher rate by adults due to research activities are more vulnerable to predation (Götmark 1992). Additionally, unattended shorebird eggs at the Salton Sea in California overheated, which caused embryo death within two minutes (Grant 1982). Since human presence can modify predator behavior (Pietz & Granfors 2000) and predators are the leading cause of nest failures for most ground-nesting avian species (Martin 1993), nest predation is often cited as the mechanism that drives observer influences on nest success. In particular, predators may be attracted or deterred from human presence; therefore, research activities may increase or decrease nest predation, depending on the focal species, field methodologies and the predator community (Pietz & Granfors 2000, Weidinger 2008).

There are three primary responses of predators to the occurrence of research activities at nests (Weidinger 2008). First, there is an immediate (short-term) response from the predator – either the research activity exposed the nest location or caused the adults to leave the site, preventing defense of the nest. In this case, depredation of the nest would occur within hours (< 24 hours) of the research activity. Second, olfactory or visual signs, left by the researchers, may modify the behavior of a predator (attract or deter from a nest) at a later date (> 24 hour after the activity). This is a long-term effect in which the cues (the measure of effect) will gradually decrease as the time since last visit increases. Finally, the observer effect at a nest may be permanent (i.e. damage to concealment is irreparable, artificial signs left to mark location, obvious nest-monitoring tools). Predator behavior modification to a permanent observer effect is predicted to be independent of the timing of last research activity (Weidinger 2008). One goal of experimental or observational study designs is to maximize data collection while simultaneously minimizing disturbance from research activities. Observer effects cannot be minimized without first understanding if and how predators respond to research activities.

Past studies have published mixed results about the overall impact of observer effects on nesting behaviors and nest success, with the majority of research reporting decreased nest attendance but little to no effect on nest success (Götmark & Åhlund 1984, Nichols *et. al* 1984, MaCivor *et al.* 1990, Hannon *et al.* 1993, Shealer & Haverland 2000, Bêty & Gauthier 2001 Sandvik & Barrett 2001, Verboven *et al.* 2001, Keedwell & Sanders 2002, Weidinger 2008, Ibáñez-Álamo *et al.* 2011). However, this past research relied on abbreviated observational measurements to estimate nest attendance as well as predator presence and behaviors. For this study, I used video cameras to continuously monitor individual Least Tern (*Sternula antillarum athalassos*; hereafter referred to as "Terns") and Piping Plover (*Charadrius melodus*; hereafter referred to as "Plovers") nests to assess the impact of observer effects on: (1) immediate nest attendance during research activities, (2) daily nest attendance and (3) nest predation risk. The breeding grounds for Plovers and Interior Least Terns on the Missouri River in North Dakota provided a unique opportunity to evaluate our objectives. Since both species are federally protected by The Endangered Species Act as endangered (Terns) or threatened (Plovers) (U.S. Fish and Wildlife Service 1985a, U.S. Fish and Wildlife Service 1985b), both populations are exposed to extensive monitoring and research. These circumstances allowed me to quantify the impacts of multiple different research activities on nesting behaviors. I expected that there would be both an immediate increase of time absent from the nest during research activities as well as a prolonged decline in daily nest attendance on days when researchers were present and that these nesting behavior differences would increase predation risk. The use of continuous camera monitoring provided direct measurements of research activity impacts on adult nest attendance and timing of nest predation, which permits a more thorough evaluation of the relationship between observer effects, nesting behaviors and nest predation.

Methods

Study Area and Species

This study was conducted on the Garrison Reach of the Missouri River in North Dakota, from the dam at Riverdale south to Bismarck, previously described by Shaffer *et al.* (2013), during May through August from 2013 to 2015. Both Terns and Plovers are small, ground-nesting shorebirds that select open, sparsely vegetated sand habitat with pebbles or gravel, such as coastal and riverine shorelines, temporary sandbars and permanent islands (Anteau *et al.* 2012, Sherfy *et al.* 2012, Stucher e*t al.* 2013). The nest predator community was previously described by Andes e*t al*. (2018), with the majority of nests depredated (76%) by American Crows (*Corvus brachyrhynchos*) and Black-billed Magpies (*Pica hudsonia*).

Field Methods

Field crews, consisting of 2-4 personnel, searched all suitable nesting habitats and monitored all Tern and Plover nests found throughout the study area on a 3-day schedule (refer to Shaffer *et al.* (2013) for a detailed description of the monitoring methodologies). Additional research activities were conducted outside of the monitoring schedule to trap adults, check nest status, install cameras, re-sight band combinations and band chicks (Shaffer *et al.* 2013). Therefore, there were instances when more than one research activity occurred at a nest or in a nesting area on a daily basis. Once a nest was found, clutch age was calculated by egg floatation at the initial nest visit (Mabee *et al.* 2006, Shaffer *et al.* 2013). Video camera systems were installed at a subset of nests after incubation reached a minimum of two days and were not removed until a nest outcome was confirmed by field personnel (refer to Andes *et al.* (2018) for a detailed description of the camera system design and installation).

Field personnel recorded the date, start and stop times as well as the specific research activity conducted during each visit to a nesting area, which was defined as a shoreline, sandbar or habitat with at least one active nest. The research activity duration was calculated as the difference between the stop and start times of activities recorded by researchers in the field. Research activities were divided into seven categories: (1) nest searches, (2) adult banding at the nest, (3) adult banding at other nests in the surrounding nesting area, (4) camera check at the nest, (5) camera check at other nests in the surrounding nesting area, (6) targeted search at the nest and (7) targeted searches at other nests in the surrounding nesting area. The nest search category included systematic "grid" searches, opportunistic "behavioral" searches (behaviors exhibited by the adults indicated the presence of a nest) and a combination of both previous search methods as well as band re-sighting research activities. The primary purpose of the research activities included in the nest search category was to either target all of the nests or none (band re-sighting) and required field personnel to walk through the entire nesting areas. In contrast to nest searching, the purpose of adult banding, camera checks and targeted searches was to target pre-specified individual nests. Adult banding involved setting a trap (bow-net or walk-in) at one or multiple nests in a nesting area in order to band the adults. Camera checks were conducted after the initial installation at the nest and consisted of changing the batteries as well as the SD cards. A targeted search indicated that only one or a few and not all nests were visited during that activity, usually to confirm nest fate or to band chicks. Adult banding, camera checks and targeted search research activities were further subdivided based on the targeted nests. In other words, these categories were divided by whether the research activity occurred at the targeted camera nest or at another nest within the surrounding nesting area.

Data analysis

After the cameras were removed from the nest site, an independent researcher reviewed the camera video to assign a fate. A nest was successful if one or more chicks were observed in the nest on video. The exact date and time of the first hatching event was recorded for the successful nest fate. For nests that failed due to predation, the exact date and time the last egg was removed or destroyed was recorded for the fate. Nest attendance of adults was also recorded from video observation. Nest attendance was defined as the adult attending or "on" the nest, which included sitting on and/or standing over the eggs. The start and stop times were recorded for all observations when the adults were absent from or "off" the nests.

I adopted a bottom-up approach to examine observer effects on shorebird nesting behaviors and ultimately nest predation risk. To assess the immediate impact of observer effect on nest attendance, I modeled the proportion of time adults were absent from nests (response variable) during the time period (TP) one hour pre, during the entire length of the research activity and one hour post using generalized linear mixed models (GLMM) with a β distribution in PROC GLIMMIX (SAS 9.4; SAS Institute, Cary, NC). The total amount of time (RAD) for each time period (pre, during, post) was added as a covariate to account for the variable lengths of individual research activities. I expected variation in the impact of each research activity category on the response variable; therefore, the type of research activity (RA) was also added as a covariate. The response variable was repeated over the categorical variables nest identification number and location on the Missouri River (random effects) to account for dependency issues due to spatial clustering of individual nests within nesting areas. Year (2013, 2014, and 2015), Date (Julian Date of the breeding season), clutch age (CA = age of the nest) and Spp (Species either Terns or Plovers) were included as covariates because these factors can potentially influence nesting behaviors (Smith & Wilson 2010). Year was added as a fixed effect because the research objective changed in 2015 and the rate of activities decreased compared to 2013 and 2014.

To examine a prolonged influence of observer effects on daily nest attendance, I modeled the daily nest attendance (total minutes adults attended ("on") nests per day) in response to the occurrence of research activities (RA, binary variable), total number of research activities (RAN) and the total duration of research activities (RAD) on each particular day using GLMM with a normal distribution in PROC GLIMMIX. The response variable was repeated over the categorical variables nest identification number and location on the Missouri River. Year, Date, Clutch Age and Species were also added as covariates in the daily nest attendance analyses. I adopted a hierarchical approach to model selection and ranked models based on their Akaike's Information Criterion (AIC), Akaike model weight (w_i) and model goodness-of-fit (-2LL) (Burnham & Anderson 2002). Models that best described the impact of observer effects on adult nest attendance had the lowest AIC scores and the largest model weights (Burnham & Anderson 2002).

Since the survival data consisted of continuously video-monitored nests, I used extended Cox proportional hazards models to estimate the impact of observer effects on nest predation risk (Hosmer Jr. *et al.* 2011). The proportional hazards model computes a conditional failure rate or hazard function, which is defined as the instantaneous potential for an individual nest to fail at time t, given that it survived up to that point in time (t). There are two assumptions of the proportional hazards model: (1) the baseline hazard function involves a time component but no covariates and (2) the exponential expression in the equation involves covariates but not a time component (Hosmer Jr. *et al.* 2011). Since observer effect covariates of interest in this study involved a time component, I used the counting process form of model specification to account for the inclusion of time-dependent covariates into the analyses. I used age (age when nest was located) as the baseline time component because it is well established from past research that nest survival is strongly influenced by age (Mayfield 1961).

All 12 *a priori* models included a set of covariates (X) that regulated confounding heterogeneity in survival rates (Weidinger 2008) including year (2013, 2014, 2015), linear and quadratic variables of Julian date and time (in minutes) from proceeding research activity to sundown of that day. Julian date was added to the candidate models to account for seasonal variation in predation rates of different predators. The time from preceding research activity to sundown of that day was added to the candidate models to account for daily variation in timing of research activities. The simplest model included just X covariates.

I was interested in testing a short-term (V=amount of time in minutes between nest fate and the preceding research activity) and long-term (N=mean number of research activities per each time interval) observer effects on nest predation risk with respect to X covariates (Weidinger 2008). I evaluated the influence of different levels of V and N on nest predation risk using 12 *a priori* models (Weidinger 2008). Due to a smaller sample size of nests and a nest-monitoring schedule of 3-days, I only evaluated nest predation risk in relation to a linear effect of N and the N*Year interaction, linear and quadratic effects of V (V_L & V_Q) and a short-term observer effect that varied depending on if the last visit occurred within 24-hr (V_{24hr}), between one to two days (V_{2d}) and between two to three days (V_{3d}) before the nest research activity or nest outcome. Since all of my *a priori* models included the same set of covariates, I only reported the parameter estimates from the individual top models (Burnham & Anderson 2002, Arnold 2010). Hazard ratios for covariates that were not included in the top model were estimated from the models with the highest w_i in which they occurred first and included for comparison between different levels of observer effects on nest predation risk.

Results

I installed cameras at 154 nests (65 of 294 Tern and 89 of 551 Plover) monitored throughout the duration (May-August) of the study period from 2013-2015. There was no statistical influence of cameras on the daily nest survival rate (DSR) of either species (Andes *et al.* 2018). The majority of research activities and nest depredations occurred between 0600 and 1200 during the day (Fig. 3). Nests were primarily depredated during the month of June, which coincided with the peak of nesting season (Fig. 4). However, corvids depredated nests throughout the nesting season.

Immediate Impacts from Research Activities

I included 70 nests (total number pre, during, and post research activity time periods = 1,569) in the GLMM analyses of immediate observer effects on nest attendance. I found that one top model (Date + Spp + TP + RA + CA + RAD + RA*Spp + RA*TP + TP*Spp + Spp*CA) best explained the immediate observer effect on nest attendance because it received the lowest AIC score and the greatest w_i (Table 6); therefore, I used this model for derivation and interpretation of parameter estimates. I considered all subsequent models as noncompetitive because their ΔAIC > two. The top model included TP (time period pre, during and post research activity), RA (research activity type) and RAD (research activity duration). Adults of both species were 5.25 times more likely to be absent from nests during research activities compared to the time period 1 hour before (Table 7). During research activities, both species spent more time absent from nests (Terns=39.7% ± 0.023 se, Plovers=26.5% ± 0.01 se) compared to the time periods directly pre (Terns=13% ± 0.013 se, Plovers=10.1% ± 0.01 se) and post (Terns=13% ± 0.013 se, Plovers=12.2% ± 0.012 se, Fig. 5). Adult banding at the nest had the greatest immediate impact on nest attendance (proportion time off nest=63.3% ± 0.029 se) followed by nest searching (proportion time off nest=44.7% ± 0.024 se) and targeted searches at other nests in the surrounding area (proportion time off nest=38.9% ± 0.043 se) compared to pre and post time periods (Fig. 6) Additionally, adults spent more time absent after adult banding at the nest compared to other research activities (23.6% ± 0.031 se, Fig. 6). Across all research activities, Terns spent more time absent from nests compared to Plovers (Fig. 7).

Daily impacts from Research Activities

There were 47 nests (254 days) included in the GLMM analyses of observer effect on daily nest attendance. The top model included Date, research activity type (RA), daily number (RAN) and duration (RAD) of activities as well as clutch age (CA) of the nest (Table 8); therefore, I used this model for derivation and interpretation of parameter estimates. I considered models two and three as noncompetitive due to the addition of an uninformative parameter (TD) that lowered the AIC but did not improve model fit (Arnold 2010). All models with a $\Delta AIC_c > 2$ were considered noncompetitive. None of the parameters included in the top model had a large impact (Table 9) on nest attendance given that their calculated odds ratios were approximately one. Overall, nest attendance was lower on days with a research activity (90.5% ± 0.011 se) compared to ones with no occurrence (91.8% ± 0.012 se, Fig. 8). Nest attendance for adults of both species was 91 % (Tern se = ± 0.017 and Plover se = ± 0.012) on days when a research activity occurred (Fig. 9).

Nest Predation Risk

I conducted Cox proportional hazard analyses on 89 Plover nests (883 research activity intervals). Due to a small sample size of nest depredations (n = 4 nests), I excluded Terns from the nest predation risk analyses. The model that best explained the relationship between nest predation risk and observer effect ($w_i = 0.51$) included the daily rate of research activities (N) as well as its interaction with year (N*year, Table 10). There was a positive influence of daily research activity rate (N) on nest predation risk. For example, the hazard or predation risk of a nest subjected to a research activity rate of one/day was 4.995 times greater than a control nest not exposed to any activities (Table 11). I considered the second model as competitive, which included the short-term linear observer effect (V_L) and its interaction with year ($w_i = 0.27$, Table 10). However, the effect of V_L on nest predation risk was minimal (HR = 1.001, 85 % CI = 0.996 – 1.01, Table 6). There was a slight increase in predation risk within 24 hours (HR = 1.227, 85% CI = 1.0 – 1.6) and 2 days (HR = 1.375, 85% = 1.1 – 1.7) after a research activity, which decreased after the 3rd day (HR = 0.95, 85% CI = 0.81 – 1.1).

Discussion

Based on the results of this study, there is strong evidence that research activities do have an immediate negative impact on nest attendance; however, these behavioral disruptions do not necessarily correspond to decreased daily nest attendance. Even though adults of both species were absent from nests three times more during research activities, similar attendance patterns pre and post research activities suggest the adults recover normal nesting behaviors quickly after a disturbance. Accordingly, the overall daily nest attendance decreased by only 1.4% on days with a research activity, which indicates minimal prolonged behavioral impacts from research activities. I can conclude that predators did not respond to the immediate disruptions of nesting behaviors from research activities since V_L was the only short-term function of observer effect that was included in the top two models, resulting in a hazard ratio = 1.001, which is interpreted as no effect of predation risk. My results contrasted those of Weidinger (2008), who reported only a short-term decrease in predation risk less than two hours after a nest visit.

However, the results from this study do indicate that there was a long-term observer effect on predation risk. Nests that were visited more frequently were at a higher risk of predation, which was evident from the inclusion of N (research activity daily rate) and N*year in the top proportional hazards model. A research activity rate of one/day, which resulted in a hazard ratio of 4.995, is unnecessarily high for accurate nest fate classification (Andes *et al.* 2018) and logistically difficult to achieve at large spatial scales. A more realistic scenario would be predation risk 1.7 (85 % CI = 1.612 – 1.793) times greater for a nest visited on a 3-day monitoring schedule (0.33 daily research activity rate) compared to a nest subjected to no daily research activities. In other words, the predation risk is almost two times greater for a nest visited at a 0.33 daily research activity rate

Visual cues such as tracks left in the sand by repeated visits may have attracted corvids, the primary predator in our system, to nest sites. Since both Terns and Plovers build their nests on the ground and in the open, human tracks surrounding a nest may be a conspicuous attraction for predators. Additionally, nest monitoring protocols were altered in 2015 compared to 2013-

2014. Crews were reduced from four to two people and nest monitoring schedules were decreased to just twice weekly with no additional visits as the estimated hatch date approached. Therefore, overall research activities decreased in 2015 compared to the two previous years. The predation risk (hazard ratios) for nests in 2013 and 2014 were 2.9 (85 % CI = 2.3 – 0.3.6) and 4.1 (85 % CI = 3.4 – 4.9) times higher compared to 2015, suggesting a positive correlation between increased research activities and greater predation risk for Tern and Plover nests. However, an alternative explanation for the difference between predation risks in 2015, compared to 2013—2014, could be a change in the predator community.

Skutch (1949) first hypothesized a correlation between parental behavior and predation rates in tropical nests of altricial species; more specifically, that foraging and feeding activities attract predators to the nest. For some shorebird species like Plovers, the Skutch hypothesis is not directly relatable because chicks are born precocial, with the ability to move and feed themselves shortly after hatch. Therefore, increased parental activity at nests may not be due to feeding chicks for most shorebirds. Tern chicks hatch with mobility within a few hours but are not capable of foraging until they fledge. However, many shorebirds, including Terns and Plovers, nest on the ground in open areas that are fully visible by predators. Therefore, any nest attendance activity conducted would be visible by nearby predators. My results correspond to a similar study conducted by Stien and Ims (2016) using cameras on Common Eider (*Somateria mollissima*) nests in Norway. Stien and Ims (2016) reported that increased absences from the nest contributed to a greater predation risk (one additional day of research activities increased the predation risk of nests by 6.42). The primary factor that contributed to differences between predation rates of shorebirds that nested at East Bay, Southhampton Island, Nunavut, Canada was nest attendance (Smith *et al.* 2007). Furthermore, reduced nest attendance and increased incubation recesses were significantly correlated with nest failure for 11 shorebird species in the Arctic (Smith *et al.* 2012). Based on this past research and that decreased nest attendance was demonstrated from research activities in the Missouri River system, increased absences from the nest may be the mechanism for increased predation risk. Absences from research activities may allow corvids to follow the adults back to the nest (Smith *et al.* 2012).

Even though the magnitude of observer effects will vary across species, habitats and methodologies, general inferences can be made from this study that may benefit research across avian orders. Based on the results of this study, there is more concern for long-term observer effects on nest predation risk, especially in systems where corvids are the primary predators. There were three primary mechanisms from research activities that may have attracted predators to nests in the Missouri River system based on previous research (Weidinger 2008, Stien & Ims 2016): 1) presence of researchers, 2) visual cues left behind by researchers or 3) nest absences. I concluded that the predators in our system primarily responded visually to nest absences during a research activity rather than the direct or indirect presence of researchers.

To my knowledge, this is the first study to quantify an immediate and daily impact of various research activities on nest attendance as well as correlate these behavioral changes to predation risk. Stien and Ims (2016) directly connected increased nest absences from research activities to higher predation risk in Common Eiders but, they failed to quantify the behavioral changes due to nest monitoring. Inferences from the results reported by Stien and Ims (2016) are limited to the eider colonies in Norway due to lack of spatial replication. Smith *et al.* (2012) also demonstrated that predation increased for shorebird nests that were left unattended for longer amounts of time. Weidinger (2008) analyzed predation risk in response to nest monitoring but did not include the impact to nesting behaviors. However, this study did attempt to connect decreased nest attendance, research activities and predation risk. The novel approach of this study increased our understanding of the relationship between research activities, nest attendance patterns and predation risk.

Research should contain a balance between accurate data collection and the welfare of the focal population(s). Both of the focal species are federally protected by The Endangered Species Act as endangered (Terns) or threatened (Plovers) (U.S. Fish and Wildlife Service 1985a, U.S. Fish and Wildlife Service 1985b). It is imperative that data is collected in a manner that does not negatively influence populations, especially if they are imperiled. Based on the long-term effects and change in research intensity in 2015, a decreased rate of research activities at and around a nest will increase daily nest attendance and allow external factors such as weather to obscure signs of human activity. Checks at a distance will minimize nest absences and visual cues left by researchers at the nest. If predator identification is not a primary objective, visits to a nest can be minimal during early incubation, while still allowing accurate nest fate determination, until the approach of the estimated hatch date (Andes *et al*. 2018). Less invasive technology, such as temperature data loggers and video cameras, may be successfully substituted for traditional methods of nest monitoring by field personnel (Weidinger 2006).

