POPULATION DYNAMICS AND MANAGEMENT IMPLICATIONS FOR AMERICAN WHITE PELICANS (*PELECANUS ERYTHRORHYNCHOS*) BREEDING AT MARSH LAKE, LAC QUI PARLE WILDLIFE MANAGEMENT AREA, MINNESOTA

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The Supervisory Committee certifies that this ***disquisition*** complies with North Dakota State University's regulations and meets the accepted standards for the degree of

DOCTOR OF PHILOSOPHY

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ABSTRACT

The American white pelican (*Pelecanus erythrorhynchos*) is a prominent breeding bird in Minnesota, but little information has been available on their production, population dynamics, growth and development, or demographic characteristics. I examined life-history traits of American white pelicans nesting colonially at Marsh Lake, Lac qui Parle Wildlife Management Area, Minnesota. Marsh Lake is an impounded river floodplain lake on the Upper Minnesota River that holds the largest American white pelican breeding colony in Minnesota (and one of the largest American white pelican breeding colonies in North America).

An analysis of colony population levels and spring streamflow data indicated that more than 84% of the variation in the number of near-fledged chicks produced per nest was related to mean daily discharge during April. In years when high water floods preferred low-elevation nesting habitat on islands in the middle of the lake, American white pelicans are forced to establish nests on high-elevation sites that are closer to the mainland. The proximity to the mainland leaves the high-elevation sites accessible to mainland mammalian predators, and production rates decline.

An examination of size at hatch and growth of American white pelican chicks showed little variation in initial size and growth rates between years. However, substantial variation in initial size and growth rates were detected within season depending on the timing of hatch. Initial mass did not vary throughout the nesting season, but initial tarsus and wing length were shorter in chicks hatched later in the season. However, growth rates for mass, tarsus, and wing were faster for late-hatched chicks, potentially allowing late-hatched chicks to fledge at an earlier age.

An analysis of demographic characteristics of American white pelicans nesting at Marsh Lake indicated timing of nest initiation was not related to age or body condition of adults.

However, nests were initiated earlier on the preferred nesting island at Marsh Lake. Although some individuals may nest at an earlier age, the estimated age of maturation for American white pelicans nesting at Marsh Lake suggests they are unlikely to begin nesting until they are at least five years old.

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GENERAL INTRODUCTION

The American white pelican (*Pelecanus erythrorhynchos*) is listed as a Species of Special Concern in Minnesota (MN DNR 2006), yet little information is available on breeding dynamics or life history traits that could be useful in formulating effective management strategies. The historical presence and widespread appeal of this charismatic species is exemplified by the numerous lakes, rivers, islands, and other geographic features named after them in Minnesota (Upham 1920). In many cases, the names are English translations of preexisting American Indian names (Upham 1920). In some instances, a form of the American Indian name has been retained, as with Lake Shetek, Murray County (U. S. House 1845; Upham 1920). Some of the names have been used for centuries. For example, the Chippewa (Ojibwe) Indians did not advance west of Lake Superior until after 1736, but by 1783 they were occupying the area around Leech Lake when they named Pelican Island because of the number of pelicans that nested there (Warren 1885). Later, a map of the Upper Mississippi River produced from Z. M. Pike's 1805-1807 expedition (Pike 1895) delineated and labeled Pelican Island on Leech Lake (Cronin 1895). The following narrative summarizes the historic record of American white pelicans in Minnesota.

Pre-1850

Although long known as a breeding bird in the state, the historical status and distribution of American white pelicans in Minnesota are not well documented. Some of the earliest reports of American white pelicans in the region include Henry (1809) who reported that American white pelicans were numerous on Lake of the Woods, Lake of the Woods County in August 1775. Carver (1778) included the species among birds he observed on his 1776-1768 expedition to Minnesota and Wisconsin. Henry and Thompson (in Coues, 1897) noted American white pelicans on the Red River of the North on the Minnesota-North Dakota border near the Pembina River Post, Pembina County, North Dakota in April 1802.