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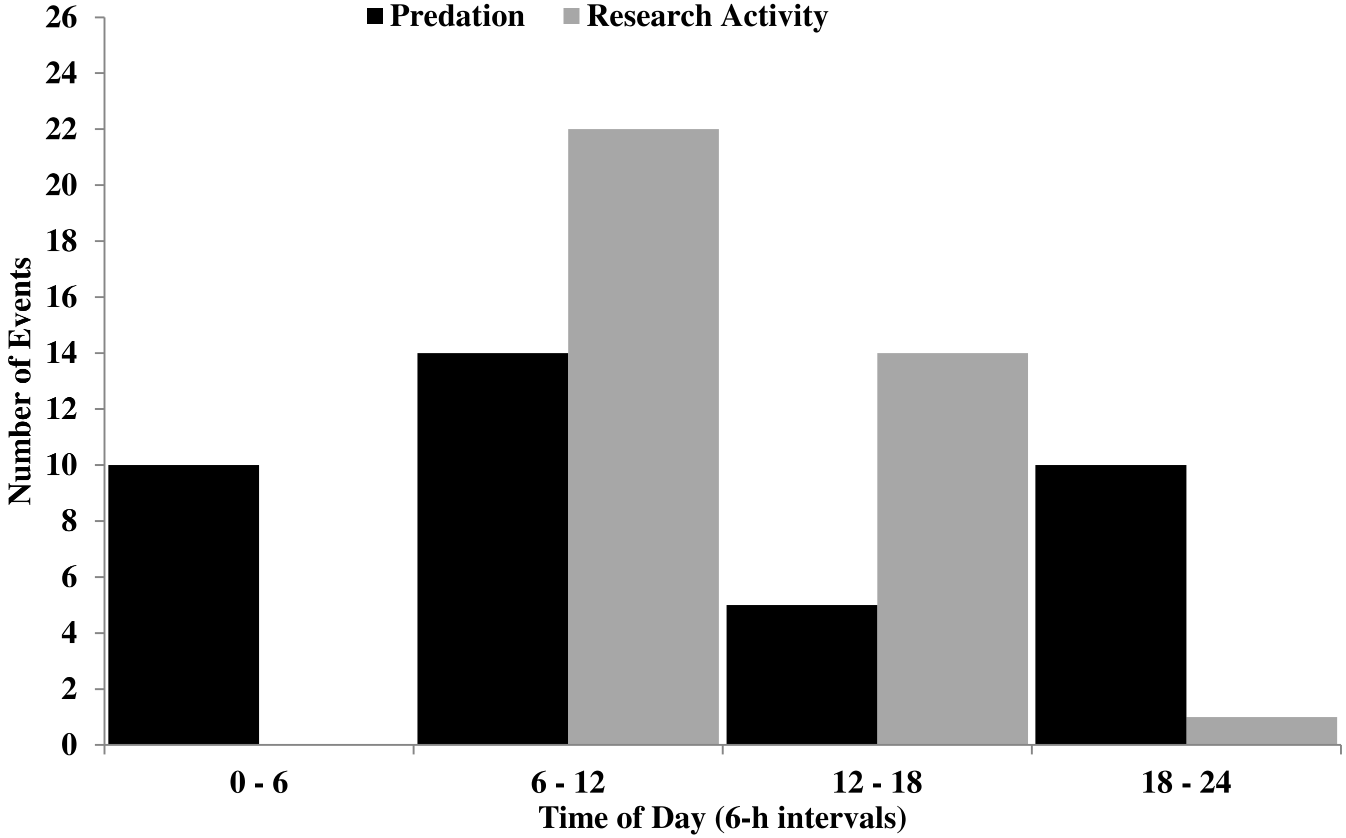

Figure 3. Daily military time of preceding research activity and corresponding predation events at interior Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius melodus*) nests on the Garrison Reach of the Missouri River, ND from 2013-2015.

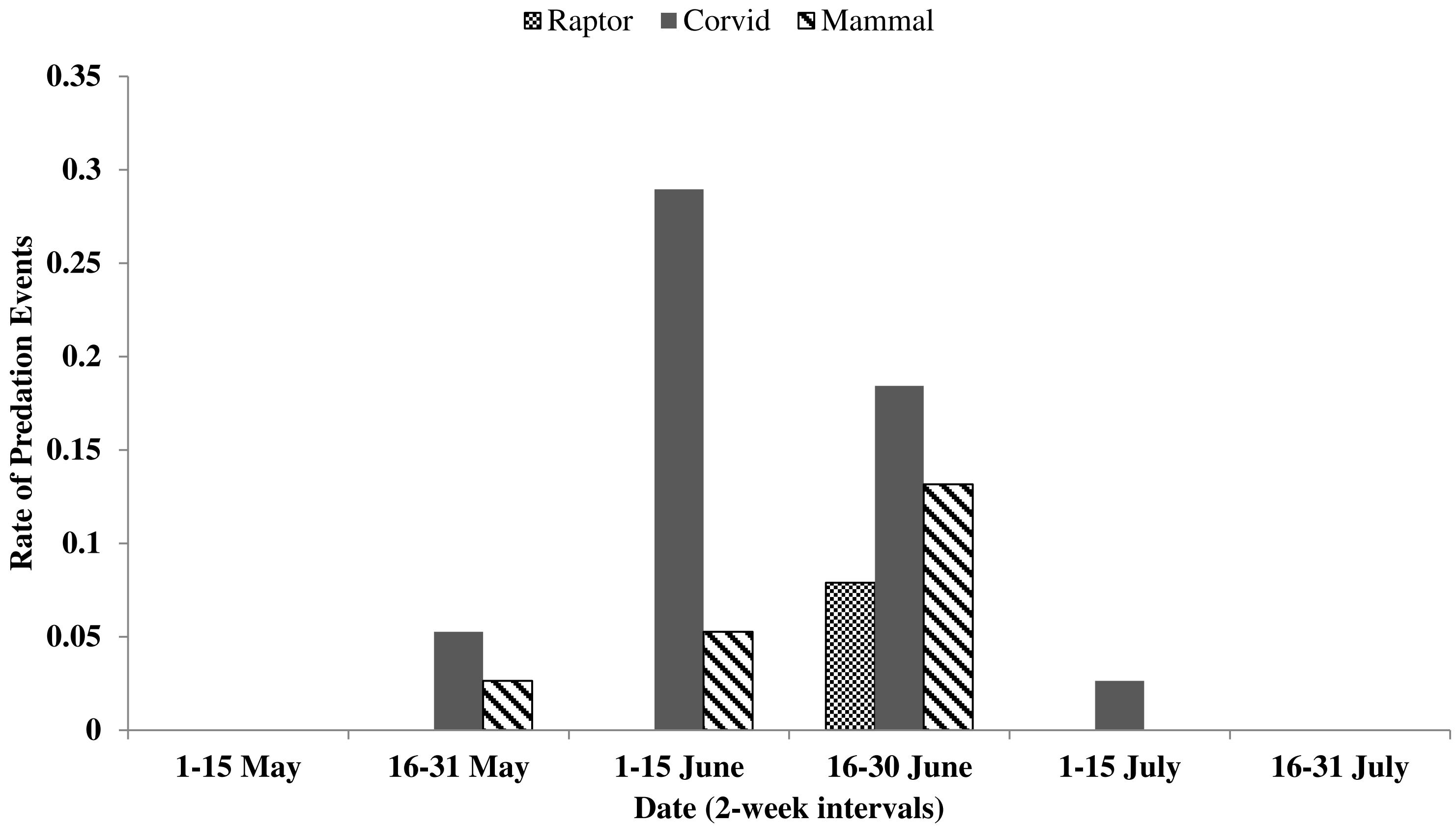

Figure 4. Seasonal rate of Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius melodus)* nest depredations (number of predation events per species per month/total number of predation events) on the Missouri River, ND from 2013-2015. Nest predators included American Crows (*Corvus brachyrhuynchos*) and Black-billed Magpies (*Pica hudsonia*) categorized as corvids, Great-horned Owls (*Bubo virginianus*) and Bald Eagles (*Haliaeetus leucocephalus*) as raptors and coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), striped skunks (*Mephitis mephitis*) and raccoons (*Procyon lotor*) as mammals.

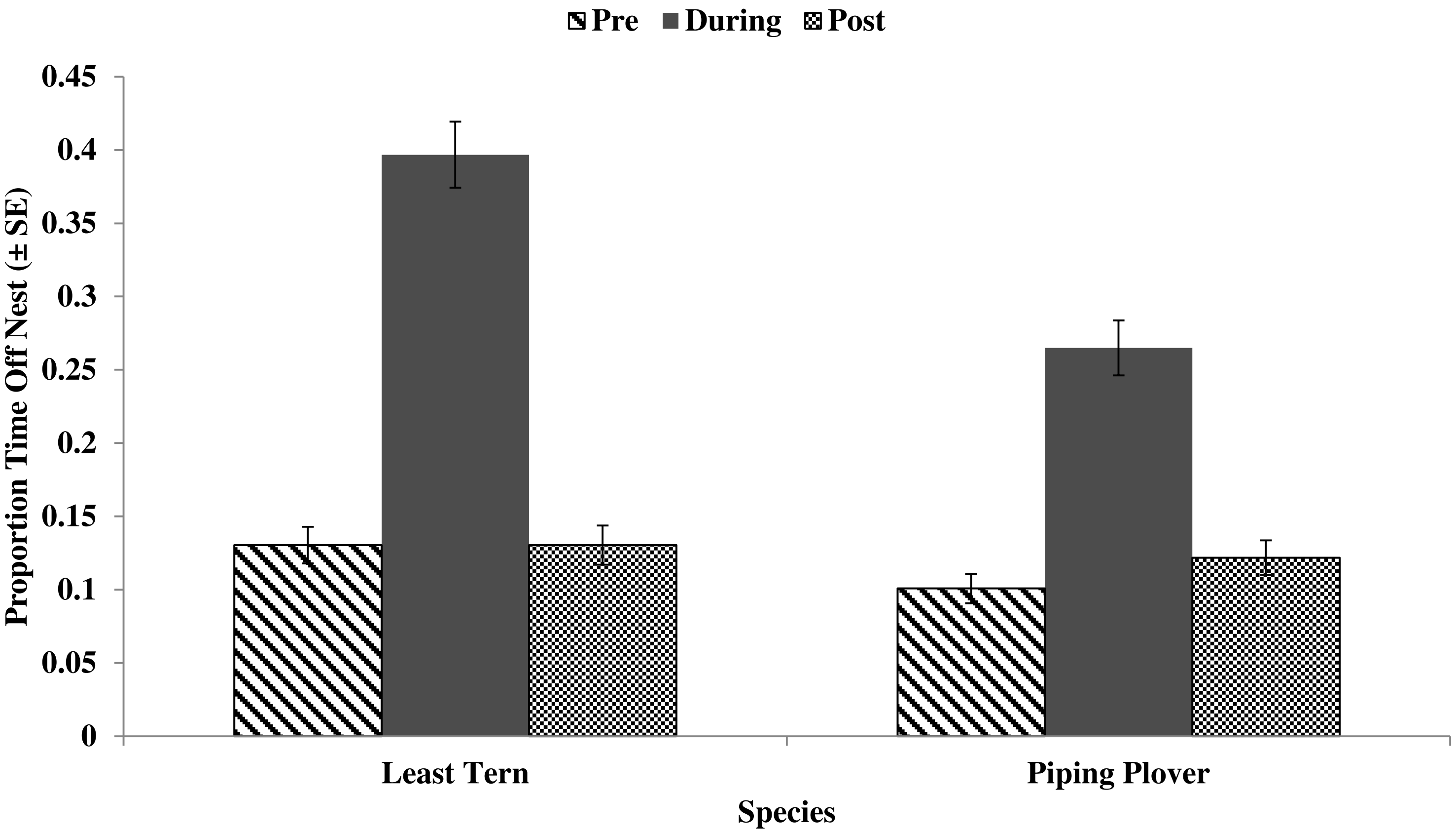

Figure 5. The proportion of time that Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius melodus*) adults spent absent from their nests one hour pre, during and one hour post (minutes off nest/total minutes of time period) all collective research activities conducted at the nest or in the surrounding nesting area on the Missouri River, ND during 2013-2015.

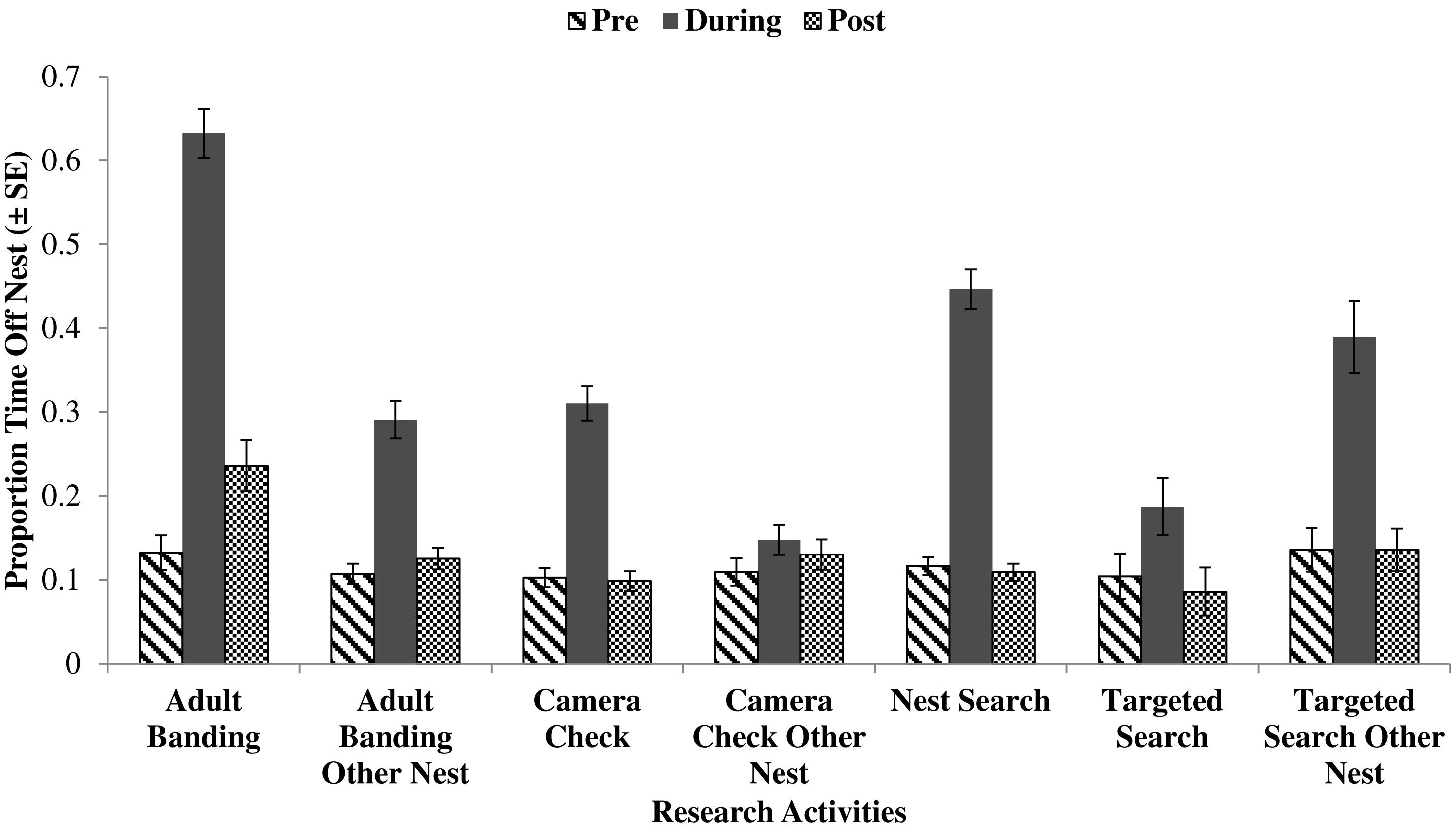

Figure 6. The proportion of time that adults (Least Terns (*Sternula antillarum athalassos)* and Piping Plovers (*Charadrius melodus)*) were absent from their nests (minutes off nest during time period/total minutes of time period) one hour pre, during and one hour post individual categories of research activities on the Missouri River, ND during 2013-2015. For adult banding, camera check and targeted searches, the research activities were further categorized as either occurring at the camera-monitored nest or at a non-target nest within the surrounding nesting areas (Adult Banding Other Nest, Camera Check Other Nest, Targeted Search Other Nest).

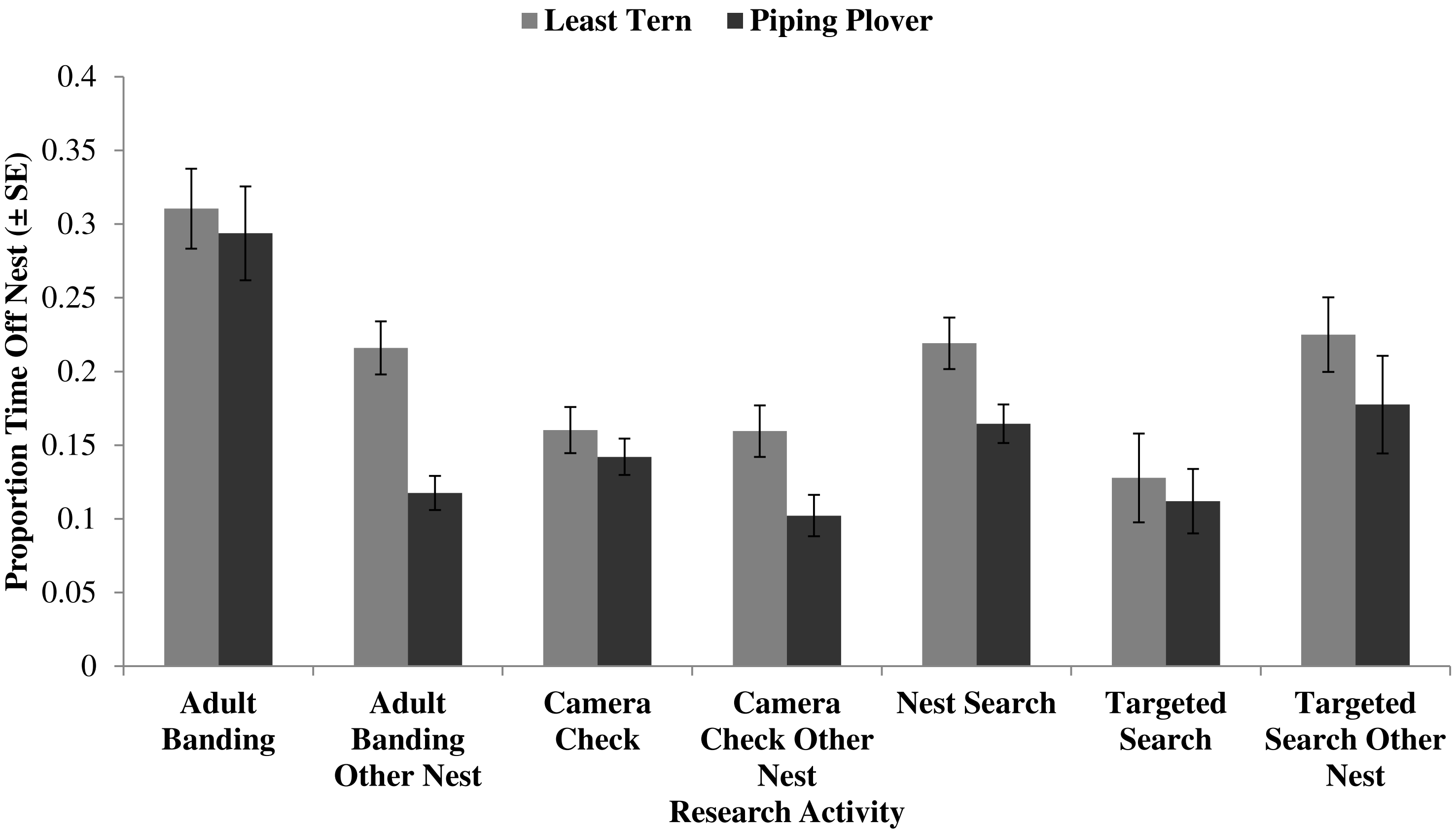

Figure 7. The proportion of time that Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius melodus*) adults were absent from their nests (minutes off nest during research activity/total minutes of research activity) during individual categories of research activities conducted at the nest or in the surrounding nesting area on the Missouri River, ND during 2013-2015. For adult banding, camera check and targeted searches, the research activities were further categorized as either occurring at the camera-monitored nest or at a non-target nest within the surrounding nesting areas (Adult Banding Other Nest, Camera Check Other Nest, Targeted Search Other Nest).

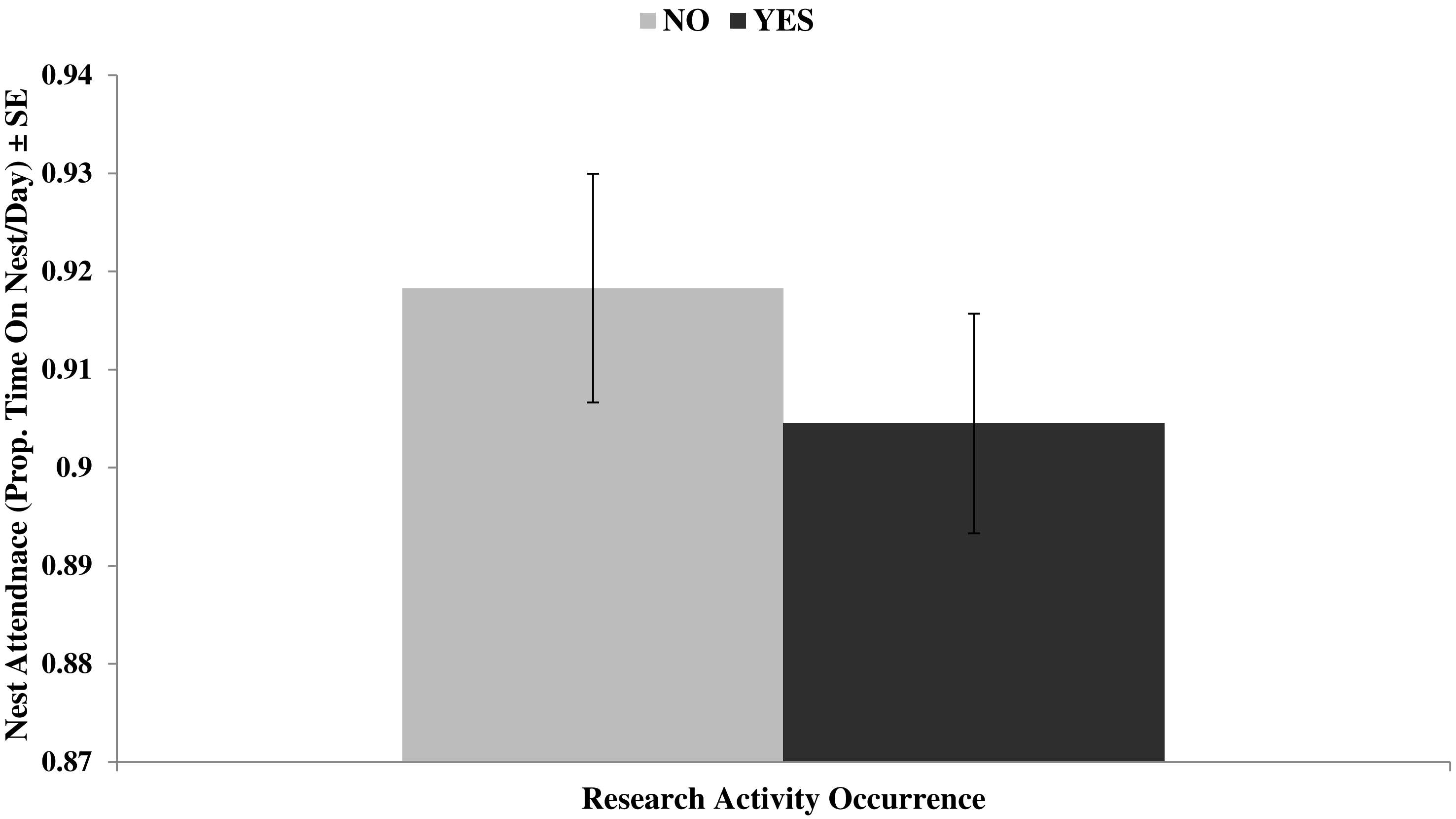

Figure 8. Daily nest attendance (daily minutes on the nest/daily total minutes) of shorebird adults (Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius melodus*)) in response to the occurrence of research activities at the nest or within the surrounding nesting area on the Missouri River, ND during 2013-2015. Nest attendance was defined as an adult sitting or standing over at least one egg in the nest.