Schoolcraft (1821; 1834), in his two expeditions to discover the source of the Mississippi, wrote of several encounters with American white pelicans in north-central Minnesota. In July 1820, on what he described as Lake Winnipec, Schoolcraft (1821) named a guano-covered island as Pelican Island, where he flushed pelicans and found a dead pelican on its shore. Lake Winnipec is referenced on Pike's earlier map (Cronin 1895) and may have been inundated following construction of the Lake Winnibigoshish dam in 1881-1884 (Winchell 1899). When descending the Mississippi River in late July 1820, Schoolcraft (1821) reported American white pelicans were common in the vicinity of Pike's former winter encampment near Little Falls, Morrison County. On his second expedition in 1832, Schoolcraft (1834) portaged to Leech Lake, where he described pelicans as annually returning to the lake. He additionally produced a map of Leech Lake, which like Pike's earlier map (Cronin 1895), depicted and labeled Pelican Island. All evidence suggests pelican nesting activity on the island.

Lanman (1847) reported American white pelicans were nesting on Pelican Island, Leech Lake in July 1846. Owen (1852) described American white pelicans as common in the region around Otter Tail Lake, Otter Tail County in June 1848.

1850-1900

Trippe (1870) described American white pelicans as common spring and fall migrants in central Minnesota in 1870, but did not mention pelican presence during the breeding season. This was the same region where both Schoolcraft (1821) and Owen (1852) had reported pelicans as a common summer resident decades earlier. Krider (1879) reported that in May 1872 American white pelicans were abundant and nesting in Minnesota. Coues (1877) reported American white pelicans on the Red River of the North and some of its tributaries, and described a specimen collected in May 1873 on the Red River near Pembina. Coues' description of fifty crayfish collected from the pelican's stomach resulted in the identification of a new crayfish species, *Cambarus couesi* (Streets 1877). Hatch (1874) wrote that American white pelicans were a common breeding bird in the state, arriving 1 April and departing 1 November. Deane (1923) cites G. B. Sennett's notes from a trip to collect scientific specimens in Minnesota; Sennett reported shooting two pelicans in April 1876 near Elbow Lake, Grant County.

McChesney (1879) reported that American white pelicans were a common spring and fall migrant, as well as summer resident, approximately 50 km west of the Minnesota border in the vicinity of Fort Sisseton, Marshall County, South Dakota during 1876-1878. Farrar (1880) reported pelicans as common in Minnesota during 1875-1879. Roberts (1919a) described American white pelicans as a once common summer resident of Minnesota, and wrote that a pelican colony on Pelican Point, Heron Lake, Jackson County had been abandoned sometime in the 1870s. Roberts and Benner (1880) reported that frequent visits by residents of Herman, Grant County to a pelican colony on the Mustinka River in 1878 resulted in the abandonment of the colony. In 1879 Roberts and Benner (1880) searched the area to see if the pelicans had established a new nesting colony. Although they observed pelicans near the South Dakota border at Brown's Valley and on Lake Traverse, Traverse County, they were unable to find any nests.

Hatch (1881) described American white pelicans as a common breeding bird in Minnesota during 1879. Cooke (1888) reported breeding by American white pelicans from southern Minnesota northward during 1884-1885, and Cantwell (1890) reported that pelicans were common in Minnesota, breeding in western parts of the state between 1883 and 1889. Goss (1891) reported American white pelicans breeding on islands in large inland lakes from

Minnesota northward. Bullis (1892) described American white pelicans as rare, but still breeding in Faribault, Martin, and Jackson counties, Minnesota. Following the abandonment of the Mustinka River colony (Roberts and Benner 1880), Hatch (1892) reported persistent claims by duck hunters that American white pelicans had resumed breeding at other locations in Minnesota, including credible reports that they were nesting at Lake Shetek, Lake Traverse, and other locations in northwestern parts of the state. Hatch (1892) concluded that American white pelicans still nested in Minnesota. Rolfe (1896) noted occasional flocks of American white pelicans seen during the breeding season, but he was unable to locate a nesting colony in eastern North Dakota or western Minnesota, whereas Chapman (1896) noted that they still bred from southern Minnesota northward. Roberts (1932) referenced reports of American white pelicans breeding at Pelican Lake, Grant County up to 1895, and Lake Shetek in 1899.