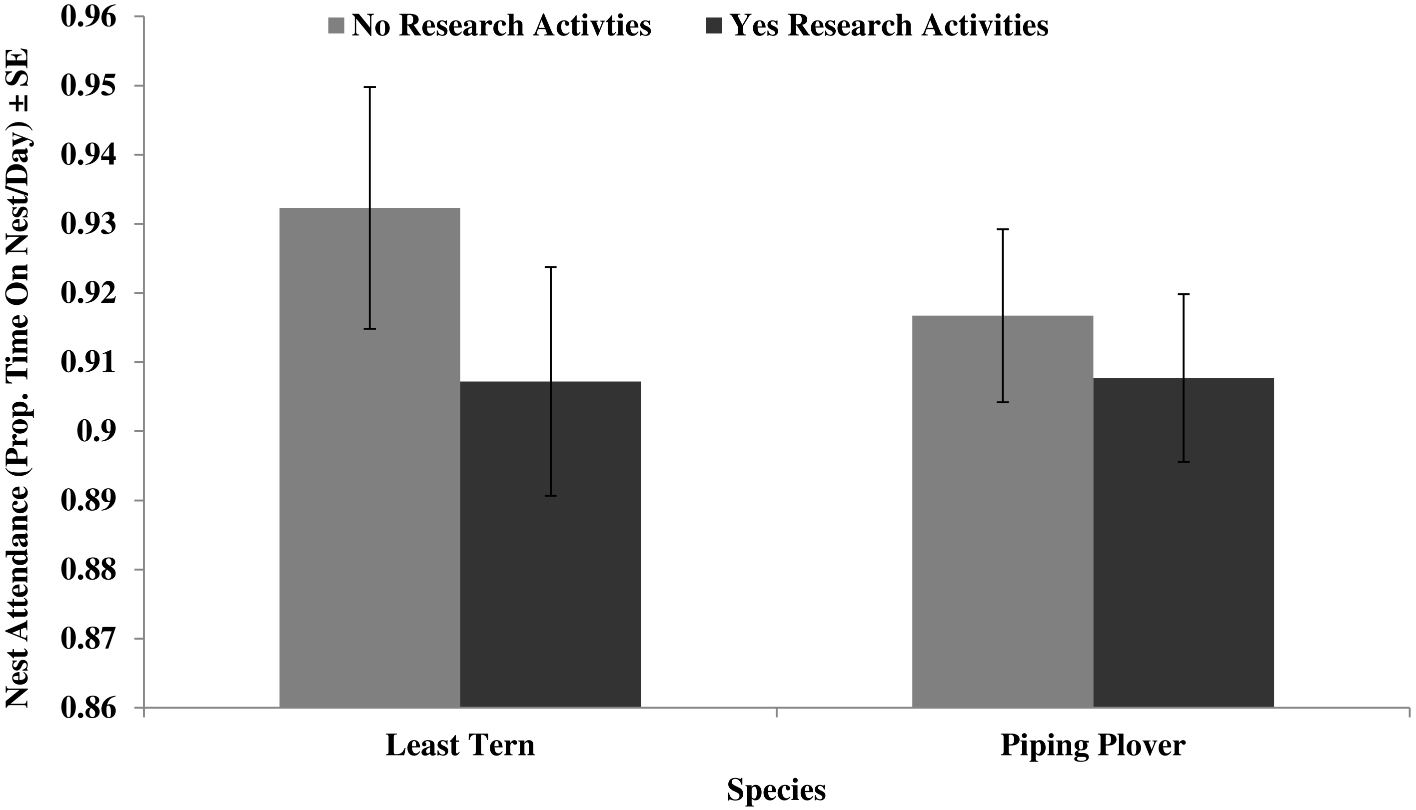

Figure 9. Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius melodus*) daily nest attendance (daily minutes on the nest/daily total minutes) in response to the occurrence of research activities at the nest or within the surrounding nesting habitat on the Missouri River, ND during 2013-2015. Nest attendance was defined as an adult sitting or standing over at least one egg in the nest.

Table 6. Model-selection results for a subset of generalized linear mixed models (β distribution) analyzing the proportion of time Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius melodus*) adults spent off their nests 1 hour pre, during and 1 hour post research activities conducted at the nests or in the surrounding nesting habitat on the Missouri River, ND during 2013-2015. Covariates include Year (2013-2015) Date (Julian date of the breeding season), Spp (species), TP (time period pre, during or post research activity), RA, (research activity type), RAD (research activity duration), CA (clutch age of the nest) and YR (year). Research activity types include adult banding at the nest, adult banding at other nests in the surrounding area, camera checks at the nest, camera checks at nests in the surrounding area, nest searches, targeted searches at the nest and targeted searchers at other nests in the surrounding area. The Full Model was Year + Date + Spp + TP + RA + RAD + CA.

Model	**k**[a]	**AIC**[b]	**ΔAIC**[c]	w_i[d]	**-2LL**[e]
Date+Spp+TP+RA+CA+RAD+RA*Spp+RA*TP+TP*Spp+Spp*CA	34	-3434.	0	0.65	-3508.0
Date+Spp+TP+RA+CA+RAD+RA*Spp+RA*TP+TP*Spp+Spp*CA+Spp*Date[f]	35	-3433	2.11	0.23	-3507.9
Date+Spp+TP+RA+CA+TotalTimeRA+RA*Spp+RA*TP+TP*Spp	33	-3430	3.8	0.097	-3502.2
Full Model + RA*TP + RA*SPP +TP*Spp	35	-3427	7.51	0.015	-3502.5
Date+Spp+TP+RA+CA+TotalTimeRA+RA*TP+TP*Spp	27	-3426	8.14	0.011	-3485.9
Intercept	1	-2778	656	0	-2786.0

[a] The number of parameters in the model

[b] Akaike's Information Criterion

[c] Distance of a model from the lowest AIC model

[d] The weight of the model

[e] Estimate of model goodness of fit

[f] Model has minimal support (Arnold 2010)

Table 7. A subset of the parameter estimates, odds ratios and corresponding 85% confidence intervals for covariates that influenced the proportion of time spent off the nest by Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius melodus*) adults one hour pre, during and one hour post research activities on the Missouri River in ND, during 2013-2015. Estimates were derived from the top model(Date+Spp+TP+RA+CA+RAD+RA*Spp+RA*TP+TP*Spp+Spp*CA). Covariates include Date (Julian date of the breeding season), Spp (Least Tern in relation to Piping Plover), TP (Time Periods During or Post research activity in relation to Pre), RA (research activity type in relation to Nest Searching: Adult Banding, Adult Banding Other Nest, Camera Check, Camera Check Other Nest, Targeted Search, Targeted Search Other Nest) as well as the interaction between Spp and Clutch Age.

Covariate	**Estimate**	**85% CI**	**se**	**Odds Ratio**	**85% CI**
Intercept	-3.33	-4.34 – -2.33	0.57	0.04	0.01 – 0.1
Date	0.01	0.01 – 0.02	0.00	1.01	1.01–1.02
Spp (Least Tern)	-0.04	-0.33 – 0.25	0.20	0.96	0.72 – 1.28
Clutch Age (CA)	-0.01	-0.02– -0.002	0.01	0.99	0.98 – 1
Research Activity Duration (RAD)	-0.01	-0.01 – -0.007	0.00	0.99	0.99 – 0.99
TP_During Research Activity	1.66	1.47 – 1.85	0.13	5.25	4.35 – 6.36
TP_Post Research Activity	0.03	-0.16 – 0.23	0.13	1.03	0.85 – 1.26
RA_Adult Banding	0.28	-0.04 – 0.61	0.23	1.33	0.96 – 1.84
RA_Adult Banding Other Nests	-0.28	-0.51 – -0.05	0.16	0.76	0.6 – 0.95
RA_Camera Check	-0.03	-0.25 – 0.18	0.15	0.97	0.78 – 1.2
RA_Camera Check Other Nests	-0.15	-0.45 – 0.16	0.21	0.86	0.64 – 1.17
RA_Targeted Search	-0.02	-0.51 – 0.47	0.34	0.98	0.6 – 1.6
RA_Targeted Search Other Nest	0.21	-0.22 – 0.63	0.29	1.23	0.8 – 1.88
Spp (Least Tern)*Clutch Age	0.027	0.01 – 0.04	0.01	1.02	1.01 – 1.04

Table 8. Model-selection results for a subset of generalized linear mixed models (normal distribution) analyzing Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius* melodus) daily nest attendance (total minutes spent attending the nest per day) in response to the occurrence of research activities at the nest or in the surrounding nesting area on the Missouri River, ND during 2013-2015. Covariates include Year (2013-2015), Date (Julian date of the breeding season), research activity occurrence (RA, "yes/no"), number of research activities (RAN), research activity duration (RAD, amount of time researchers spent conducting activities in a nesting area), clutch age (CA, age of the nest) and species (Spp, either Least Tern or Piping Plover).

Model	**k**[a]	**AIC$_c$**[b]	**ΔAIC$_c$**[c]	**w_i**[d]	**-2LL**[e]
Date + RA + RAN + RAD + CA	6	-862.25	0.00	0.41	-880.25
Date + RA + RAN + RAD + CA + Spp[f]	7	-860.88	1.37	0.21	-880.88
Date + RA + RAN + RAD + CA + Spp*RA[f]	7	-860.50	1.75	0.17	-882.5
Year + Date + RA + RAN + RAD + CA	8	-858.84	3.41	0.08	-880.84
Date + RA + RAN + RAD + CA + Spp + RA*Date	9	-858.48	3.77	0.06	-880.49
Year + Date + RA + RAN + RAD + CA + Spp + RA*Spp	10	-856.33	5.92	0.02	-883.85
Year + Date + RA + RAN + RAD + CA + Spp + SPP*Date + RA*Spp + RA*Date	12	-856.30	5.95	0.02	-884.3
Year + Date + RA + RAN + RAD + CA + Spp	9	-855.96	6.29	0.02	-881.25
Year + Date + RA + RAN + RAD + CA + Spp + Spp*JDATE	10	-853.82	8.43	0.01	-879.82
Intercept	1	-732.38	129.87	0.00	-739.08

[a] The number of parameters in the model

[b] Akaike's Information Criterion corrected for small sample sizes

[c] Distance of a model from the lowest AIC$_c$ model

[d] The weight of the model

[e] Estimate of model goodness of fit

[f] Model has minimal support (Arnold 2010)

Table 9. Parameter estimates, odds ratios and corresponding 85% confidence intervals for covariates that influenced the daily nest attendance (total minutes spent on the nest per day) of Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius melodus*) adults in response to research activities. Estimates were derived from the top model (Date+RA+RAN+RAD+CA). Covariates include Date (Julian date of the breeding season), research activity occurrence (RA_None = days without research activities in relation to days with research activities), research activity number (RAN = daily number of research activities), research activity duration (RAD = total time researchers spent conducting activities in the nesting area) and clutch age (CA = age of the nest).

Covariate	**Estimate**	**85% CI**	**se**	**Odds Ratio**	**85% CI**
Intercept	1.11	1.045 – 1.172	0.04	–	–
Date	-1.0e-03	-0.002 – -0.001	3.0e-04	0.999	0.998-0.999
RA_None	0.014	-0.001 – 0.029	0.01	1.014	0.999-1.029
RAN	8.0e-03	-0.005 – 0.021	0.01	1.008	0.995-1.021
RAD	-3.00e-04	-0.0004 – -0.0002	7.0e-05	1	1-1
CA	1.0e-03	0.001 – 0.002	5.0e-04	1.001	1.001-1.002

Table 10. Extended Cox Proportional Hazard models fitted to the time of survival or predation of Piping Plover (*Charadrius melodus)* nests using nest age as the baseline time. All models included the same set of covariates (*X*): year (2013, 2014 and 2015) as well as the linear and quadratic functions of Julian date and the time to sundown of the last preceding research activity. Covariates of observer effects on nest predation risk included: (1) rate of research activities per time interval (N), (2) linear and quadratic functions of time since last research activity (V_L and V_Q), (3) time to event within 24 hour of last research activity (V_{24hr}), (4) time to event between 24 hour and 2 days after research activity (V_{2d}) and (5) time to event between 2-3 days after research activity (V_{3d}).

Model	k[a]	-2LL[b]	AIC[c]	ΔAIC[d]	w_i[e]
X + N + N*year	9	17.4	35.4	0	0.506
X + N + V_L + V_L*year	10	16.7	36.7	1.29	0.266
X + N +V_Q + V_Q*year	10	18.6	38.6	3.24	0.100
X + N	8	26.0	40.0	4.57	0.0515
X + N +V_Q	9	25.9	41.9	6.49	0.0197
X + N + V_{24hr}	9	25.9	41.9	6.54	0.0193
X + N +V_L	9	26.0	42.0	6.59	0.0190
X	7	31.2	43.2	7.83	0.0101
X + N + V_{3d} + V_{3d}*year	10	25.8	45.5	10.1	0.00327
X + N + V_{2d}	9	30.4	46.4	11.0	0.00208
X + N + V_{3d}	9	31.2	46.5	11.1	0.00198
X + N + V_{2d} +V_{2d}*year	10	29.9	49.9	14.5	0.000367

[a] The number of parameters in the model

[b] Estimate of model goodness of fit

[c] Akaike's Information Criterion

[d] Distance of a model from the lowest AIC model

[e] The weight of the model

Table 11. Hazard ratios (HR) with 85% confidence intervals for observer effects on the predation risk of Piping Plover (*Charadrius melodus*) nests on the Missouri River, ND from 2013-2015. Covariates from the two top models, that were measures of observer effects, included the rate of research activities per time period (N derived from the top model: X + N + N*year) and the linear function of time since last research activity (V_L derived from the second model: X + N +V_L + V_L*year). Additional functions of V derived from noncompetitive models included an observer effect comparing predation risk among the first three days after research activity.

Covariate	HR	85% CI
N	4.995	4.252 – 5.868
V_L (Linear)	1.001	0.996 – 1.006
V_{24hr} (1st 24 hours vs later)	1.227	1 – 1.632
V_{2d} (1st day vs 2nd day)	1.375	1.139 – 1.659
V_{3d} (2nd day vs 3rd day)	0.95	0.805 – 1.12

CHAPTER IV

LEAST TERN AND PIPING PLOVER NESTING BEHAVIORS IN RESPONSE TO RISING SAND TEMPERATURE

Abstract

Birds that nest on the ground in open areas, like federally threatened Piping Plovers (*Charadrius melodus*) and endangered Least Terns (*Sternula antillarum*), are exposed to high temperatures in thermally stressful environments. Nests that are left unattended, even for short periods of time, in hot environments, can have lethal consequences for embryo development. As a result, birds have adapted behavioral techniques to maintain thermal regulation of eggs and themselves. Our objective was to assess the impact of temperature on Least Tern and Piping Plover nesting behaviors. We installed video cameras and thermocouples at 52 Least Tern and 55 Piping Plover nests on the Missouri River in North Dakota during the 2014—2015 breeding seasons. Daily maximum sand temperature was included in the top model(s) that best explained the variation in nest attendance as well as shading behaviors. Nest attendance decreased by 1.2 minutes with one degree increase in temperature. On average, daily nest attendance was greater for Least Terns (0.97 % ± 13.9 se) compared to Piping Plovers (0.94 % ± 14.4 se). The number and duration of shading behaviors increased by 0.22 and 0.32 min per day with one degree increase in maximum sand temperature. Piping Plovers exhibited more and longer shading behaviors (frequency of daily shades = 5.83 ± 3.16 se, duration of daily shades = 4.13 minutes ± 2.69 se) compared to

Least Terns (number of daily shades = 0.46 ± 0.26, duration of daily shades = 0.33 minutes ± 0.23 se). Temperature had less of an influence on nest exchange behaviors. The examination of possible effects that sand temperature inflict on avian ground-nesting behavior will be critical to understand in order to adapt or develop recovery plans in response to climate change.

Keywords: shorebirds, *Charadrius melodus*, *Sternula antillarum*, temperature, nest attendance, shading behaviors, nest exchanges, Missouri River

Introduction

It is well documented that many shorebird species, including interior Least Terns (*Sternula antillarum athalassos*; hereafter "Terns") and (Piping Plovers (*Charadrius melodus;* hereafter "Plovers") on the Missouri River, avoid predominantly vegetated habitats to establish nests in order to decrease predation risk from earlier predator detection (Götmark et al. 1995, Catlin et al. 2011, Saalfeld et al. 2012, Sherfy et al. 2012). However, the exchange for increased visual range around the nest is prolonged exposure to extreme summer temperatures. Incubating shorebirds face two problems when nesting on the ground in open, hot environments: (1) overheating of the adult while on the nest and (2) maintaining egg temperatures below lethal levels. When exposed nests of ground-nesting birds are left unattended during high temperatures (> 42˚C), even for short periods of time, the eggs are more vulnerable to hyperthermia, which results in lethal overheating of the embryos (Grant 1982, Webb 1987, Brown & Downs 2003). Therefore, incubating birds in hot climates must prevent themselves and their nests from overheating by cooling their body temperatures as well as the eggs, a reversal of the normal incubation process.

Hyperthermia of incubating adults and eggs is primarily avoided or reduced by adaptive behaviors that facilitate heat loss at the nest. Shorebirds that nest in climates characterized by extreme temperatures have developed several behavioral adaptations to manage thermal stress and egg thermoregulation during incubation such as bi-parental nest attendance, shading eggs, belly-soaking, panting and gular fluttering (Purdue 1976, Grant 1982, Amat and Masero 2004, Saalfeld et al. 2012). Bi-parental nest attendance (the sharing of adult attendance at the nest) facilitates thermoregulation of the eggs by almost continuous control of egg temperature through incubation and thermal stress management by allowing the adults to leave when overheated (Grant 1982). Nest attendance of Snowy Plovers (*C. nivosus*), Wilson's Plovers (*C. wilsonia*) and Killdeer (*C. vociferous*) decreased during diurnal moderate temperatures (68 — 76 %) and increased to > 90 % during the hottest times of the day (Purdue 1976, Grant 1982, Bergstrom 1989). In response to rising ambient air temperatures, Lesser Black-winged Plovers (*Vanellus lugubris*) increased bi-parental nest attendance (Ward 1990). Kentish Plovers (*C. alexandrinus)* that incubated covered nests exhibited no behavior related to heat stress (Amat & Masero 2004). Conversely, Kentish Plover female incubation bouts decreased (primarily female uniparental incubation during the daytime) and bi-parental care of uncovered nests increased as temperatures rose. Overall, past research reported a positive relationship between nest attendance and temperature.

The thermoregulatory role of shading behaviors (the bird elevates its tibiotarsi until the incubation patch is extended above the eggs by 2-3 cm) is less defined (Downs & Ward 1997). Shading eggs was first considered a thermoregulatory mechanism to cool egg temperature by convection (Dixon & Louw 1978, Bennett *et al.* 1981). However, more recent evidence indicates that the primary purpose of shading eggs is to prevent overheating of the incubating adult (Downs & Ward 1997, Brown & Downs 2003). Wilson's Plovers and Killdeer spent 27.6% and 28.1% of their time shading eggs at temperatures >23-25˚C at the Aransas National Wildlife Refuge in Texas (Bergstrom 1989). Amat and Masero (2004) reported that female Kentish Plovers exhibited shading behaviors for 10.4 % ± 12.8 of their time at a mean ambient temperature of ≥ 31˚C. There is a general consensus from past research that the occurrence of shading behaviors increases with higher temperatures.

Indirect or abbreviated behavior measurements were a common shortcoming of most past research that attempted to quantify shorebird responses to thermal stress. In addition, the use of personnel to directly observe nests to measure nesting behaviors was another limitation that decreased sample sizes for analyses. An alternative approach to direct field observations of nest attendance is indirect measurements via probes placed in the nest. Saalfeld *et al.* (2012) used iButtons placed in and around Snowy Plover nests in the Texas panhandle to indirectly measure and correlate nest attendance to temperature and habitat selection. The use of thermocouples to indirectly calculate nest attendance increased sample size (n = 104 nests) in the preceding study (Saalfeld *et al.* 2012) but may reduce precision of nest attendance measurements according to Schneider and McWilliams (2007), who reported that temperature data loggers were unsuccessful to determine nest attendance of Plovers at Cape Cod National Seashore.