1900-1950

Mindwell (1901) described the main breeding grounds for American white pelicans as including Minnesota northward. Currier (1904) noted a flock of American white pelicans flying over Leech Lake in June 1902; however, he reported seeing no pelicans on the lake during the summer of 1903. Chapman and Reed (1903) and Cory (1909) expressed uncertainty over the breeding status of American white pelicans in Minnesota. However, Lano (1922) described two pre-fledging American white pelican chicks collected by a hunter on the shore of (Big) Sandy Lake, Aitkin County in August 1904, providing evidence of pelicans nesting in Minnesota during this period.

Meeker (1907) noted that American white pelicans no longer nested on Pelican Lake in Becker County, and Roberts (1907) added that although pelicans were once abundant in Becker County, they were greatly reduced in numbers, and occurred only in small flocks. Widmann

(1907) reported American white pelicans still bred from Minnesota northward, whereas Chapman (1908) suggested that pelicans had not nested in Minnesota for 30 years. By 1910, the American Ornithologists' Union (Allen 1910) indicated that American white pelicans no longer bred in Minnesota and South Dakota. Hornaday (1913) stated that by 1912, pelicans were extirpated as a breeding bird from Iowa and Minnesota, and were threatened in North Dakota and Wisconsin. Skinner (1917) reported that American white pelicans no longer nested in North Dakota and Minnesota, and Reagan (1917) described them as occasional to frequent migrants in north central Minnesota. Bent (1922) wrote that pelicans still nested in North Dakota, but no longer nested in Wisconsin, Minnesota, or South Dakota.

Roberts (1932) indicated the Mustinka River colony was the last American white pelican colony in Minnesota for which he had knowledge; however, as with Hatch (1892) earlier, he referenced reports of pelicans nesting in the state since that time, including the vicinity of Leech Lake in 1902 and Heron Lake in 1914. Offered as an update of McChesney's (1879) report from six decades earlier, Youngworth (1935) described American white pelicans as a regular migrant in the vicinity of Fort Sisseton, South Dakota, sometimes summering on the Waubay lakes, Day County, in 1929-1930, and 1935. In July 1938, four American white pelican nests were found on a small island in Lake of the Woods, Ontario, Canada less than four km from the Minnesota border (Erickson and Upson 1938). By the late 1940s and early 1950s, pelicans attempted nesting on South Waubay Lake (Adolphson and Adolphson 1968).

Post-1950

Breckenridge (1968) described a credible report by a game warden of American white pelicans nesting in Lac qui Parle County around 1950. Lee (1951) provided April and May pelican counts, primarily from southwest and west-central Minnesota, documented during spring

1950 waterfowl surveys. Many of his counts were of several hundred pelicans, up to 1,000-2,000 in Nobles and Traverse counties. One of the lakes where American white pelicans were counted in Lee's (1951) report was Ocheda Lake, Nobles County. In July 1955, 100 pre-fledging pelican chicks were banded at Ocheda Lake (U. S. G. S. Bird Banding Laboratory 2013).

Lies and Behle (1966) reported that pelicans had abandoned the Lake of the Woods islands colonized in the late-1930s but returned around 1958, whereas Magnus (1960) reported nesting pelicans were present there during 1956-1958. By 1960 the colony expanded to two other islands approximately 0.5 km south (Lies and Behle 1966). The colony on South Waubay Lake grew to 200-250 nests by the early 1960s, up to 1,500 by 1965 (Adolphson and Adolphson 1968). A much larger colony formed approximately 15 km southeast on Bitter Lake, initially in 1964 and then from 1987 to the present (Sovada *et al*. 2013), and pelicans no longer nest at South Waubay Lake. Breckenridge (1968) reported 25 active American white pelican nests on a small island on Marsh Lake, Big Stone County in July 1968. An annual banding program was initiated in the Marsh Lake pelican colony in 1972 by A. H. Grewe, Jr., St. Cloud State University that has been ongoing through 2015. American white pelicans were reported summering in Jackson County in 1971, with three pelican chicks seen in August (Eckert 1971). That report was clarified by Baumhofer (1972) who identified the colony location as North Heron Lake, and reported an additional 90 adult pelicans and 40 pre-fledging chicks were present in June 1972.