One method that would improve research focused on the relationship between temperature and nesting behaviors is the combination of video cameras with temperature data loggers placed at or near the nest. The integration of video cameras to quantify behaviors allows direct measurement of responses to temperatures and increases sample sizes for analyses. Terns and Plovers that nest along the Missouri River system are perfectly suited to study the influences of temperature on nesting behaviors for several reasons including: (1) both species nest on the ground in the open with full exposure to the sun, (2) both species have known adaptive behaviors to cope with thermal stress and (3) sand temperatures range on a daily basis from 4.4˚C to 50˚C. Our primary objective was to assess the potential impact of sand temperatures on shorebird nest behavior patterns. I hypothesized that as sand temperatures increased, adult Terns and Plovers would exhibit more behaviors associated with thermal stress such as shading eggs and nest exchanges. I expected that nest attendance would increase as temperature rises.

Methods

Study Area and Species

This study was conducted on the Garrison Reach of the Missouri River in North Dakota, from the dam at Riverdale south to Bismarck, previously described by Shaffer *et al.* (2013), during May through August from 2013 to 2015. Both Terns and Plovers are small, ground-nesting shorebirds that select open, sparsely vegetated sand habitat with pebbles or gravel, such as coastal and riverine shorelines, temporary sandbars and permanent islands (Anteau *et al.* 2012, Sherfy *et al.* 2012, Stucker *et al.* 2013). Female Terns lay 2-3 eggs in a clutch, one every day, that are oval, beige in color and speckled to camouflage against the nest substrate (Kirsch 1996, Thompson *et al.* 1997). Incubation begins at the start of the egg laying stage and lasts approximately 19-25 days (Thompson *et al.* 1997). Unless the nest is depredated or destroyed, pairs only breed once a season (Thompson *et al.* 1997). Both adults share parental responsibilities; however, the female parent contributes the most time to incubation and chick-rearing duties (Keane 1987).

Unless the nest is a failure, there is only one nest attempt per year for Plovers. First attempt clutches typically contain four eggs, laid every other day, that are oval, sand colored with evenly distributed spots that camouflage into the substrate (Cairns 1982, Elliott-Smith & Haig 2004). Multiple re-nests are possible if the previous attempts are depredated or destroyed in any way; however, clutch size for re-nests decrease with attempts (Bottitta *et al.* 1997, Elliott-Smith & Haig 2004). Full incubation begins after the last egg is laid. However, there are reported instances when short incubation periods were observed during the egg-laying period (Cairns 1977, Whyte 1985). Both sexes incubate the nest, which lasts around 25 to 28 days (Wilcox 1959, Cairns 1977, Whyte 1985, Haig & Oring 1988).

Field Methods

I used systematic grid and behavioral searches to locate and monitor Tern and Plover nests throughout the 2014 and 2015 breeding seasons from May through August (refer to Shaffer *et al.* (2013) for a detailed description of the monitoring methodologies). Clutch age was calculated by egg floatation at the initial nest visit (Mabee *et al.* 2006, Shaffer *et al.* 2013). Egg floatation allowed researchers to determine incubation stage as well as estimate initiation (date first egg was laid) and hatching dates for nests of both species (assuming 18- and 25-day incubation periods for Terns and Plovers (Shaffer *et al.* 2013)). Clutch size was recorded at the onset of incubation. Nests were monitored on a 3-day schedule until the estimated hatch date approached (< 3 days) when visits were increased to daily. Monitoring continued until nest completion when the fate was determined as either successful (hatched with chicks observed in the nest bowl), probable successful (evidence of hatching but no chicks present in the nest bowl, failed (nest could not have hatched based on estimated hatch date or evidence suggested infertile eggs, depredation, abandonment, destruction by weather or livestock) or unknown (Andes *et al.* 2018).

To observe nesting behaviors, video camera systems (miniature infrared surveillance cameras equipped with 24 LEDs and 4.3-mm lenses (Jet Security USA, Buena Park, CA) were installed at a subset of nests after incubation reached a minimum of two days and were not removed until a nest outcome was confirmed by field personnel (refer to Andes *et al. (2018)* for a detailed description of the camera system design and installation). The camera was installed ≥ one m away from the nests at a height of 15 – 25 cm. The 12 V, 35-amp-hour batteries and 32-GB SD cards housed in a weatherproof case (SEAHORSE Protective Equipment Cases, Fuertes Cases, La Mesa, CA) were buried in the sand at least 25-30 m away from the nest and exchanged every 3-4 days to ensure continuous recording of the nests. Since Terns and Plovers are both federally protected under the Endangered Species Act (U.S. Fish and Wildlife Service 1985a, U.S. Fish and Wildlife Service 1985b), the existing permit prohibited the placement of data loggers near the nest bowl. Alternatively, I measured sand temperature with thermocouples (Onset Computer Corporation, Cape Cod, MA; hereafter “HOBO”) installed, at least one meter away from the weatherproof case and battery (which were at least 25 meters away from the nest), in substrate (sand, gravel, pebble or mud) similar to the surrounding nest bowl habitat. The thermocouples were pushed into the ground, at a depth of 2-3 inches, until the temperature sensor at the top was level with the sand surface. Sand temperatures were recorded on a 30-minute interval starting at camera installation until removal after nest outcome. Both the camera system and thermocouple were removed once the brood vacated the nesting area or a nest fate was assigned in the field by researchers.

Recording Nesting Behaviors

I was interested in documenting behaviors that are impacted by temperature such as nest attendance as well as shading and nest exchange behaviors. Nest attendance was defined as the adult attending or "on" the nest, which included sitting or standing over at least one egg in the nest. I defined shading behaviors as the adults visibly standing over the nest for a period > 3 seconds. I was unable to distinguish between shading and belly-soaking behaviors due to low resolution video quality. Therefore, I started recording shading behaviors when an adult first arrived to attend the nest and stood over the eggs or stood up during incubation. Behaviors classified as shading when the bird first arrived to the nest and stood over the eggs may have actually been belly-soaking. I classified nest exchange behaviors as one adult leaving or moving "off" the nest and a different adult moving "onto" the nest to attend. Since Terns and Plovers are not sexually dimorphic and video quality was too poor to determine band combinations, I only recorded a nest exchange when both adults were visible in the video screen. I recorded start and stop times for all observations when adults were attending the nest, shading or exchanging nest attendance duties. All behavioral observations were recorded within one calendar day (24 hour period) from 00:00:00 in the morning till 23:59:59 at night. Since the presence of researchers decreased nest attendance (Andes *et al.* 2018), I only included days with no research activities at the nest or within the nesting area for analyses.

I was unable to watch all of the video collected from the 107 camera nests; therefore, a subsample of those nests was first selected to review based on the spatial and temporal distribution of cameras on the Missouri River to ensure independence between nests. In other words, camera nests were selected from each segment (lower, middle and upper) of the Missouri River as well as across the breeding season (early, middle and late initiation dates). Within individual sampled camera nests, days were selected to ensure equal representation of incubation stage (early, middle and late) as well as seasonal temperature variation (early, middle and late breeding season dates). I recorded the total duration in minutes per day of nest attendance and shading behaviors as well as the total frequency per day of shading and nest exchange behaviors for analyses.

Data Analysis

Sand temperature measurements were graphically summarized as daily minimum, maximum and mean by year, nest and date. I conducted generalized linear mixed models (GLMM) using the program PROC GLIMMIX (SAS 9.4; SAS Institute, Cary, NC) for all statistical analyses. The response variables included daily nest attendance duration, daily frequency and duration of shading behaviors, as well as daily frequency of nest exchange behaviors. Daily nest attendance was defined as the total minutes per day the adults attended at least one egg in the nest per day. Daily duration of shading behaviors was defined as the total minutes per day the adults spent standing over at least one egg in the nest. Daily frequency of shading and nest exchange behaviors were defined as the total number of occurrences of each activity per day. Year, individual nest identifications and categorical locations on the Missouri River were included as random effects to account for repeated measures (multiple days/nest and multiple nests/location on the Missouri River). I modeled the response variables (nest attendance, shading and nest exchange behaviors) in relation to daily minimum (MIN), mean (MEAN) and maximum (MAX) sand temperatures. Additionally, the covariates Species (Least Tern or Piping Plover), Date (Julian date of the breeding season) and Clutch Age (age of the nest) were included as predictor variables in all GLMM analyses because previous research determined that they may influence nesting behaviors (Smith & Wilson 2010). I adopted an information-theoretic approach to model selection and ranked models based on their Akaike's Information Criterion corrected for small sample sizes (AIC$_c$), Akaike model weight (w_i) and model goodness-of-fit (-2LL) (Burnham & Anderson 2002). I conducted model selection on a set of 41 *a priori* models for nest attendance and shading behavior response variables. Model selection was also conducted on 48 *a priori* models of nest exchange behaviors. Models that best described the impact of temperature on nesting behaviors had the lowest AIC$_c$ and the largest model weights (Burnham & Anderson 2002). Estimates and 85 % confidence intervals were derived from the top model(s) (Burnham & Anderson 2002).

Results

I installed video cameras and thermocouples at 52 Tern and 55 Plover nests on the Missouri River in North Dakota during the 2014-2015 breeding seasons. Of the 107 nests with cameras and thermocouples, a subset of 39 were included in the GLMM analyses (Tern nests =22, Plover nests =17). There was continuous variation in daily minimum, mean and maximum temperatures throughout both nesting seasons (2014-2015) during the duration of this study (Figs. 10, 11). Average mean and maximum temperatures were slightly higher in 2015 (mean = 24.6˚C, maximum = 42˚C) compared to 2014 (mean = 23.6˚C, maximum = 39˚C), while the minimum was similar for both years (2014 = 13.9˚C, 2015 = 13.6˚C). In general, Plover nest attendance was greater at cooler rather than hotter temperatures (Fig. 12). In contrast, there was more variation in Tern nest attendance responses to maximum sand temperature differences (Fig. 12). The time spent (duration in minutes) and frequency of shading behaviors for both species was higher for hotter temperatures, with the sharpest increase of these activities at ≥ 35˚C (Figs. 13, 14). Temperature had the least influence on the occurrence of nest exchange behaviors with consistent variation in frequency throughout the range of temperatures for both species (Fig. 15).

Daily Nest Attendance

There were 152 days (Tern nests = 22, Plover = 17) included in the analysis of temperature influences on nest attendance, shading and nest exchange behaviors. The top model for nest attendance, Species + Date + Clutch Age + MAX + Species*Date, had the lowest AIC_c (1634.6) and -2LL (1611.56) as well as the greatest w_i (0.334) (Table 12). I considered models two and three as noncompetitive due to the addition of an uninformative parameter that lowered the AIC_c within two units of the top model but did not improve model fit (-2LL) (Arnold 2010). With the exclusion of models two and three, the top model accounted for 63.3% of the w_i. Model four was also considered competitive because it was not nested within the top-ranking model and had a better model fit compared to subsequent models. I considered the rest of the models as noncompetitive (starting at five) due to their ΔAIC_c > two.

Nest attendance was related to all of the parameter estimates included in the top model, as evidenced by confidence intervals excluding zero (Table 13). Generally, Terns spent more time (proportion of total time/day) attending their nests (nest attendance = 0.96 ± 0.0096 se) compared to Plovers (nest attendance = 0.94 ± 0.0096 se) (Fig.16). There was a negative relationship between nest attendance and temperature (Table 13). As daily maximum temperature increased by one degree, nest attendance was reduced by 1.2 minutes.

Shading Behaviors

The variation in daily frequency of shading behaviors was best explained by the top model (Date + Clutch Age + MAX + Species + Species*Clutch Age), which accounted for the majority of the variation in the data (w_i =0.948) (Table 14). Date, MAX and the interaction between Clutch Age and Species had a significant influence (confidence intervals excluded zero) on the daily frequency of shading behaviors (Table 15). Plovers exhibited a higher frequency of shading their eggs compared to Terns (Fig. 17). As daily maximum temperature increased by one degree, the daily frequency of shading behaviors increased by 0.21 behaviors per day.

There was more model uncertainty (more top models with less w_i) for duration of daily shading behaviors. I concluded that the top two models best explained the variation in the duration of shading behaviors because they had the lowest -2LL values (Table 14), which included Date, Clutch Age, MAX, Species as well as the interaction between MAX and Date (model two). I disregarded models three and four as competitive due to the addition of a non-informative parameter (species) that increased the AIC_c within two of the top model but did not improve model fit (-2LL) (Arnold 2010). We considered the rest of the models as noncompetitive (starting at five) due to their ΔAIC_c > two. Model estimates were derived from the top model (Date + Clutch Age + MAX + Species). Date, Species, MAX and Clutch Age all had a significant influence on the daily duration of shading behaviors. On average, shading behavior duration was 0.32 minutes longer per day for each one degree increase in temperature.

Nest Exchange Behaviors

There were no top model(s) that best explained the variation in daily frequency of nest exchange behaviors (Table 16). The top model, which included the interaction between clutch age and MEAN, only accounted for 20 % of the w_i. I considered the top two models as competitive because they had the lowest AIC_c, were not nested and accounted for the most w_i. Models three and four were considered noncompetitive due to the addition of an uninformative parameter that lowered AIC_c to within two units of the top model but did not improve model fit (-2LL) (Arnold 2010). The rest of the models (starting at five) were considered noncompetitive because their $\Delta AIC_c >$ two. There was a slight positive relationship between daily nest exchange frequency and Clutch Age*MEAN (estimate = 0.0014, 85 % CI = 0—0.002) as well as Clutch Age*MAX (estimate = 0.00088, 85 % CI = 0.0005 — 0.0012).

Discussion

Terns and Plovers expressed behaviors related to thermal stress while nesting on the Missouri River in North Dakota with sand temperatures that ranged from 2.7˚C to 54.7˚C during the two-year study. Appropriately, these shorebirds exhibited adaptive plasticity in their nesting behaviors in response to rising temperatures. Adults increased the frequency and duration of shading behaviors at higher sand temperatures. However, I observed only a modest response of shorebird thermal behaviors to higher temperatures compared to past studies (Purdue 1976, Grant 1982, Bergstrom 1989, Ward 1990, Amat & Masero 2004). Concurrently, daily nest attendance decreased with a corresponding increase in temperature, which conflicts with results reported from past research (Purdue 1976, Grant 1982, Bergstrom 1989, Ward 1990, Amat & Masero 2004). I expected a positive relationship between next attendance behaviors and sand temperature, which was not supported by the results. Sand temperatures in this system only briefly (approximately 2-3 hours/day) increased to ranges when thermal behaviors were exhibited. It is likely sand temperatures were not high enough to require prolonged expenditure of thermally adapted behaviors for Terns and Plovers in the Missouri River system.

Next exchange behaviors were the least responsive to fluctuations in temperature. My definition of nest exchange behavior resulted in conservative counts from video observation. I only documented nest exchanges in which both parents were observed in the video and visibly switched attendance at the nest. Due to my limited field of view at the nest, I suspect there were nest exchanges that occurred beyond the field of view. Nonetheless, the purpose of nest exchange behaviors was not to exclusively respond to thermal stress. Adults of both species rotate nest attendance duties to forage as well, which is a possible explanation for the lack of relationship between temperature and nest exchange behaviors.

There was a distinct pattern in the shading behaviors between Terns and Plovers in response to increased temperatures. Plovers exhibited more frequent and longer shading behaviors compared to Terns. One potential reason for this behavioral difference between species is clutch size. Since Plovers lay larger clutches (3-4 eggs), they may expend more energy to regulate egg temperatures compared to Terns (2-3 eggs). This increased energy expenditure by Plovers may increase their core temperatures faster, resulting in overheating more quickly, when the adults responded by exhibiting more and longer shading behaviors. On the other hand, the low estimates of Tern shading behaviors may be due to observational challenges. Much shorter legs combined with poor video quality made it difficult to distinguish shading behaviors for Terns compared to Plovers. Therefore, our estimates for Tern shading behaviors may be negatively biased. Even if the estimates of Tern shading behaviors are slightly under-biased, past research reported that clutch size does not influence mean incubation temperatures (Clauser &

McRae 2016), which provides support that Plovers may have overheated faster in order to maintain incubation temperature of more eggs, resulting in increased shading behaviors.

There are two primary hypotheses for adaptive plasticity of shading responses to temperature fluctuations at the nest: (1) cool egg temperatures within a nonlethal range (DuRant *et al.* 2013) and (2) to prevent overheating of adults while incubating (Downs & Ward 1997, Brown & Downs 2003). Crowned Plover (*Vanellus coronatus*) nesting adult temperatures were always lower during shading behaviors compared to incubation time periods; while egg temperatures were always higher during shading rather than when incubated (Brown & Downs 2003), suggesting that shading behaviors increased the risk of egg hyperthermia compared to incubation. Since both Plovers and Terns are federally protected, I was unable to measure egg or adult temperatures to definitively determine the role of shading behaviors. However, the positive relationship between shading behaviors and sand temperature in this system suggests the primary purpose of shading is to cool the adult and not the eggs. Based on the results of Brown and Downs (2003), if the purpose of shorebird behavior in this system was to maintain egg temperatures, nest attendance should increase with the rise in temperature. Instead, daily nest attendance decreased and shading behaviors increased, which may be more indicative that the purpose of the behavior was to prevent overheating of the adults.

It is crucial that breeding adults of shorebirds be able to cope with fluctuating temperatures in response to climate change. Increased temperature fluctuations may result in breeding pairs of shorebirds that may not be able to cope with high levels of thermal stress during incubation, which may decrease egg survival. The results of this study add to mounting evidence that ground-nesting avian species adapt their nesting behaviors appropriately to temperature variation (Grant 1982, Bergstrom 1989, Ward 1990, Amat & Masero 2004, Saalfeld *et al.* 2012, Clauser & McRae 2016). The occurrence of thermal behaviors in Plovers and Terns suggests that these populations may be able to adapt to future temperature fluctuations due to climate change.

Care should be taken to develop monitoring programs that do not disrupt nesting behaviors during extreme temperatures, especially for protected species such as Terns and Plovers (Andes *et al.* 2018). The examination of possible effects that sand temperatures inflict on avian ground-nesting behavior will be critical to understand in order to adapt or develop monitoring programs in response to climate change. For Terns and Plovers, nest attendance decreased and shading behaviors increased at sand temperatures ≥ 35˚C. Unattended shorebird eggs at the Salton Sea in California, exposed to a similar range of temperatures observed at the Missouri River, overheated and caused embryo death within two minutes (Grant 1982). Therefore, research activities should be conducted at sand temperatures that are within the thermal zone for normal embryo development (35.5˚C-37.5˚C) to prevent prolonged exposure of eggs from unattended nests (Grant 1982). Likewise, extended adult absences from the nest due to researcher presence should be minimized. In the Missouri River system, research activities were prohibited once the ambient temperature exceeded 32.2˚C. Additionally, research and monitoring should be designed to minimize disturbance to normal nesting behaviors (Andes *et al*. 2018). Once a nest is located and then subsequently monitored, personnel should move far enough away from the nest to allow normal nesting behaviors to resume while data is recorded. Since accuracy of nest fate determination decreases as clutch age increases (it is easier to determine fates for nests that fail during early incubation stages), nest monitoring can be minimized until the approach of the estimated hatch date (Andes *et al*. 2018).

To my knowledge, this is the first large scale study to use video cameras paired with thermocouples to evaluate the behavioral responses of nesting shorebirds to temperature variation. My results were similar to those reported from a video camera study conducted on King Rails (*Rallus elegans)* at the Mackay Island National Wildlife Refuge (Clauser & McRae 2016). King Rails spent significantly less time incubating and more time exhibiting shading behaviors as ambient temperature increased (Clauser & McRae 2016). The primary difference between the study conducted by Clauser and McRae (2016) and mine was choice of video camera equipment. There is a trade-off between video quality (greater resolution) and battery life (longer recording hours). I employed continuously recording camera systems, which sacrificed video quality for longer recording hours, resulting in increased sample size of nesting behaviors (1,648 hours of nesting behaviors). Clauser and McRae (2016) conceded battery life for higher video quality by using higher resolution cameras (Sony Handycam, Sony Handycam HD, Go-Pro Hero 3, or Go-Pro Hero 3+), causing a smaller sample size of recorded nesting behaviors (375 hours). Decreased video resolution prohibited our ability to distinguish between individuals (unique band combination), a capability exercised by Clauser and McRae (2016) with their use of high quality video camera equipment. However, I presented a more complete picture of the daily nesting activities of Plovers and Terns with the use of continuously recording video cameras. The integration of video cameras to nest monitoring allows direct measurement of parental responses and increases sample sizes for analyses. Camera systems reduce time and number of research visits to the nest, which may mitigate possible negative impacts to adult nesting behavior. However, my video camera systems experienced technological difficulties (failed to record video) as sand temperature increased. Since my recording systems were buried, battery power loss due to rising substrate temperatures was the primary reason for video loss. This issue was rectified by increasing the exchange of batteries as temperatures increased later in the nesting season. Recent technological advances increased the ease to adapt and incorporate video camera systems into experimental design methods to study avian nesting ecology, especially for shorebirds (Andes *et al.* 2018).