In 1973, the nesting colony of American white pelicans expanded from the Ontario side of Lake of the Woods to an island on the Minnesota side of the lake, with reports of 200 adult pelicans and 80-100 chicks (Sloan 1973; Janssen 1974). Sloan (1973) noted that American white pelicans were still nesting at Heron Lake in 1973, but by 1983, pelicans were no longer nesting on the lake (Guertin 1984).

Mortensen and Ringle (2007) described finding a single American white pelican egg on Little Pelican Island on Leech Lake in 1993. Hiemenz (1994) found three American white pelican nests on an island on Lake Johanna, Pope County in June 1994. Two of the nests held chicks, and the third still contained eggs. Also in 1994, Fall (1994) observed American white pelicans nesting on an island on Minnesota Lake, Faribault County, where he estimated 70-80 pre-fledging chicks in July. The landowner adjacent to the nesting island reported the pelicans had nested on the island for 20 years (Fall 1994). Mortensen and Ringle (2007) reported a single nest with two pelican eggs on Little Pelican Island on Leech Lake in 1998. While early nesting attempts failed, five young were fledged from eight nests on Little Pelican Island in 1999 (Mortensen and Ringle 2007).

American white pelicans began nesting on a mainland point separating Upper and Lower Red Lake, Red Lake Indian Reservation, Beltrami County in the mid-1990s (J. Huseby, Red Lake Department of Natural Resources, personal communication). When visited in July 2006, 300-400 adult pelicans were present, along with the remains of 200-300 nests that were destroyed by predators (J. J. DiMatteo, personal observations). During the late 1990s or early 2000s, American white pelicans also began nesting at Pigeon Lake, Meeker County and Swartout Lake, Wright County (F. Bengtson, Minnesota Department of Natural Resources, personal communication). Pelicans nested on Leech Lake in 2001, 2004, 2006, and 2007; however, the nesting attempts failed in those years. Competition from other colonial waterbirds and human disturbance were implicated as contributing factors to the pelican’s lack of success (Mortensen and Ringle 2007). In 2008, 23 pelican nests were initiated on Little Pelican Island, Leech Lake from which four chicks fledged (Mortensen and Ringle 2008), with additional nests reported in 2010 (Wires *et al*. 2011).

With the exception of Heron Lake, the previously mentioned American white pelican colonies since 1968 all represent sustained efforts. In that period, an estimated 70-85% of Minnesota's breeding population nested in the Marsh Lake colony (Wires *et al*. 2006; 2011). Additional short-term and failed nesting attempts also have occurred in Minnesota, as in 2006 when 20-23 pairs of American white pelicans fledged 14 chicks from a small island on Artichoke Lake, Big Stone County (J. J. DiMatteo, personal observations). A larger single year nesting effort occurred in 2012, when 280 pairs of American white pelicans nested on an island at Big Stone National Wildlife Refuge, Lac qui Parle County (J. J. DiMatteo, personal observations). Additional unsustained or short-term nesting attempts in other parts of Minnesota have been reported since the 2000s (Wires *et al*. 2006; 2011).

Summary

American white pelican numbers and distribution were reduced in Minnesota and across their continental range in the late 1800s, but since the 1970s pelican populations have been recovering and former nesting areas have been reoccupied (Evans and Knopf. 2004; Keith 2005). Although the historical record demonstrates the continued attractiveness of Minnesota wetlands to breeding American white pelicans, insufficient documentation exists to provide a complete historical account of Minnesota pelican populations and distribution, or possible periods of extirpation. Hatch (1892) and Roberts (1919b, 1932) both indicated American white pelicans experienced declines as a breeding bird in Minnesota by the end of the nineteenth century, but disagreed on if, or when pelican nesting was absent in the state. Documentation of reasons for declines is limited, although in some cases excessive disturbance during the nesting period has been implicated (Roberts and Benner 1880; Mortensen and Ringle 2007). Some authors have suggested there may have been periods of extirpation in Minnesota, but nesting of American white pelicans in Minnesota has been documented intermittently through the 1950s, and annually since 1968.