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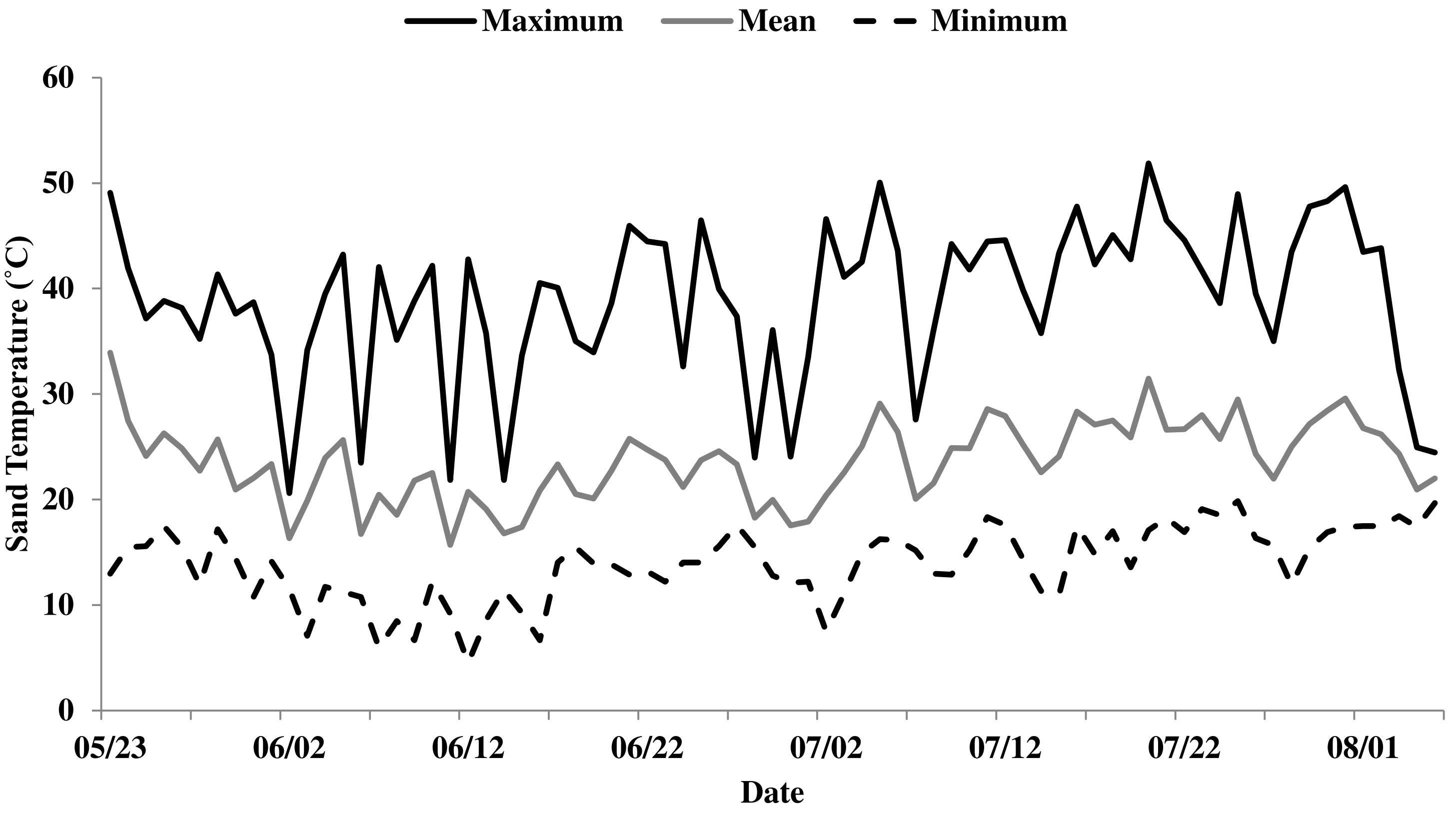

Figure 10. Daily minimum, maximum and mean sand temperatures at sites representative of Least Tern (*Sternula antillarumathalassos*) and Piping Plover (*Charadrius melodus*) nests (n=24) on the Garrison Reach of the Missouri River in 2014.

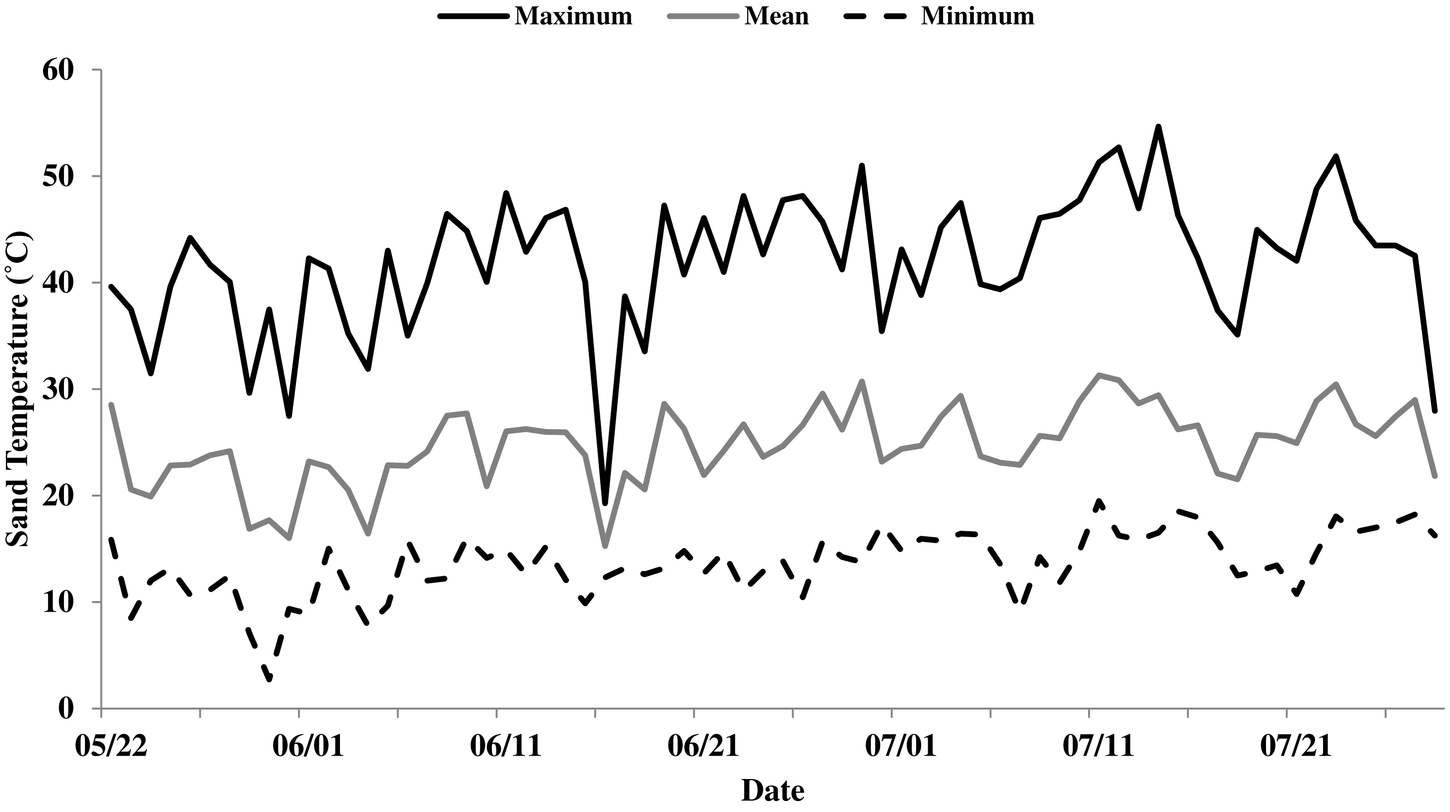

Figure 11. Daily minimum, maximum and mean sand temperatures at sites representative of Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius melodus*) nests (n=15) on the Garrison Reach of the Missouri River in 2015.

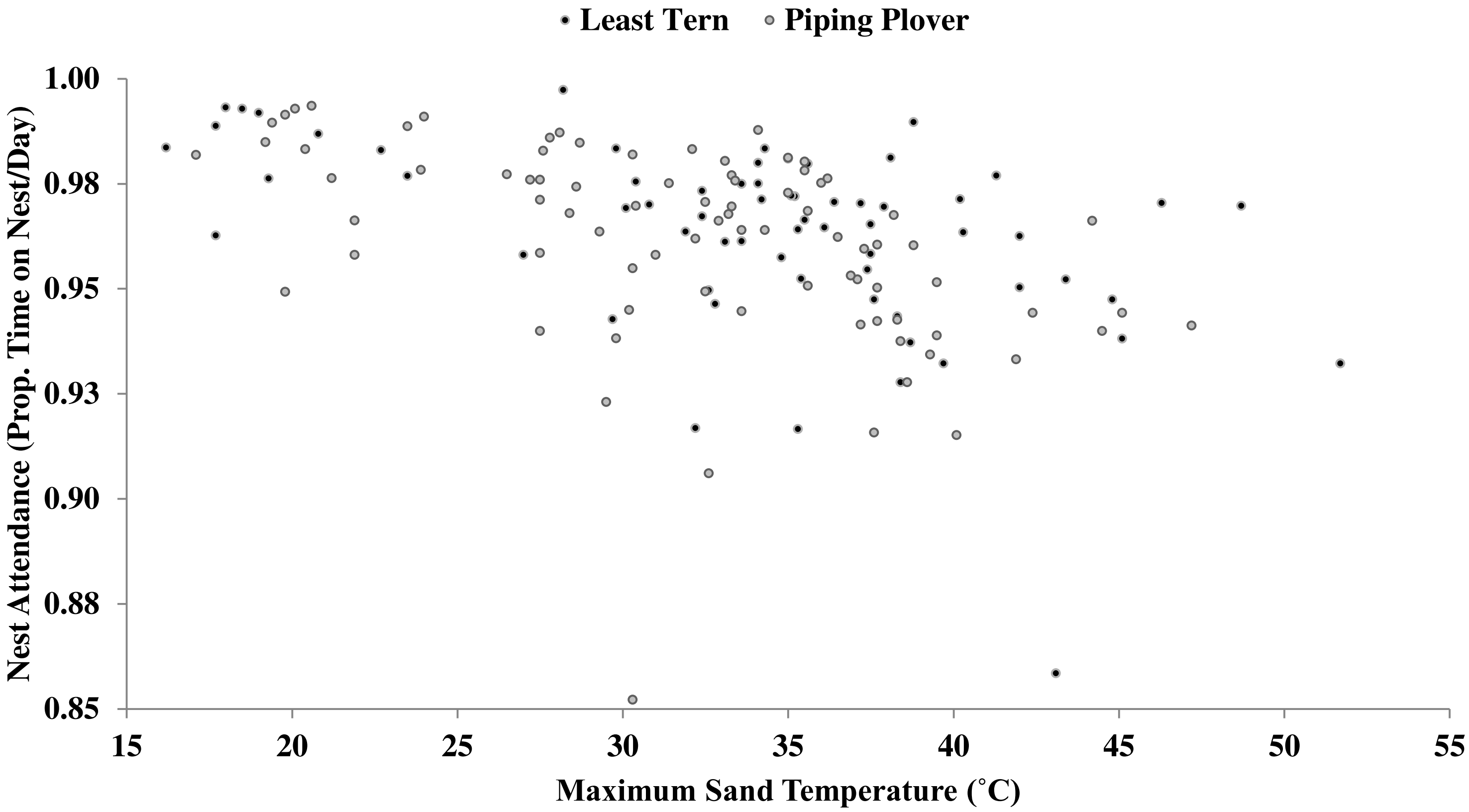

Figure 12. Least Tern (S*ternula antillarum athalassos)* and Piping Plover (*Charadrius melodus*) daily nest attendance (number of minutes spent sitting on or standing over at least one egg in the nest/ total minutes in a day) in relation to maximum sand temperatures on the Missouri River in North Dakota during 2014—2015 in relation to maximum daily sand temperature. Each dot represents the daily nest attendance at a single nest (total days = 152, Least Tern nests =22, Piping Plover nests =17).

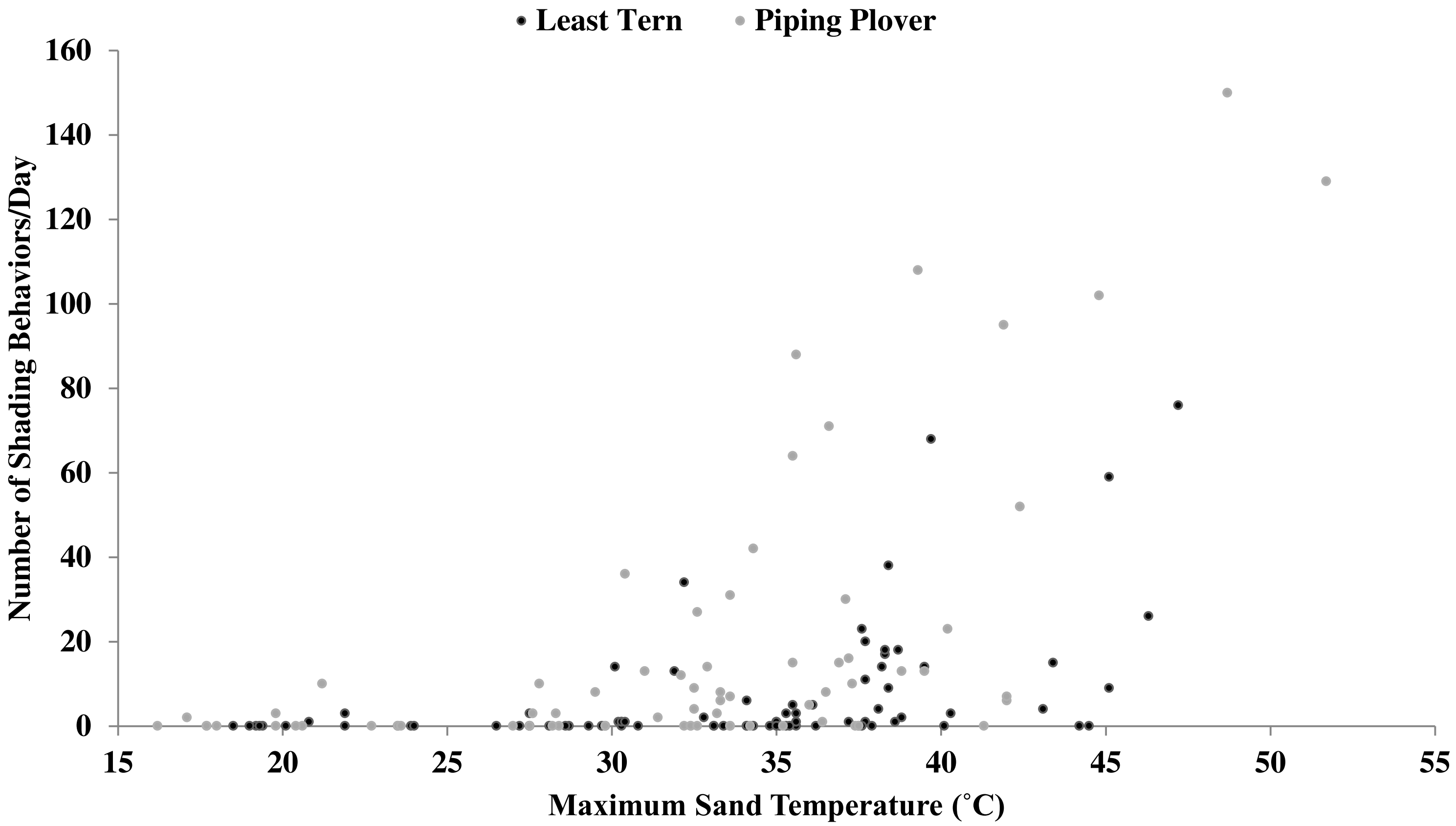

Figure 13. Daily frequency of shading behaviors exhibited by Least Terns (*Sternula antillarum athalassos*) and Piping Plovers (*Charadrius* melodus) that nested on the Missouri River in North Dakota during 2014—2015 in relation to maximum daily sand temperatures. Each dot represents the daily shading behavior frequency at a single nest (total days = 152, Least Tern nests =22, Piping Plover nests =17). Shading behaviors were defined as an adult visibly standing over at least one egg in the nest for > 3 seconds.

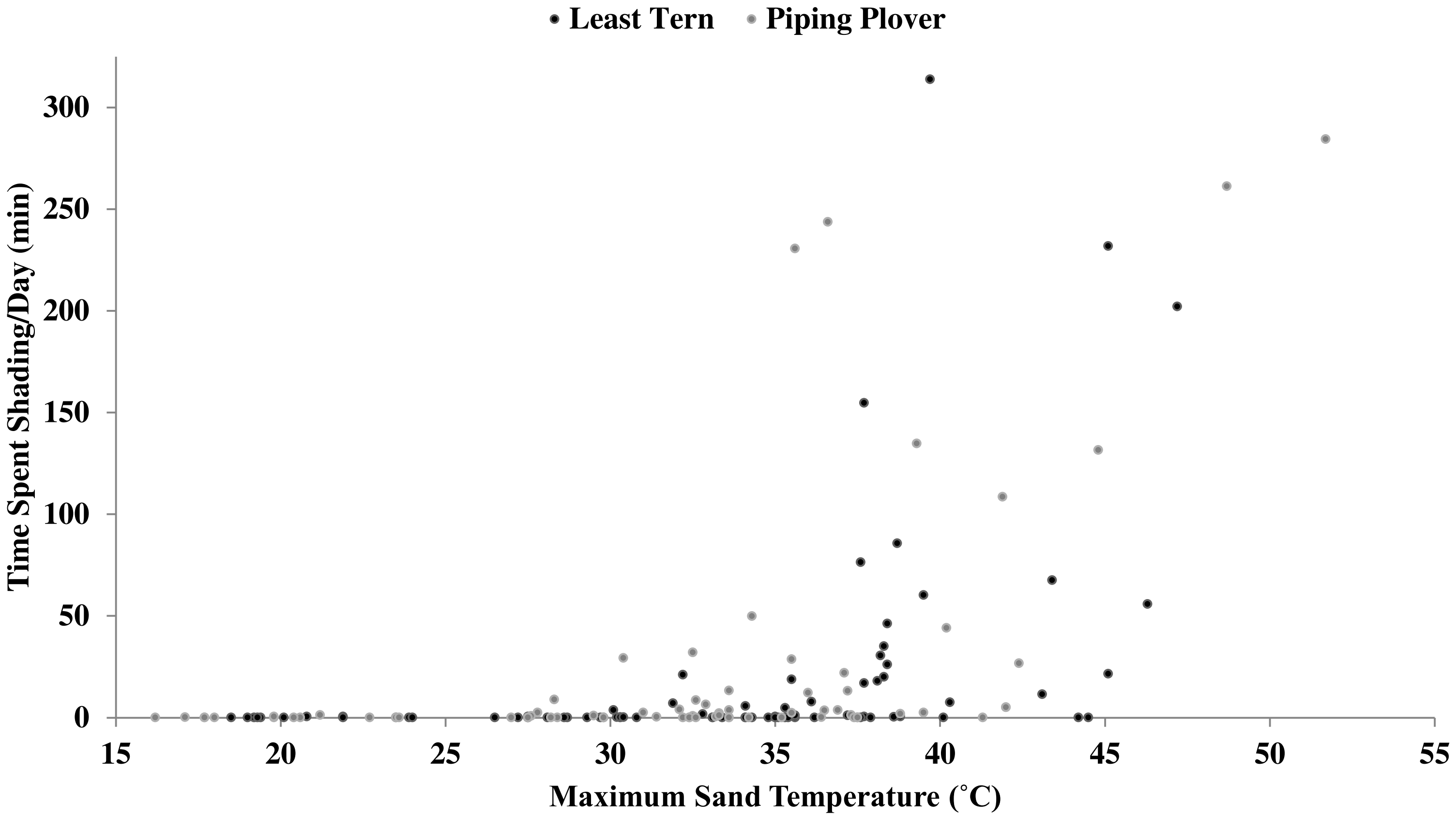

Figure 14. Daily duration of shading behaviors (total minutes spent shading or standing over at least one egg in the nest per day) exhibited by Least Terns (*Sternula antillarum athalassos*) and Piping Plovers (*Charadrius* melodus) that nested on the Missouri River in North Dakota during 2014—2015 in relation to maximum daily sand temperature. Each dot represents the daily shading behavior duration at a single nest (total days = 152, Least Tern nests =22, Piping Plover nests =17). Shading behaviors were defined as an adult visibly standing over at least one egg in the nest for > 3 seconds.

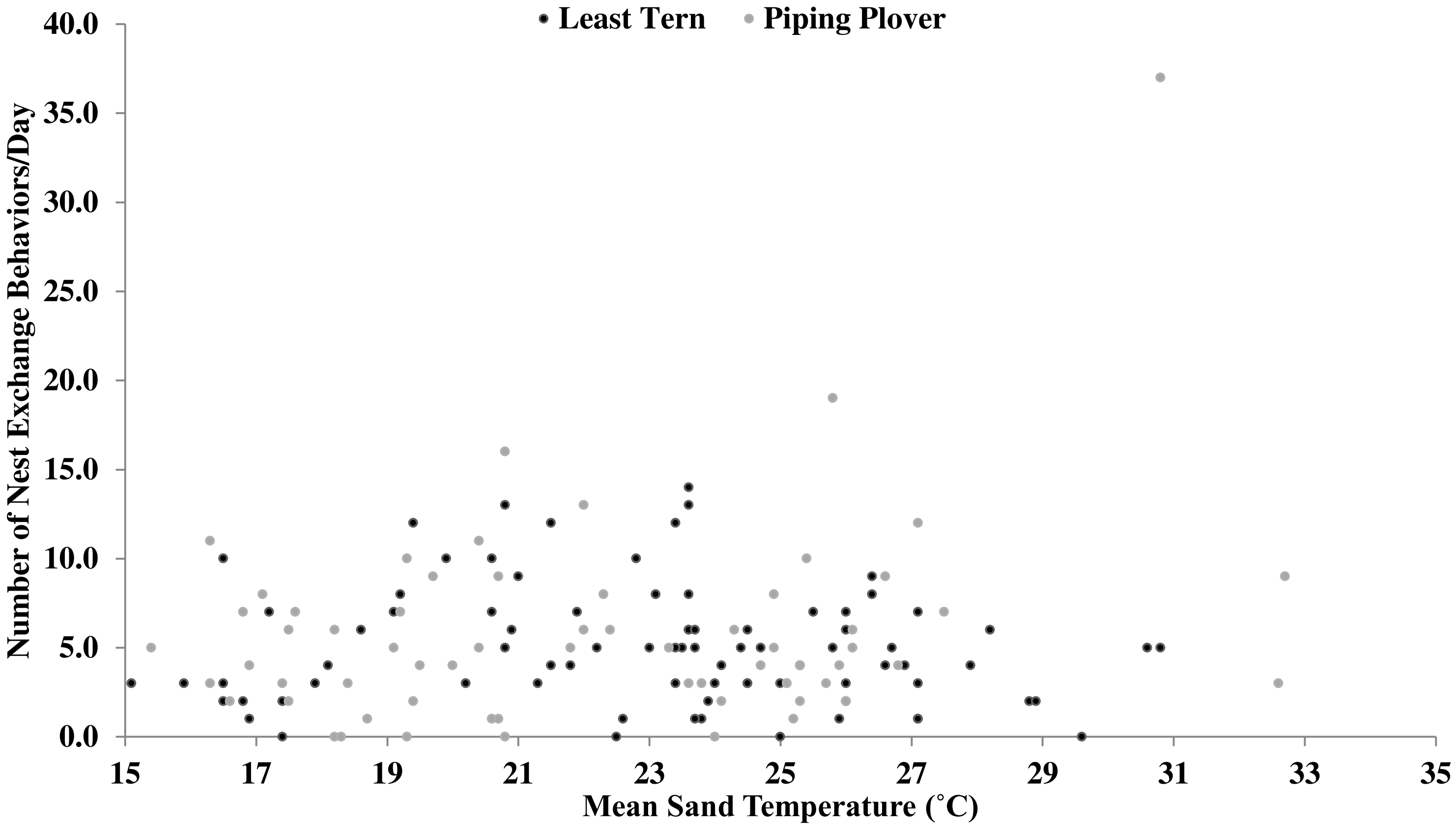

Figure 15. Daily frequency of nest exchange behaviors exhibited by Least Terns (*Sternula antillarum athalassos*) and Piping Plovers (*Charadrius melodus*) that nested on the Missouri River in North Dakota during 2014—2015 in relation to daily mean sand temperatures. Nest exchange behaviors were defined as the trade of attendance duties at the nest. Each dot represents the daily nest exchange frequency at a single nest (total days = 152, Least Tern nests =22, Piping Plover nests =17).

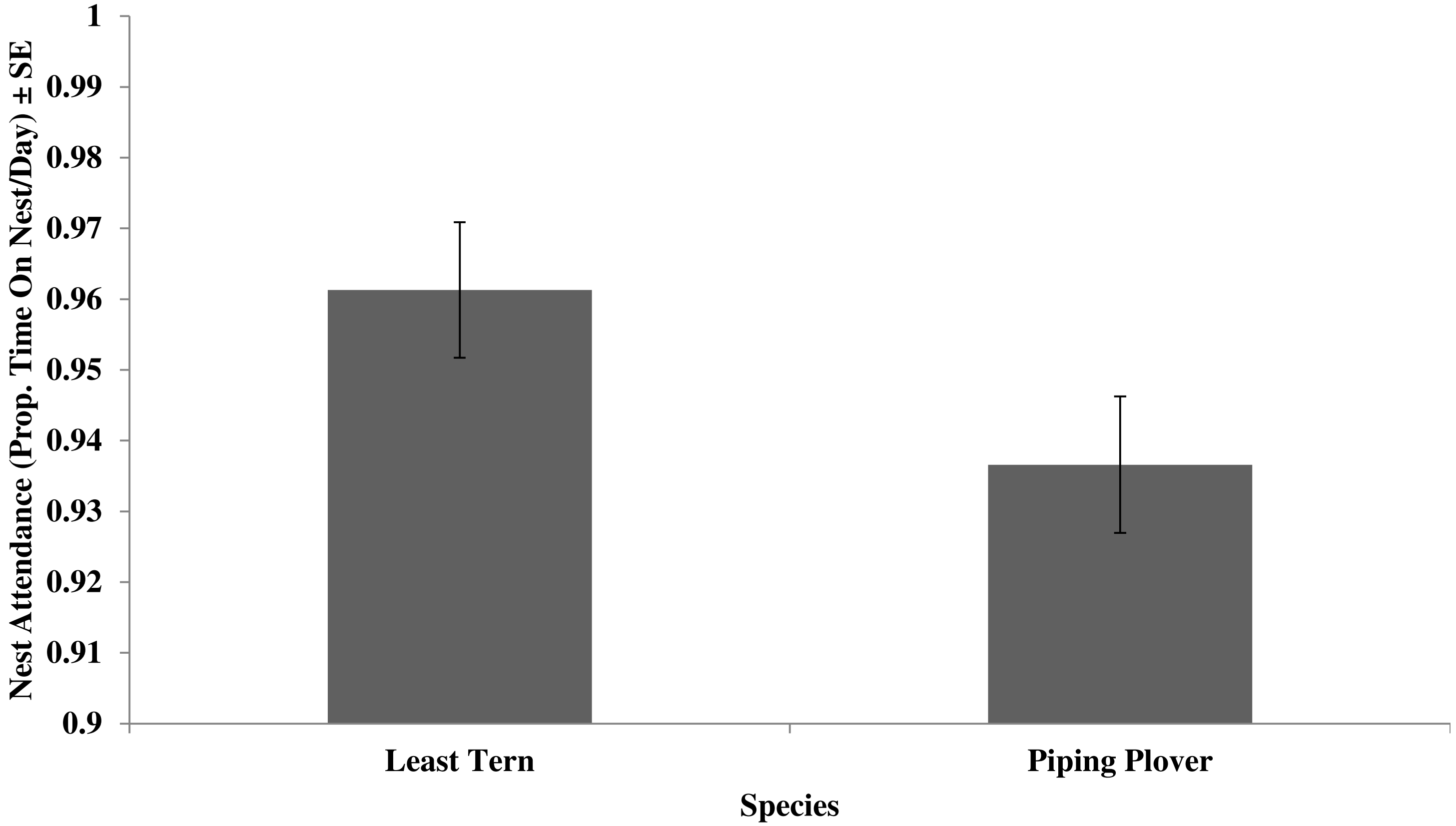

Figure 16. Mean nest attendance (number of minutes spent sitting on or standing over at least one egg in the nest/total minutes in a day) of Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius melodus*) adults that nested (nests=39) on the Garrison Reach of the Missouri River in North Dakota during 2014—2015.

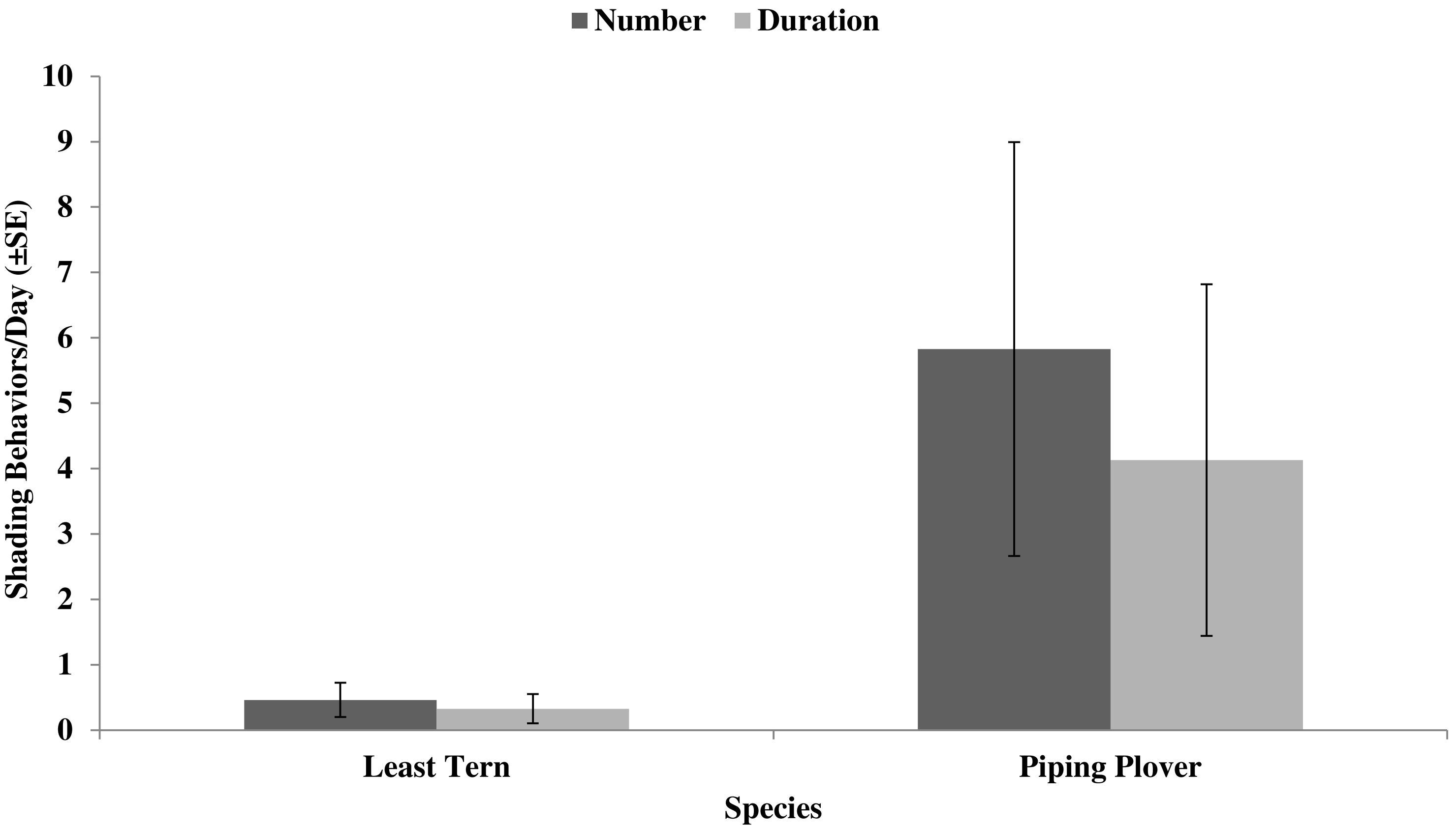

Figure 17. Mean number and duration (minutes) of shading behaviors exhibited by Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius melodus*) adults that nested (nests=39) on the Garrison Reach of the Missouri River in North Dakota from 2014—2015. Shading behaviors were defined as an adult visibly standing over at least one egg in the nest for > 3 seconds.

Table 12. Model-selection results for a subset of generalized linear mixed model (normal distribution) analyses of Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius melodus*) nest attendance on the Missouri River in North Dakota during 2014—2015. Nest attendance (total minutes spent sitting on or standing over at least one egg in the nest per day) was modeled in relation to the covariates: Species (Least Tern or Piping Plover), Date (Julian day of the nesting season), Clutch Age (age of the nest), MAX (maximum sand temperature), MEAN (mean sand temperature) and MIN (minimum sand temperature).

Model	**k**[a]	**-2LL**[b]	**AIC**[c]	**ΔAIC**[d]	**w_i**[e]
Species + Date + Clutch Age + MAX + Species*Date	6	1615.4	1634.6	0	0.334
Species + Date + Clutch Age + MAX + Species*Clutch Age[f]	6	1616.9	1636.1	1.5	0.156
Species + Date + Clutch Age + MAX + Species*MAX[f]	6	1617.3	1636.3	1.7	0.143
Species + Date + Clutch Age + MAX	5	1619.9	1636.9	2.3	0.106
Species + Date + Clutch Age	4	1623.5	1638.3	3.6	0.054
Species + Date + Clutch Age + MEAN	5	1621.6	1638.6	4.0	0.046
Date + Clutch Age + MAX	4	1624.5	1639.3	4.7	0.033
Species + Date + Clutch Age + MIN	5	1622.8	1639.8	5.2	0.025
Intercept	1	1638.2	1646.4	11.8	0.001

[a] The number of parameters in the model

[b] Estimate of model goodness of fit

[c] Akaike's Information Criterion

[d] Distance of a model from the lowest AIC model

[e] The weight of the model

[f] Model has minimal support (Arnold 2010)

Table 13. Estimates for covariates that influenced daily nest attendance of Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius melodus*) adults nesting on the Missouri River in North Dakota from 2014—2015. Nest attendance was defined as the total minutes spent by adults sitting on or standing over at least one egg in the nest per day. Estimates were derived from the top model: Species+ Date + Clutch Age+ MAX + Species*Date). Covariates included Species (Piping Plovers in relation to Least Terns), Date (Julian date of the breeding season), Clutch Age (age of the nest), MAX (maximum sand temperature) and Date*Species (interaction between Piping Plovers and Julian date in relation to Least Terns).

Covariate	**Estimate**	**se**	**85 % CI**
Intercept	1855.01	120.87	—
Species (Piping Plover)	-323.62	169.01	-568.7 — -78.6
Date	-2.9	0.730	-4.0 — -1.9
Clutch Age	2.3	1.01	0.8 — 3.7
MAX	-1.2	0.556	-2.0 — -0.4
Date*Species (Piping Plover)	2.1	0.973	0.7 — 3.5

Table 14. Model-selection results for a subset of generalized linear mixed model (negative binomial distribution) analyses of Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius melodus*) shading behaviors on the Missouri River in North Dakota during 2014—2015. Shading behaviors (frequency and duration in minutes that adults stood over and shaded at least one egg in the nest per day) was modeled in relation to Species (Least Tern or Piping Plover), Date (Julian date of the nesting season), Clutch Age (age of the nest), MAX (maximum sand temperature), MEAN (mean sand temperature) and MIN (minimum sand temperature).

	Model	**k**[a]	**-2LL**[b]	**AIC**[c]	**ΔAIC**[d]	w_i[e]
Frequency	Date + Clutch Age + MAX + Species + Species*Clutch Age	6	746.54	765.81	0.00	0.948
	Date + Clutch Age + MAX + Species + MAX*Date	6	754.57	773.83	8.02	0.017
	Date + Clutch Age + MAX + Species + Species*Date	6	754.57	773.83	8.02	0.017
	Date + Clutch Age + MAX + Species + Species*MAX	6	754.81	774.08	8.27	0.015
	Date + MAX + Species	4	765.01	779.79	13.98	0.001
	Date + Clutch Age + MAX	4	766.04	780.81	15.0	0.001
	MAX*Date	2	773.18	783.6	17.79	0
	Intercept	1	862.47	870.74	104.93	0
Duration	Date + Clutch Age + MAX + Species	5	723.2	740.2	0.00	0.376
	Date + Clutch Age + MAX + Species + MAX*Date	6	722.1	741.4	1.2	0.206
	Date + Clutch Age + MAX + Species + Species*Date[f]	6	722.3	741.6	1.4	0.190
	Date + Clutch Age + MAX + Species + Species*MAX[f]	6	722.4	741.7	1.5	0.180
	Date + MAX + Species	4	731.3	746.0	5.9	0.020
	Date + Clutch Age + MAX	4	731.8	746.6	6.4	0.015
	MAX*Date	2	737.1	747.5	7.4	0.009
	Intercept	1	835.8	844.1	103.9	0

[a] The number of parameters in the model

[b] Estimate of model goodness of fit

[c] Akaike's Information Criterion

[d] Distance of a model from the lowest AIC model

[e] The weight of the model

[f] Model has minimal support (Arnold 2010)

Table 15. Estimates for covariates that influenced daily frequency and duration of Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius melodus*) shading behaviors on the Missouri River in North Dakota during 2014—2015. Estimates for the daily number of shading behaviors were derived from the top ranked model in Table 14 (frequency): (Date + Clutch Age + MAX + Species + Species*Clutch Age). Estimates for the duration of daily shading behaviors were derived from the top model in Table 14 (duration): Date + Clutch Age + MAX + Species). Covariates included Date (Julian date of the breeding season), Clutch Age (age of the nest), MAX (maximum sand temperature), Species (Least Tern in relation to Piping Plover) and the interaction between Species and Clutch Age (influence of clutch age on Least Terns compared to Piping Plovers.

	Covariate	**Estimate**	**se**	**85 % CI**
Frequency	Intercept	-19.7	3.1	—
	Date	0.084	0.017	0.059 — 0.11
	MAX	0.21	0.024	0.18 — 0.25
	Species (Least Tern)	-0.80	0.77	-1.92 — 0.33
	Clutch Age	-0.043	0.031	-0.089 — 1.9e-3
	Clutch Age*Species (Least Tern)	-0.14	0.05	-0.22 — -0.07
Duration	Intercept	-25.14	3.98	—
	Date	0.10	0.021	0.07 — 0.13
	MAX	0.31	0.038	0.25 — 0.36
	Species (Least Tern)	-2.37	0.73	-3.44 — -1.31
	Clutch Age	-0.11	0.036	-0.16 — -0.05

Table 16. Model-selection results for generalized linear mixed model (Poisson distribution) analyses of Least Tern and Piping Plover nest exchange behaviors on the Missouri River in North Dakota during 2014—2015. Nest Exchange behavior (number of times the adults exchanged attendance duties at the nest/day) was modeled in relation Species (Least Tern or Piping Plover), Date (Julian date of the nesting season), Clutch Age (age of the nest), MAX (maximum sand temperature), MEAN (mean sand temperature) and MIN (minimum sand temperature).

Model	**k**[a]	**-2LL**[b]	**AIC$_c$**[c]	**ΔAIC$_c$**[d]	**w$_i$**[e]
Clutch Age*MEAN	2	787.3	795.6	0	0.201
Clutch Age*MAX	2	788.7	797.0	1.43	0.098
Clutch Age*MEAN + Clutch Age*Date[f]	3	787.3	797.3	1.71	0.086
Clutch Age*MEAN + Clutch Age[f]	3	787.3	797.7	2.09	0.071
Clutch Age + MEAN	3	787.4	797.8	2.19	0.067
Clutch Age + MIN	3	788.0	798.4	2.79	0.050
Clutch Age + Date + MEAN	4	786.0	798.6	3.03	0.044
Intercept	1	802.9	809.0	13.46	0

[a] The number of parameters in the model
b

[b] Estimate of model goodness of fit
[c] Akaike's Information Criterion
[d] Distance of a model from the lowest AIC model
[e] The weight of the model
[f] Model has minimal support (Arnold 2010)

CHAPTER V

HETEROSPECIFIC COLONY INFLUENCES ON THE NESTING BEHAVIORS OF LEAST TERNS AND PIPING PLOVERS

Abstract

Nesting behaviors are an intrinsic factor that can have an impact on nest survival. Protection from predators is the primary benefit of colonial nesting strategies and mixed-species colonies can consist of various nest defenses that may alter the nesting behaviors and nest survival of non-target nests. Interior Least Terns (*Sternula antillarum athalassos*) and Piping Plovers (*Charadrius melodus*) nest in mixed-species colonies on the Missouri River in North Dakota. Therefore, my objective was to evaluate the impact of colonial dynamics on the nest attendance of both species. I used generalized linear mixed models to evaluate the relationship between nest attendance and measures of colonial dynamics, including Least Tern and Piping Plover nest densities as well as the distance to the nearest nest for both species. Julian date, clutch age and species were also included as covariates to account for additional factors that influence nest attendance. I installed cameras at 154 nests (65 of 294 Least Tern and 89 of 551 Piping Plover) monitored throughout the duration (May-August) of the study period from 2013-2015. My four top models included distance to the nearest Least Tern nest as a measure of colonial dynamics, which accounted for 45.3 % of the model weight (w_i) and also contained the variables species, clutch age and Julian Date. Tern and Plover nest densities also impacted nest attendance of both species since it they included two of the top ranked models. As Least Tern and Piping Plover nest densities increased by each additional nest/hectare, there was a corresponding rise in the nest attendance of both species by 0.55 and 0.88 minutes respectively. Adults of both species increased their daily nest attendance by 0.031 minutes as distance to the nearest Least Tern nest increased by one meter, which suggests advantages from additional nest defense behaviors of nearby nesting Least Tern adults. The influence of colonial dynamics may have been confounded by habitat quantity and quality and other life-history differences, primarily differences in arrival to the breeding grounds. The influence of heterospecific colonies of Plovers and Terns has important implications for potential management decisions in the future, especially as habitat quality continues to decline.

Keywords: mixed-species colonies, nest defense, *Sternula antillarum*, *Chradrius melodus*, shorebirds, nesting behaviors, nest attendance

Introduction

There is considerable past and current research devoted to determining the limiting factors that influence nest survival, since it is a crucial demographic parameter that influences population dynamics over time. Much of this research focused on extrinsic factors that affected nest survival such as habitat quality, predator communities, human activities, disease, parasites and climate (Benson *et al.* 2010, Stucker *et al.* 2013, Clauser & McRae 2016, Stien & Ims 2016). However, nest survival is also dependent on intrinsic characteristics such as body condition, breeding experience and nesting behaviors (Grant 1982, Eichholz & Sedinger 1998, Smith *et al.* 2012). Nest attendance and incubation constancy are positively correlated with nest survival

(Smith *et al.* 2012). In particular, nesting behaviors are less studied in relation to nest survival, because it is logistically difficult to record unbiased observations in the environment, especially using personnel. Furthermore nesting behaviors, such as nest attendance and incubation constancy, are complicated by the influence of breeding strategies, individual variation and external factors (Martin *et al.* 2000, Palmer *et al.* 2001, Spiegel *et al.* 2012). For example, species that adapted bi-parental care (both adults participate in nesting behaviors) generally are not constrained by trade-offs between energy requirements and incubation, resulting in more time spent attending the nest (Conway & Martin 2000). Past research has demonstrated that adults have the ability to modify their nesting behaviors in response to external factors, such as temperature variation and predation risk, while simultaneously maintaining an ideal nest environment for embryo development (Clauser & McRae 2016).

Colonial dynamics are another external factor that likely influences the nesting behaviors and nest survival of species that form nesting colonies. Protection from predators is the primary benefit of colonial nesting strategies (Götmark & Andersson 1984). Single species colonies include social factors that consist of location in the colony, nest density and nearest neighbor distance. For example, several studies suggest that nest survival increases toward the center of the colony, where incubation constancy increased and adults spent less time defending the nest (Yorio & Quintana 1997, Brown & Brown 2001, Rendón *et al.* 200, Minias & Kaczmarek 2013). However, mixed-species colonies can consist of various nest defense strategies that may alter the nesting behaviors and nest survival of non-target nests. Additional defense from other species may permit riskier nesting behaviors (reduced nest attendance) and allow more time for self-maintenance or foraging (Coates *et al.* 2016) Nest survival for docile species may benefit from the more aggressive nest defense of another genus present in the colony. Several past reports have now confirmed the nest survival advantages of mixed-species colonies for more passive aggressive populations (Veen 1977, Burger 1984, Forbes 1989, Bogliani *et al.* 1999, Powell 2001, Quinn & Ueta 2008). More recently, a comprehensive study was conducted on the influences of Black-crowned Night Herons (*Nycticorax nycticorax*) nesting in colonies with Western Gulls (*Larus occidentalis*) and California gulls (*L. californicus*) (Brussee *et al.* 2016, Coates *et al.* 2016). Incubation constancy and nest attendance decreased by 9% (almost doubled from five) and 2% (quadruple decline from 0.5) respectively for Night Herons that nested within three meter of a gull (Coates *et al.* 2016). In contrast, the probability of heron nest survival was 7.3% more likely with every one meter farther from the gull colony boundary (Brussee *et al.* 2016). These conflicting results highlight the continued need to investigate the influence of mixed-species colonial dynamics on nesting behaviors and ultimately nest survival.