Less information is available on the reproductive ecology and population dynamics of American white pelicans nesting in Minnesota, or on the strategies for their management. Other than protection, few methods have been available for management of American white pelican populations. The only systematic study of the ecology of American white pelicans nesting in Minnesota was at Marsh Lake during 1976-1978 (Orr 1980), but the colony has increased significantly in size and complexity since then. American white pelicans present management challenges in balancing efforts to sustain populations while limiting human conflicts (Anderson and King 2005). Knowledge of life history traits and demographic processes that influence how pelican populations change is essential in developing sound predictions of outcomes for effective adaptive management.

The conservation of American white pelicans requires knowledge of their current population size, density, and demographic trends to aid in the evaluation of potential beneficial or detrimental factors that might influence population stability or change. Although available studies of other American white pelican populations (e.g., Johnson and Sloan 1978; Lingle and Sloan 1980; Diem and Pugesek 1994; Evans 1996; Madden and Restani 2005; Moreno-Matiella *et al*. 2005; Sovada *et al*. 2005; Sovada *et al*. 2008; Sovada *et al*. 2013) provide insight into pelican dynamics at Marsh Lake, direct comparisons are problematic as populations can vary by size, density, trends, age and the influences of environmental factors (e.g., latitude, elevation, climate, disease, parasites, contaminants, predators, or available food). Differences in dynamics among populations underscore a need for colony-specific management strategies that account for local influences on colonies.

The following study was initiated to document population size and reproductive rate of the Marsh Lake American white pelican colony (the largest Minnesota pelican colony), and to identify key demographic influences on population dynamics to provide baseline data on which future studies can expand and compare, in addition to providing management recommendations specific to Marsh Lake with implications for other American white pelican and waterbird colonies. This dissertation is organized into three stand-alone chapters meant for individual publication. Nest-site selection, disturbance, and spring water-level effects on pelican reproduction was investigated and reported on in Chapter 2. American white pelican chick size, condition, and growth as related to timing of nesting and survival also were examined with results presented in Chapter 3. Finally, relationships among timing of nest initiation, age, size, condition, and age at maturation of American white pelicans nesting in the Marsh Lake colony were assessed with outcomes described in Chapter 4.

IMPLICATIONS OF SPRING WATER LEVELS ON THE PRODUCTION OF AMERICAN WHITE PELICANS NESTING AT MARSH LAKE, MINNESOTA[1]

Abstract

We investigated the relationship between spring water levels and production of American white pelicans (*Pelecanus erythrorhynchos*) nesting colonially at Marsh Lake in southwest Minnesota during 2003–2012. We obtained estimates of pelican nest and chick numbers from aerial photographs to determine population levels. We used historical streamflow data to characterize April water conditions, a period when nest-site selection typically occurs. Pelicans used four islands and one peninsula for nesting, ranging from relatively high-elevation sites connected to or near the mainland to more distant low-elevation sites in the middle of the lake. The number and proportion of nests on high-elevation sites are positively related to discharge in the Upper Minnesota River during April. In years when high water inundates low-elevation sites during pelican nest-site selection, pelican nests were located on the high-elevation locations near or connected to the mainland. Over 90% of the variation in the number of nests on high-elevation sites is related to the mean daily discharge in the Upper Minnesota River during April. In addition, the proportion of nests on high-elevation sites also increases as mean daily discharge during April increases. However, chick production was negatively related to discharge during April. More than 84% of the variation in the number of near-fledged chicks produced per nest was related to mean daily discharge during April. Although high-elevation sites in close