The breeding grounds for Interior Least Terns (*Sternula antillarum athalassos*; hereafter "Terns") and Piping Plovers (*Charadrius melodus*; hereafter "Plovers") on the Missouri River system provide a unique opportunity to evaluate the influence of mixed-species colonial dynamics on nesting behaviors for multiple reasons. First, both Terns and Plovers nest in mixed-colonies, selecting sparsely vegetated sand and gravel habitat, such as temporary sandbars and permanent islands (Catlin *et al.* 2011, Anteau *et al.* 2012, Sherfy *et al.* 2012, Stucker *et al.* 2013). Second, Terns exhibit an aggressive approach to nest defense that includes aerial mobbing and defecation (Burger 1989, Thompson *et al.* 1997). On the other hand, Plover nest defense strategy consists of distracting predators away from nests, a more passive and less aggressive method compared to Terns (Cairns 1982). Both species are protected by The Endangered Species Act as endangered (Terns) and threatened (Plovers) (U.S. Fish and Wildlife Service 1985a, U.S. Fish and Wildlife Service 1985b) due to habitat loss from the Garrison Dam. As habitat quality and quantity continues to decline and competition for nest site selection increases, there is a need to understand how dynamics of this mixed-species colony will influence nesting behaviors and nest survival.

The primary objective of this study was to evaluate the effects of colony characteristics on Tern and Plover nesting behaviors and nest survival. In regards to nesting behaviors, I hypothesized a positive relationship between the nest attendance of both species and distance to the nearest Tern nest. More specifically, Tern and Plover nest attendance will decrease with decreased distance to the nearest Tern nest. Conversely, nest attendance of both species will decrease with an increase in Tern nest density. I expect little influence on the nest attendance of both species in relation to Plover colonial characteristics (nearest Plover nest and nest density). Overall, I expect that Terns and Plovers will benefit from the nest defense behaviors of Terns, which will allow more time spent off the nest.

Methods

Study Site and Species

This study was conducted on the Garrison Reach of the Missouri River in North Dakota, from the dam at Riverdale south to Bismarck, previously described by Shaffer *et al.* (2013), during May through August from 2013 to 2015. Both Terns and Plovers are small, ground-nesting shorebirds that select open, sparsely vegetated sand habitat with pebbles or gravel, such as coastal and riverine shorelines, temporary sandbars and permanent islands

(Anteau *et al.* 2012, Sherfy *et al.* 2012, Stucker *et al.* 2013). Female Terns lay 2-3 eggs in a clutch, one every day (Kirsch 1996, Thompson *et al.* 1997). First Plover attempt clutches typically contain four eggs, laid every other day (Cairns 1982, Elliott-Smith & Haig 2004). Both species exhibit bi-parental care (Keane 1987, Haig & Oring 1988). Tern incubation begins at the start of the egg laying stage and lasts approximately 19-25 days (Thompson *et al.* 1997). Full Plover incubation begins after the last egg is laid. However, there are reported instances when short incubation periods were observed during the egg-laying period (Cairns 1977, Whyte 1985). Terns feed primarily on small fish, shrimp and occasionally invertebrates (Atwood & Kelly 1984) and social feeding between mates at the nest allows for increased rates of nest attendance. Plovers forage alone or in groups along the shoreline for freshwater invertebrates (Nicholls 1989).

Field Methods

I used systematic grid and behavioral searches to locate and monitor Tern and Plover nests throughout the 2013—2015 breeding seasons from May through August (refer to Shaffer *et al.* (2013) for a detailed description of the monitoring methodologies). Nest location was determined by GPS and recorded as UTMs. Clutch age was calculated by egg floatation at the initial nest visit (Mabee *et al.* 2006, Shaffer *et al.* 2013). Egg floatation allowed researchers to determine incubation stage as well as estimate initiation (date first egg was laid) and hatching dates for nests of both species (assuming 18- and 25-day incubation periods for Terns and Plovers (Shaffer *et al.* 2013)). Clutch size was recorded at the onset of incubation. Nests were monitored on a 3-day schedule until the estimated hatch date approached (< 3 days) when visits were increased to daily. Monitoring continued until nest completion when the fate was determined as either successful (hatched with chicks observed in the nest bowl), probable successful (evidence of hatching but no chicks present in the nest bowl, failed (nest could not have hatched based on estimated hatch date or evidence suggested infertile eggs, depredation, abandonment, destruction by weather or livestock) or unknown (Andes *et al.* 2018).

To observe nesting behaviors, video camera systems (miniature infrared surveillance cameras equipped with 24 LEDs and 4.3-mm lenses (Jet Security USA, Buena Park, CA) were installed at 65 of 294 Tern and 89 of 551 Plover nests after incubation reached a minimum of two days and were not removed until a nest outcome was confirmed by field personnel (refer to Andes *et al.* (2018) for a detailed description of the camera system design and installation). The camera was installed ≥ one meter away from the nests at a height of 15 – 25 cm. The 12 V, 35-amp-hour batteries and 32-GB SD cards housed in a weatherproof case (SEAHORSE Protective Equipment Cases, Fuertes Cases, La Mesa, CA) were buried in the sand at least 25-30 meters away from the nest and exchanged every 3-4 days to ensure continuous recording of the nests. Video of nesting behaviors was continuously recorded from installation until the cameras were removed after the nest outcome was classified by researchers in the field.

Recording Nesting Behaviors

I was unable to watch all of the video collected from the 154 camera nests; therefore, a subsample of those nests was first selected to review based on the spatial and temporal distribution of cameras on the Missouri River to ensure independence between nests. In other words, camera nests were selected from each segment (lower, middle and upper) of the Missouri River as well as across the breeding season (early, middle and late initiation dates). Within individual sampled camera nests, days were selected to ensure equal representation of incubation stage (early, middle and late) as well as seasonal temperature variation (early, middle and late breeding season dates). I was interested in documenting nest attendance behaviors defined as the adults attending or "on" the nest, which included sitting on or standing over at least one egg. I recorded start and stop times for all observations when adults were attending the nest. All behavioral observations were recorded within one calendar day (24 hour period) from 00:00:00 in the morning till 23:59:59 at night. Since the presence of researchers decreased nest attendance (Andes *et al.* 2018), I only included days with no research activities at the nest or within the nesting area for analyses. A nesting area was defined as a shoreline, sandbar or habitat with at least one active nest. I recorded the total duration per day in minutes of nest attendance.

Data Analysis

I used ArcMap 10.2 (ESRI) to calculate Tern and Plover nest densities within their specific nesting area boundaries. General aquatic versus terrestrial habitats were first classified from remote sensing of RapidEye Satellite imagery. All suitable Tern and Plover nesting habitat was further partitioned by manual digitization and area was calculated in hectares using the Spatial Analyst toolbox (ESRI). Next, I calculated daily active Tern and Plover nest densities (number nests/hectares) per nesting area. To determine the nearest Tern and Plover nests, I used the Proximity toolset to generate a near table of the distance in meters between the closest Tern-Tern, Tern-Plover, Plover-Plover nests (ESRI).

I conducted generalized linear mixed models (GLMM) using the program PROC GLIMMIX in SAS 9.4 (SAS 9.4; SAS Institute, Cary, NC) for all statistical analyses. I summarized daily nest attendance (total duration of nest attendance in minutes/total minutes in one day) in relation to Tern and Plover colony densities and distance to the nearest nests of both species. I logit transformed the response variable, proportion of daily nest attendance, to facilitate the use of linear models (Warton & Hui 2011). I included year, nest identification number and location on the Missouri River (all categorical variables) as random effects to account for repeated measures (multiple days/nest and multiple nests/location). The heterospecific colony predictor variables used to model variation in nest attendance patterns included: 1) density of active Tern nests (TernDen), 2) density of active Plover nests (PloverDen), 3) distance to the nearest Tern nest (nnTern) and 4) distance to the nearest Plover nest (nnPlover). Species (Tern and Plover), Clutch Age (incubation stage of the nest in days) and Date (Julian date of the nesting season) were also added as predictor variables since past research established that they influence adult nesting behaviors (Smith & Wilson, Smith *et al.* 2012). I adopted an information-theoretic approach to model selection and ranked models based on their Akaike's Information Criterion corrected for small sample sizes (AIC_c), Akaike model weight (w_i) and model goodness-of-fit (-2LL) (Burnham & Anderson 2002). I conducted model selection on a set of 127 *a priori* models (all combinations of the seven predictor variables). Models that best described the impact of colonial dynamics on nest attendance had the lowest AIC_c scores and the largest model weights (Burnham & Anderson 2002). Parameter estimates and 85 % confidence intervals were derived from the top model(s) (Burnham & Anderson 2002).

Results

I installed cameras at 154 nests (65 of 294 Tern and 89 of 551 Plover) monitored throughout the duration (May-August) of the study period from 2013-2015. From the sample size of camera nests, 179 days of nest attendance behaviors (total nests = 49, Tern nests = 23, Plover nests = 26) were included in the analyses. Plover nest densities ranged from 0—0.54 nests/hectare, with a median = 0.13 nests/hectare (Fig. 18). Tern nest densities ranged from 0—1.03 nests/hectare, with a median = 0.061 nests/hectare (Fig. 19). There was a positive trend between nest attendance of both species and Plover nest density (Figure 18). Conversely, no relationship was exhibited between Tern nest density and the nest attendance of both species (Fig. 19). Graphically, there was no relationship between the nest attendance of both species in relation to the nearest Plover or Tern nest (Figs. 20—21).

Model selection resulted in four models (from the 127 *a priori* candidate models) with a ΔAIC_c < two (Table 17). There were four top models that accounted for 45.3% of the variation in daily nest attendance: 1) Date + Clutch Age + Species + nnTern + PloverDen ,2) Date + Clutch Age + Species + nnTern + TernDen + PloverDen, 3) Date + Clutch Age + Species + nnTern + TernDen and 4) Date + Clutch Age + Species + nnTern. However, I derived and interpreted model parameter estimates from the second model because it had the best model fit (lowest -2LL = 343.04). Factors that influenced nest attendance patterns the most included Date, Clutch Age, Species and nnTern, which were present in all top models. Plover nest density (PloverDen) had a moderate impact on nest attendance sine it was only included in the top two models. Whereas, Tern nest density (TernDen) had the least influence on nest attendance patterns since it was only included in the second and third models. Even though there were two top models with similar AIC_c scores, I reported parameter estimates from the second model because it had a better model fit (-2LL was lower).

Parameter estimates from the top model revealed a positive relationship between nest attendance and the distance to the nearest Tern nest, active Tern and Plover nest densities, species and clutch age (Table 18). As Tern and Plover nest densities increased by each additional nest/hectare, there was a corresponding rise in the daily nest attendance of both species by 0.55 and 0.88 minutes/day. Adults of both species increased their daily nest attendance by 0.031 minutes/day as distance to the nearest Least Tern nest increased by one meter. Terns had a higher daily nest attendance rate compared to Plovers. As clutch age increased by one day, the daily nest attendance for both species also increased by 0.048 minutes/day. Conversely, date had a negative effect on nest attendance. With each increase in day during the nesting season, daily nest attendance for both species decreased by -0.021 minutes/day.

Discussion

Colonial dynamics did influence the nesting behaviors of Terns and Plovers on the Missouri River. Adults of both species exhibited riskier nesting behaviors (decreased nest attendance) as distance to the nearest Tern nest decreased. I expected this impact on nest attendance given past evidence that Terns positively influenced Plover (Burger 1987) and Snowy Plover (*Charadrius alexandrinus*) nest success (Powell 2001). Predator protection of Plover nests from Tern defense behaviors was maximized within ten meters of Tern nests in New Jersey (Burger 1987). Likewise, Plover nests within Tern colonies (20 Tern nests per 100 m^2) had higher hatching success compared to those located outside the colony (Burger 1987). Similarly, Powell (2001) reported that Snowy Plover nest success in California was highest within 100 meters of a Tern nest. Our results also indicate benefits to Plovers nesting in proximity to Tern nests. Plover nest attendance decreased (a riskier nest behavior) with decreased distance to the nearest Tern nest. Therefore, Plover adults and nests may benefit from the more aggressive mobbing behaviors of Terns (Burger 1987, Powell 2001). These nest defense behaviors from Terns may be perceived as additional security by Plovers, allowing them to exhibit riskier nesting behaviors (Coates *et al*. 2016). For example, Plover adults nesting in close proximity to a Tern nest may devote less time toward nest attendance while increasing self-maintenance and foraging behaviors. However, I observed only a modest influence of distance to the nearest Tern nest on the nesting behaviors of both species compared to past studies (Coates *et al.* 2016). One potential explanation for this result is spatial scale. The Missouri River system was characterized by low nest densities due to the quantity of available habitat and small population sizes of both species. Past research reported indirect protection of other more passive nesting species within four meters of a gull nest (Veen 1977). The nearest Tern neighbor for a Plover in my sample was generally > 1000 meters away. It is possible that the nest densities in this system are still too small to have a larger effect on nest attendance. Lastly, my study design may have biased the magnitude of colonial effects on nest attendance in the results. While there was no minimum distance between nests, care was taken not to install a camera at a nest that was in close proximity to another of either species, especially if the distance < three meters. Therefore, my sample was biased toward longer distances between nests. There may indeed be a larger effect of distance to nearest neighbor on nest attendance between Terns and Plovers at a much smaller spatial scale.

The density of active Plover nests had the greatest impact on the nest attendance of both species. I suspect there are three reasons why Plover nest density positively influenced the nesting behaviors of both species. First, Plovers begin to arrive at the breeding areas (mid-late April) and begin nesting before Terns (mid-late May). Therefore, Plovers that arrive early in the nesting season have the advantage of selecting the highest quality nesting habitat. For Plovers and Terns that arrive later in the nesting season, it may be advantageous to nest in closer proximity to Plovers that have already selected optimal habitat conditions. The higher rate of nest attendance for both species that nest in larger Plover densities may also be an artifact of habitat quality. The amount of time spent foraging and defending the nest may be reduced by higher quality habitat, resulting in a higher rate of daily nest attendance. There is growing evidence that demonstrates the importance of habitat quality on Plover and Tern nest survival (Catlin *et al.* 2011, Sherfy *et al.* 2012, Stucker *et al.* 2013). Additionally, more food availability from higher quality habitat may reduce the amount of time needed for foraging, resulting in increased time for nest attendance (Rastogi *et al.* 2006, Londoño *et al.* 2008)

To my knowledge, this is the first large scale study to evaluate the impacts of a mixed-species colony on the nesting behavior of two imperiled and federally protected species. Current habitat management on the Missouri River is focused primarily on Plovers, with the assumption that the Tern population will also benefit. My results suggest that the effect of current heterospecific colonial dynamics on Tern and Plover nesting behaviors is not large enough to warrant a refinement to current management practices. In other words, since Plover nest density had the greatest effect on the nesting behaviors of both species, the results support the continued approach to focus Missouri River habitat management on Plovers. However, the dynamics of Tern and Plover heterospecific colonies may have important implications for potential management decisions in the future, especially as habitat quantity and quality continues to decline on the Missouri River. If nest densities and competition for nest-site selection increases due to the decline in habitat quantity and quality, the impact of heterospecific colony dynamics on Tern and Plover nesting behaviors may increase. In other words, the protection benefits to Plovers nesting in close proximity to Tern nests or within colonies may become more important to manage. Therefore, it will be advantageous to determine which species provides a positive or negative influence within the colony.

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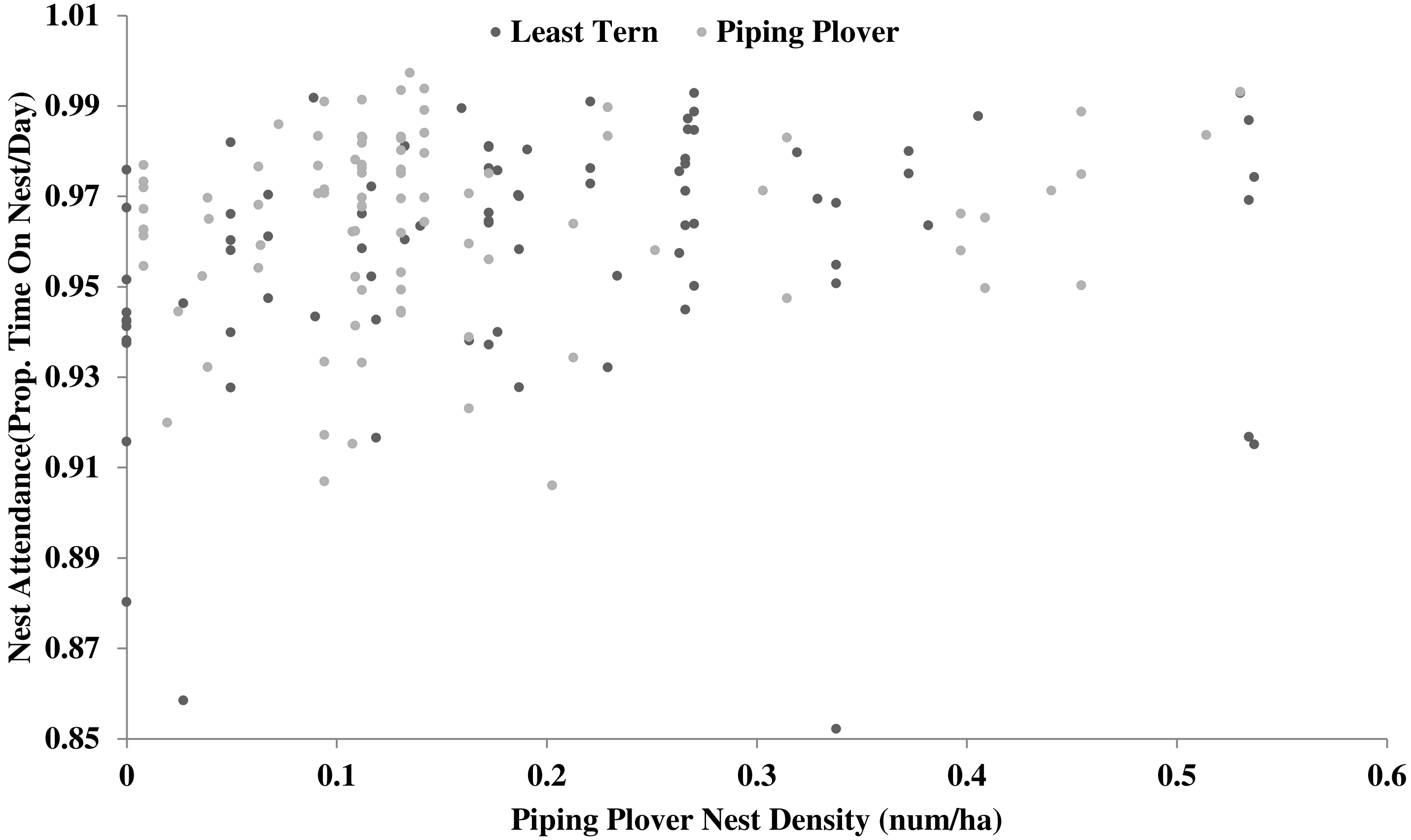

Figure 18. Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius* melodus) daily nest attendance (time spent sitting on or standing over at least one egg in the nest/day) in relation to Piping Plover nest densities on the Missouri River in North Dakota from 2013—2015. Each dot represents the daily attendance at a single nest (total days = 179, Least Tern nests = 23, Piping Plover nests = 26).

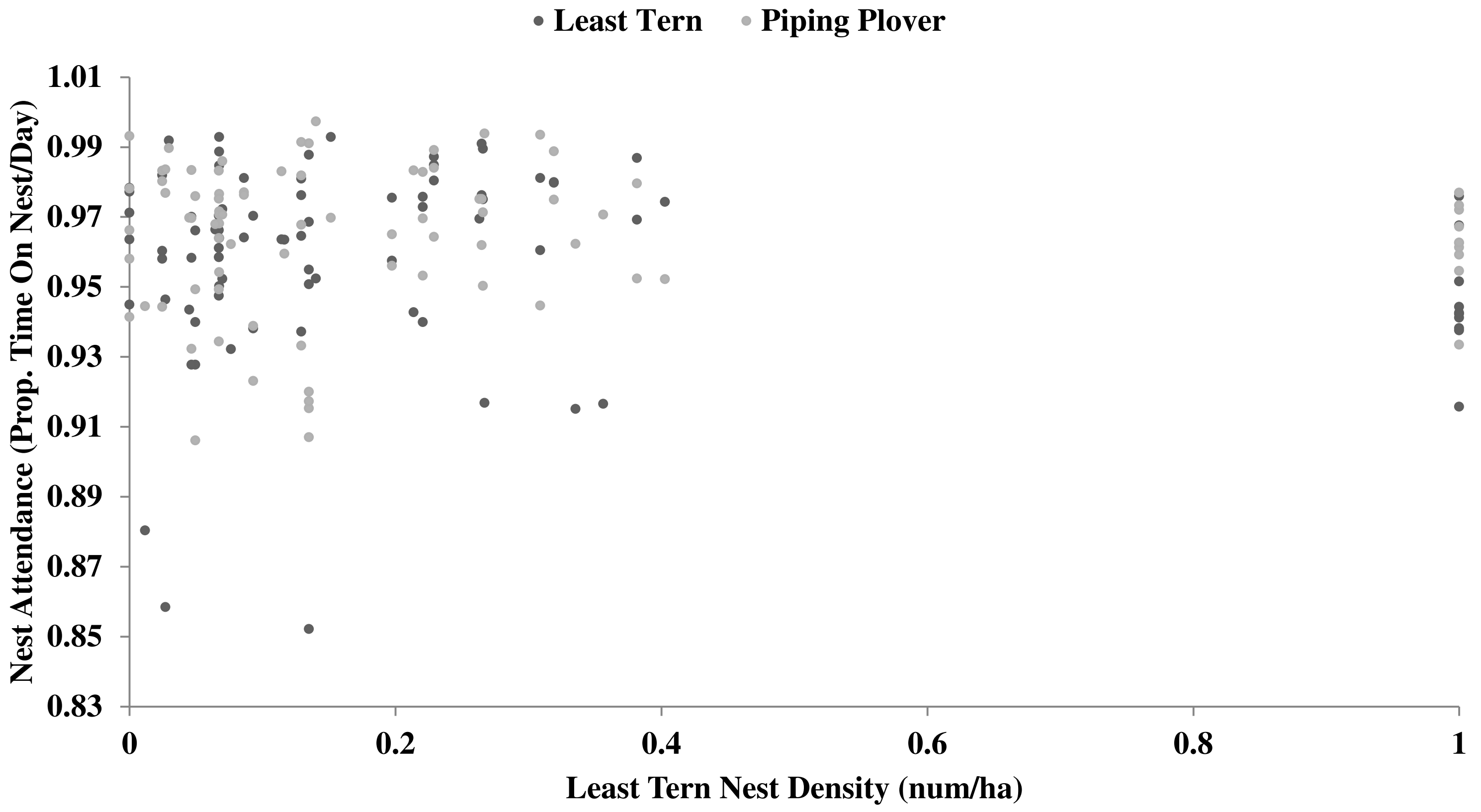

Figure 19. Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius* melodus) daily nest attendance (time spent sitting on or standing over at least one egg in the nest/day) in relation to Least Tern nest densities on the Missouri River in North Dakota from 2013—2015. Each dot represents the daily attendance at a single nest (total days = 179, Least Tern nests = 23, Piping Plover nests = 26).