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[1] The material in this chapter was co-authored by Jon J. DiMatteo, John E. Wollenberg, and Mark E. Clark and published in *Journal of Wildlife Management* 79:1129-1140 (2015). Jon J. DiMatteo was the principal investigator responsible for project design, data collection and analysis, description of results, and development of conclusions. Jon J. DiMatteo also drafted and revised all versions of this chapter. John E. Wollenberg served as a proofreader and photographer for survey flights. Mark E. Clark served as a proofreader and corroborated the math in the statistical analysis conducted by Jon J. DiMatteo.

proximity to the mainland offered nesting pelicans refuge from high water levels, they also expose American white pelican nests to greater predator risk. Nest camera monitoring indicated that high-elevation sites exhibited significantly higher predator activity than low-elevation sites, and experienced lower nest success (i.e., probability that at least one egg from the nest hatched). Proposed changes in the management of Marsh Lake call for the installation of a water control structure at the Marsh Lake dam that will allow for active management of lake levels. Our study provides managers with models for predicting impacts of water levels on American white pelican production.

Introduction

The American white pelican (*Pelecanus erythrorhynchos*) is a species of management interest, yet much of its reproductive ecology remains unknown (Evans and Knopf 2004). American white pelicans lay two eggs per clutch in a nest on the ground (Evans and Knopf 2004) in large, mixed flock colonies in the Upper Midwest, where it is listed as a species of conservation concern in Minnesota (Minnesota Department of Natural Resources [MN DNR] 2006), North Dakota (Hagen *et al*. 2005) and South Dakota (South Dakota Department of Game, Fish and Parks 2005). Anecdotal observations suggest American white pelicans prefer to nest on islands to minimize disturbance during the nesting period (Evans and Knopf 2004). Habitat availability on islands and proximity to mainland will vary with water level, especially in riverine systems or reservoirs. However, the effects of nest-site location on nest success, pelican reaction to disturbance, and water-level effects on island habitat and chick production have not been quantified for American white pelicans.

Insular nesting habitat may provide protection from predators but may expose American white pelican colonies to flooding. Vermeer (1970) hypothesized that the distribution of

American white pelican colonies in Canada was determined by the availability of remote, isolated islands, which provided refuge from mammalian predators that outweighed the cost in distance to food resources (the island hypothesis). Diem and Pugesek (1994) observed no fledgling production in years with high inflows to Yellowstone Lake, Wyoming that flooded the Molly Islands' nesting colony of the American white pelicans. However, at Pyramid Lake, Nevada, production of the American white pelican nesting colony on Anaho Island was positively correlated with spring flows on the lower Truckee River (Murphy and Tracy 2005). At Chase Lake, North Dakota, rising lake levels in the mid-1990s flooded the islands where American white pelicans historically nested, and the colony relocated to a nearby peninsula where evidence of mammalian predation was observed (Sovada *et al*. 2005). High rates of predation at the peninsula site are hypothesized to have caused subsequent colony abandonment in 2004 (Cohn 2006). Effects of river flow and predator presence on nest distribution have not been quantified at American white pelican colonies.

The American white pelican colony on Marsh Lake (an impoundment along the Minnesota River) in the Lac qui Parle Wildlife Management Area (WMA), Minnesota is among the largest in North America. Recent estimates of the number of nesting adults at Marsh Lake (this study) indicate this colony annually supports at least 15,000 breeding pairs, which is comparable to the number of breeding pairs in the largest American white pelican colonies in North America (Evans and Knopf 2004, King and Anderson 2005). Based on these estimates, the colony at Lac qui Parle WMA is an integral component of the continental American white pelican population. Changes in the management of spring river flows in the Upper Minnesota River have recently been proposed by the United States Army Corps of Engineers (USACE 2011), and we investigate the implications for American white pelican nesting and production at

Marsh Lake. Moreover, the most recent survey of American white pelican colonies in North America found approximately 30% (13 of 45) of the colonies were located on rivers, reservoirs, or impoundments (King and Anderson 2005). Thus, our findings may have implications for management of nesting habitat at many of the North American colonies. We examined historical streamflow data, nest counts, nesting behavior, nesting success, and chick production to 1) determine if pelican preference for insular nesting habitat was consistent with the island hypothesis, 2) quantify the effects of streamflow on colony production, and 3) evaluate potential density limitations in island habitat at the Marsh Lake American white pelican colony. We discuss the implications of our findings for the management of American white pelicans and more broadly for colony-nesting waterbirds.