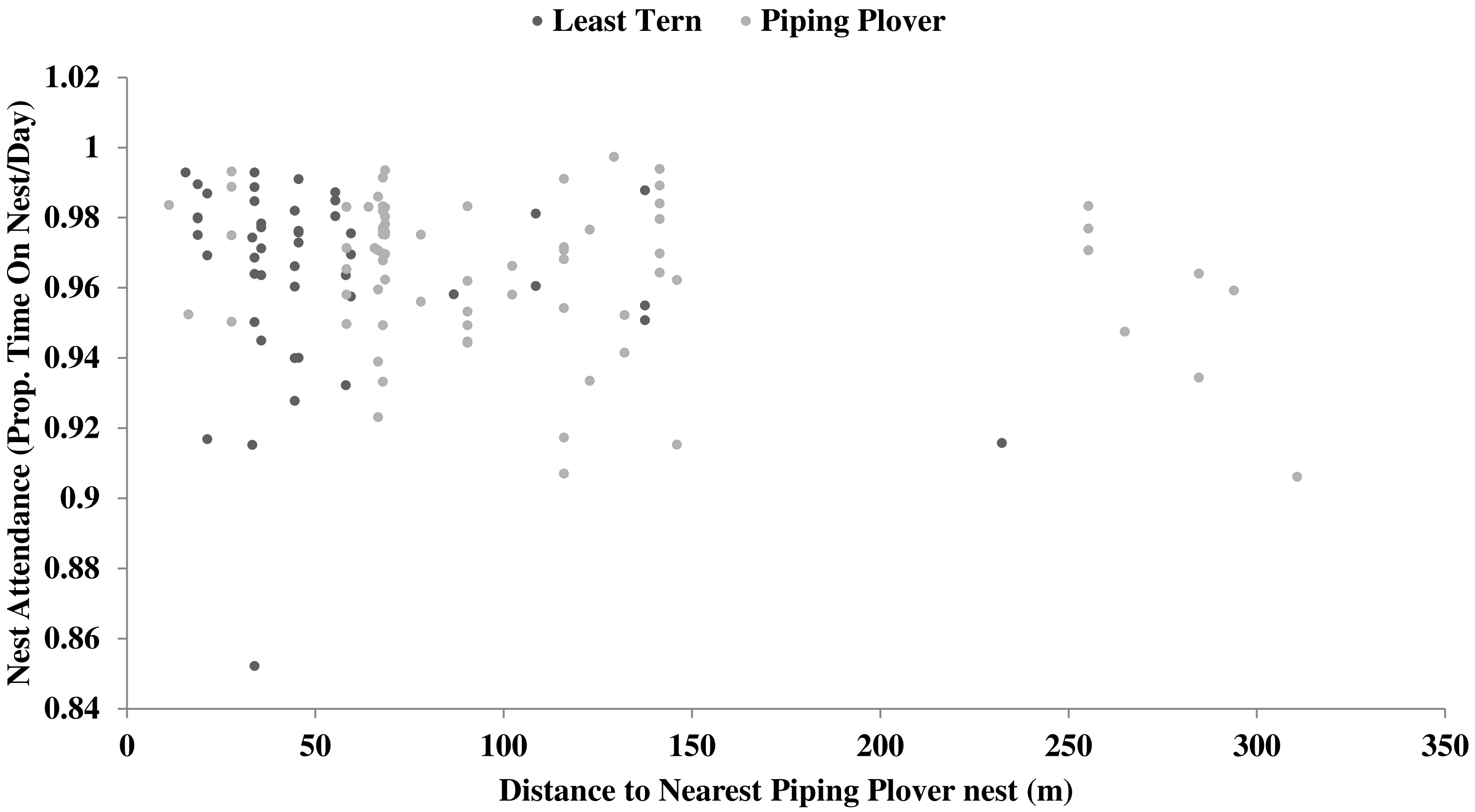

Figure 20. Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius melodus*) daily nest attendance (time spent sitting on or standing over at least one egg in the nest/day) in relation to the distance to the nearest Piping Plover nest on the Missouri River in North Dakota from 2013—2015. Only nests located with 350 m of another Piping Plover nest were included on the graph. Each dot represents the daily attendance at a single nest (total days = 179, Least Tern nests = 23, Piping Plover nests = 26).

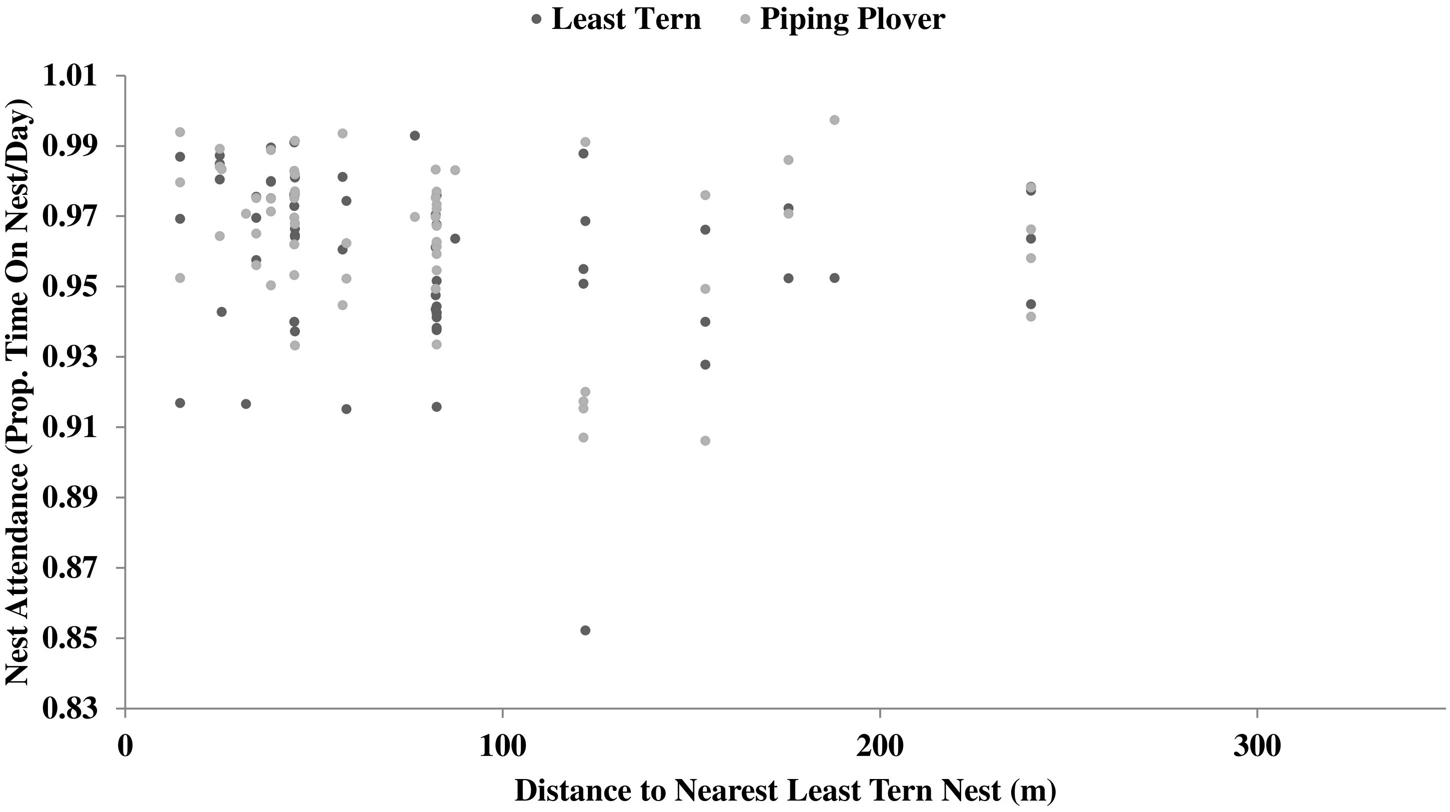

Figure 21. Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius melodus*) daily nest attendance (time spent sitting on or standing over at least one egg in the nest/day) in relation to the distance to the nearest Least Tern nest on the Missouri River in North Dakota from 2013—2015. Only nests located with 350 m of another Least Tern nest were included on the graph. Each dot represents the daily attendance at a single nest (total days = 179, Least Tern nests = 23, Piping Plover nests = 26).

Table 17. Model-selection results for a subset of generalized linear mixed models to determine heterospecifc colonial factors that influence Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius melodus*) nest attendance (time spent sitting on or standing over at least one egg in the nest/day) on the Missouri River in North Dakota from 2013—2015. Heterospecific colonial predictor variables included Piping Plover (PloverDen) and Least Tern (TernDen) nest densities (number/hectare) as well as the distance to the nearest Piping Plover (nnPlover) and Least Tern nests in meters (nnTern). Other variables that influenced nest attendance included Date (Julian date of the breeding season), Clutch Age (incubation stage of nest in days) and Species (Piping Plover or Least Tern).

Model	**k**[a]	**-2LL**[b]	**AIC$_c$**[c]	**ΔAIC$_c$**[d]	w_i[e]
Date + Clutch Age + Species + nnTern + PloverDen	6	344.73	363.8	0.00	0.175
Date + Clutch Age + Species + nnTern + TernDen + PloverDen	7	343.04	364.35	0.55	0.113
Date + Clutch Age + Species + nnTern + TernDen[f]	6	346.09	365.16	1.36	0.089
Date + Clutch Age + Species + nnTern[f]	5	348.62	365.48	1.68	0.076
Date + Clutch Age + Species + nnTern + nnPlover + PloverDen	7	344.79	366.11	2.31	0.055
Date + Clutch Age + Species + PloverDen	5	349.38	366.23	2.43	0.052
Date + Clutch Age + Species + nnTern + nnPlover	6	347.69	366.76	2.96	0.040
Date + Clutch Age + Species + nnTern + TernDen + nnPlover + PloverDen	8	343.23	366.82	3.02	0.039
Date + Clutch Age + Species	4	352.18	366.84	3.04	0.038
Date + Clutch Age + Species + nnTern + TernDen + nnPlover	7	346.05	367.36	3.56	0.030
Intercept	1	374.22	380.36	16.56	0

[a] The number of parameters estimated in the model

[b] Estimate of model goodness of fit

[c] Akaike's Information Criterion corrected for small sample sizes

[d] AIC$_c$ distance of a model from the lowest AIC$_c$ model

[e] weight of a model

[f] Model has minimal support (Arnold 2010)

Table 18. Parameter estimates and 85% confidence intervals for covariates that influenced nest attendance (time spent sitting on or standing over at least one egg in the nest/day) of Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius melodus*) adults on the Missouri River in North Dakota from 2013—2015. Estimates were derived from the model: Date + Clutch Age + Species + nnTern + TernDen + PloverDen. Covariates included Date (Julian date of the breeding season), Clutch Age (age of the nest in days), Species(Least Tern) (Least Tern in relation to Piping Plover), nnTern (distance to nearest Least Tern nest in meters), TernDen (density of Least Tern nests in num/ha) and PloverDen (density of Piping Plover nests in num/ha).

Covariate	**Estimate**	**se**	**85 % CI**
Intercept	6.9	0.84	3.3 — 10.4
Date	-0.027	0.0052	-0.035 — -0.02
Clutch Age	0.048	0.011	0.032 — 0.063
PloverDen	0.88	0.5	0.16 —1.6
TernDen	0.55	0.42	-0.054—1.1
nnTern	0.031	0.013	0.012—0.049
Species (Least Tern)	0.38	0.16	0.15—0.6

CHAPTER VI

CONCLUSION

Least Terns (*Sternula antillarum athalassos*, endangered) and Piping Plovers (*Charadrius melodus,* threatened) are both small shorebirds that have been federally protected by the Endangered Species Act in North Dakota since 1985 (U.S. Fish and Wildlife Service 1985a, U.S. Fish and Wildlife Service 1985b). The continued monitoring and recovery of these species are necessary in order to increase their populations to a sustainable level. In order to effectively manage these populations, repeated research activities are needed to collect vital data on nest survival, adult population size and fledgling rates, which measure their overall productivity. However, management should contain a balance between accurate data collection and the welfare of the focal populations. Inaccurate data can potentially introduce bias in demographic models and causal analyses of nest survival that underpin management plans (Manolis *et al.* 2000). Therefore, it is imperative that data is collected accurately and in a manner that does not negatively influence populations, especially if they are imperiled. The standard protocols implemented to locate and monitor nests of both species have been used for years (Shaffer *et al.* 2013). However, the accuracy of researchers using these nest monitoring techniques to determine nest fate as well as any potential impacts of other research activities on adult nesting behavior remained unknown until this study.

Additionally, monitoring programs may be refined and improved based on the increased understanding of Least Tern and Piping Plover breeding biology. For example, the examination of possible effects that sand temperatures inflict on avian ground-nesting behavior will be critical to understand in order to adapt or develop monitoring programs in response to climate change. Likewise, the dynamics of Least Tern and Piping Plover heterospecific colonies have important implications for potential future management decisions, especially as habitat quality continues to decline on the Missouri River (Sherfy *et al.* 2012, Stucker *et al.* 2013). If competition for nest-site selection and colony densities increases, the dynamics of this mixed-species association may become an influential factor for future management decisions. Therefore, the primary purpose of this research was to refine current research and monitoring programs based on: 1) the evaluation of researchers to accurately classify nest fates, 2) the impacts of various research activities on nesting behaviors and nest survival, 3) adult behavioral responses to increasing sand temperatures at the nest and 4) Least Tern and Piping Plover species interactions.

With increased picture quality and reduced size and cost, the use of video cameras has increased in wildlife research, especially for nest monitoring applications (Cox *et al.* 2012). Cameras allow an unbiased assessment of current protocol efficiency to monitor and measure Least Tern and Piping Plover productivity. This study was conducted on the Garrison Reach of the Missouri River in North Dakota, from the dam at Riverdale south to Bismarck during May through August from 2013 to 2015. Cameras were installed to monitor Least Tern and Piping Plover nesting behaviors and nest survival at a subset of monitored nests. I also monitored temperatures using data loggers pushed into the sand substrate near each camera nest during the 2014 and 2015 reproductive seasons.

In summary, I found no evidence for a negative effect of cameras on Least Tern and Piping Plover nest survival during the duration of this study (Chapter 2). Actually, daily survival rates were higher, albeit not statistically significant, for nests with cameras than ones without, which were attributed to later stages of incubation when the cameras were installed. These results correspond to previously published research that reported a slight positive to no effect of cameras on overall avian nest survival (Richardson *et al.* 2009). We also determined that the accurate estimation of hatch date significantly reduced the probability of nest fate misclassification. Nests that failed early in incubation were easier to classify because there was no probability of hatching based on estimated hatch date. Nest fate determination became more difficult as clutch age increased because frequent weather events, predators, adults and chicks often altered or destroyed evidence of nest outcomes in a short amount of time. Other factors that influenced misclassification of nest fates included monitoring interval, species breeding attributes, and termination date. I found that hatch date estimates were more accurate than the 2.1 ± 2 days reported by Mabee *et al.* (2006) when utilized in combination by experienced researchers conducting systematic nest searching with decreased monitoring intervals (regular nest searches and checks every 3 days). The accuracy of nest fate classification can be increased by locating nests during the egg-laying stage or early incubation, which will result in more reliable estimated hatch dates. It is possible to continuously monitor multiple nests of a population throughout the reproductive season with video cameras to increase the accurate identification of predators and fates, as well as document all nesting activity. Recent technological advances increase the ease to adapt and incorporate digital camera systems into experimental design methods in order to study avian nesting ecology, especially for shorebirds.

Even though an increased monitoring interval resulted in more accurate nest fate classifications, I found that research activities do have an immediate negative impact on adult nesting behaviors as well as a long-term influence on nest survival (Chapter 3). Overall, adults left the nest unattended three times longer during research activities compared to the one hour time periods directly before and after activities. This result is important in combination with adult behavioral responses to temperature changes at the nest. Unattended shorebird eggs at the Salton Sea in California overheated and caused embryo death within two minutes (Grant 1982). For Least Terns and Piping Plovers, nest attendance decreased and shading behaviors increased in response to sand temperatures ≥ 35˚C (Chapter 4). Nests left unattended for prolonged periods of time during research activities conducted at high temperatures may cause eggs to be exposed to heat, leading to embryo death due to hyperthermia. I also determined that the adults resumed normal nesting behaviors shortly after the conclusion of research activities, which resulted in a 1.4 % decline in daily nest attendance. Therefore, research activities should be conducted at temperatures that are within the thermal zone, 35.5˚C—37.5˚C (Grant 1982), for normal embryo development to prevent prolonged exposure of eggs to sand temperatures from unattended nests. Likewise, extended adult absences from the nest due to researcher presence should be minimized.

Past studies have published mixed results about the overall impact of observer effects on nest survival, with the majority of research reporting little to no effect (Weidinger 2008, Ibáñez-Álamo *et al.* 2011). I was also concerned with the impact of research activities on predation risk of nests. The results from this study did indicate that there was a long-term observer effect on predation risk. Nests that were visited more frequently were at a higher risk of predation. Visual cues, such as tracks left in the sand by repeated visits, may have attracted corvids, the primary predator in our system, to nest sites. Since both Least Terns and Piping Plovers build their nests on the ground and in the open, human tracks surrounding a nest may be a conspicuous attraction for predators. Additionally, absences from the nest during research activities may allow corvids to follow the adults back to the nest (Smith *et al.* 2012, Stien & Ims 2016).

The challenge of all experimental designs is to rectify the conflict between accurate data collection and negative impacts to the focal population(s). Based on the results of this research, there are conflicting management implications for Least Terns and Piping Plovers. On the one hand, an increased monitoring interval will result in more accurate nest fate classifications and predator identification. However, an increase in the rate of research activities also corresponded to higher predation risk, which may result in lower nest survival. For Least Terns and Piping Plovers, the key to rectifying the conflict between accurate data collection and negative impacts to nest survival is reliable estimation of hatch dates. If a primary objective is not predator identification, the majority of the monitoring effort can focus on locating nests during the egg-laying stage or early in incubation, which will result in more accurate estimated hatch dates. An accurate estimated hatch date will allow nest monitoring to be minimized early in incubation, decreasing the rate of research activities (that was the primary cause of long-term increased predation risk). Nest monitoring can increase as the estimated hatch date approaches to ensure accurate nest fate classification by researchers. More than one research activity can be combined to decrease the rate of nest visitation. For example, a nest visit can be combined with adult banding to reduce the rate of research activities. In other words, a nest does not need to be visited again within days after a banding activity. Additionally, nest checks can be conducted at a distance to minimize adult absences from the nest as well as visual cues left behind by researchers. Finally, less invasive technology, such as temperature data loggers and video cameras, may be successfully substituted for traditional methods of nest monitoring by field personnel (Weidinger 2008), which will reduce observer effects on nesting behaviors and nest survival.

Current management of both species on the Missouri River is focused primarily on Piping Plovers, with the assumption that benefits to that population will also be advantageous for Least Terns (Shaffer *et al.* 2013). However, these two species form heterospecific colonies on the Missouri River and species interactions may influence nest survival. For example, results from studies conducted in New Jersey and California suggests that Piping Plovers and Snowy Plovers (*C. nivosus*) nesting closer to an active Least Tern nest had greater success (Burger 1987, Powell 2001). Therefore, I hypothesized that adults of both species nesting in heterospecific colonies would exhibit riskier nesting behaviors (decreased nest attendance) due to the additional protection from the more aggressive nest defense of Least Terns. I found that Piping Plover and Least Tern nest densities as well as the distance to the nearest Least Tern nest positively influenced the nest attendance of both species. There was a slight decline in nest attendance of both species as distance to the nearest Least Tern nest also decreased, which did support my hypothesis. I suspect that habitat quality and quantity as well as low nesting densities may be the reason why Least Tern colonies had only a modest influence on the nesting behaviors of both species. The results of this study support current habitat management practices on the Missouri River that focus on Piping Plovers rather than Least Terns. If nest densities and competition for nest-site selection increases due to the decline in habitat quantity and quality, the impact of heterospecific colony dynamics on Tern and Plover nesting behaviors may increase. In other words, the protection benefits to Plovers nesting in close proximity to Tern nests or within colonies may become more important to manage. Therefore, it will be advantageous to determine which species provides a positive or negative influence within the colony.

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