Study Area

We monitored American white pelican nesting on Marsh Lake at Lac qui Parle WMA (N 45° 11’, W 096° 09’) in southwestern Minnesota from 2003–2012. Lac qui Parle WMA is a 12,545-ha area along the Upper Minnesota River in Chippewa, Swift, Big Stone, and Lac qui Parle counties, Minnesota managed by the Minnesota Department of Natural Resources for waterbirds and other resources (MN DNR 1997). Prior to the discovery of American white pelicans nesting at Marsh Lake in 1968 (Breckenridge 1968), the last report of pelicans nesting in the vicinity was approximately 80 km north-northwest of Marsh Lake on the Mustinka River in 1878 (Roberts and Benner 1880).

Marsh Lake is a river floodplain lake originally formed behind the alluvial sediment deposited at the confluence of the Pomme de Terre and Minnesota rivers (Covert *et al*. 1912). Approximately 6.5 km long and 1.5 km wide, the shallow lake dominated by emergent vegetation was mostly drained by 1920 (Upham 1920). The Marsh Lake dam was constructed between 1936 and 1939 by the Works Progress Administration, and improved by the United States Army Corps of Engineers between 1941 and 1951. The dam was originally intended to serve flood control and recreational purposes by creating a static pool on the river; however, its flood control benefits are minimal because of downstream capacity of the Lac qui Parle reservoir (USACE 2011). There are currently no means to manipulate outflow or to manage water levels on Marsh Lake.

Methods

Streamflow Data

To characterize spring water conditions at Marsh Lake, we calculated the mean rate of daily discharge during April from historical streamflow data in the Upper Minnesota River. We obtained mean daily discharge (m^3/s) for 2003–2012 for the Minnesota River at Ortonville (United States Geological Survey [USGS] site 05292000, available at http://waterdata.usgs.gov/mn/nwis/uv/?site_no=05292000&PARAmeter_cd=00065,00060), which is approximately 26 km upstream from Marsh Lake. We then computed the monthly mean daily discharge (m^3/s) for 1 April to 30 April for each year to compare with nest and chick counts. We obtained mean monthly water levels from USACE station MLDM5, which is at the Marsh Lake dam near Appelton, Minnesota (available at http://rivergages.mvr.usace.army.mil/WaterControl/stationinfo2.cfm?sid=MLDM5&fid=MLDM5&dt=S). Mean monthly discharge was significantly related to mean monthly water-level elevations at Marsh Lake (mean April water-level elevation [m] = 286.0–0.07·[1 – mean monthly discharge in April$^{0.71}$]; $F_{2,12} = 222.0$, $P < 0.001$, $r2 = 0.97$). However, the water-level elevations were not available for parts of April in both 2007 and 2010, and we elected to use discharge data to obtain a longer record for comparison. Mean daily discharge for April was selected to represent water conditions during the period when pelican nest-site selection typically occurs. We combined a digital elevation model (available via http://arcgis.dnr.state.mn.us/gis/lidarviewer/) with the mean water-level elevation at Marsh Lake during April to estimate the area (ha) of each island and the Peninsula site that was above water during April so that nest density (number/ha) could be calculated from the nest count data at each site.

Within the WMA, Marsh Lake is a 1,820–2,470-ha impoundment on the Minnesota River, characterized by shallow, eutrophic waters (MN DNR 1997). There are four islands present in Marsh Lake which have been used intermittently for nesting by American white pelicans since at least 1968 (Orr 1980): One-acre Island, approximately 0.3 ha (all island areas determined when water level elevation is 286.5 m above mean sea level); Big Island, approximately 3.9 ha; Eight-acre Island, approximately 3.4 ha; and Currie Island, approximately 8.8 ha.. A fifth island (Hermit Island, approx. 0.5 ha) was used by pelicans for nesting only through 1996 (A. H. Grewe, Jr., St. Cloud State University, personal communication), and thus we did not include it in the analysis presented here. In addition to the insular nesting sites, pelicans also have nested on a peninsula (approx. 12.6 ha and henceforth referred to as the Peninsula site) adjacent to these islands (Fig. 2.1). Of the nesting sites used by the pelican colony, both Currie Island (mean = 287.6 m, max. = 289.7 m above mean sea level) and the Peninsula site (mean = 288.6 m and max. = 289.8 m) have higher elevations than One-acre (mean = 286.7 m and max. = 287.4 m), Big (mean = 286.7 m and max. = 288.7 m) and Eight-acre (mean = 287.5 m and max. = 288.3 m) islands. Therefore, we considered Currie Island and the Peninsula site as high-elevation sites, and the remaining islands as low-elevation sites.

Figure 2.1. Marsh Lake impoundment on the Upper Minnesota River (A), located in southwestern Minnesota (inset B), and detailed view of the nesting sites (C) used by American white pelicans, 2003–2012. Map data: Google, U. S. Department of Agriculture Farm Service Agency.

American white pelicans typically initiate nesting at Marsh Lake by early or mid-April (J. J. DiMatteo, personal observations).

Nest and Chick Counts

We estimated the number of American white pelican nests on Marsh Lake from aerial photographs of the colony. We obtained photographs and counts of nests for 2003 and 2006–2012; no flights occurred in 2004 and 2005 because of logistical complications. Based on ground observations of the colony, we scheduled flights to occur mid- to late May near the peak of nesting when chicks were beginning to hatch in the earliest initiated nests, and adults were beginning continuous incubation in the latest initiated nests. Flights occurred between 0830–0930 CDT when adults were most likely on the nests to brood young chicks or incubate eggs but prior to any changeover bouts between mates, which occur later in the day (J. J. DiMatteo, personal observations). A photographer produced near-vertical oriented photographs taken at an altitude of 150–200 m. We scanned traditional 35-mm film photographs taken through 2009 to produce digital images for counts. We obtained digital photographs in 2010 and afterwards.

We estimated counts of nesting birds from digital images using UTHSCSA ImageTool software (University of Texas Health Science Center, San Antonio, Texas). We made manual counts as well as automated counts from the UTHSCSA ImageTool count routine (Laliberte and Ripple 2003). Manual and automated counts were significantly correlated ($\rho^2 = 0.89$, $P = 0.008$ for counts from 2003, 2006–2008, and 2010–2012), but we report (and analyze) only results of manual counts here. Adult pelicans that are not tending eggs or chicks at a nest do not loaf or linger in the colony, nor do they forage on Marsh Lake, so we assumed each pelican identified on land that displayed a uniform spacing between adjacent birds in nesting areas occupied a nest (Fig. 2.2A). We assumed each nest indicated a breeding pair so that the number of breeding

Figure 2.2. Aerial photographs of incubating adult American white pelicans (A) and a crèche (pod) of near-fledged chicks (B) at Marsh Lake, Minnesota, 2011.

adults would be twice the number of nests identified in the images. We also noted the island or Peninsula site that the nest was located.

We also determined the number of American white pelican chicks produced at the Marsh Lake colony from aerial photographs. Since 2006, we used a second flight (in late Jul or early Aug at 150–200 m altitude) to obtain photographs of near-fledged chicks at a time (approx. 0900 CDT) when previous observations suggest few adults were present in the colony. However, the second flight in 2008 was delayed because of scheduling difficulties beyond the point of fledging and we could not obtain reliable aerial images of chicks. As with nesting pelicans earlier, adult pelicans that are not in the colony to feed chicks do not loaf or linger in the colony, so we determined chick counts in the same manner as the nest counts, assuming all birds counted were chicks (Fig. 2.2B). Photographs from 2011 and 2013 were of sufficient quality to distinguish adults from chicks based on the orange coloration of the bill and legs, and gray coloration of the crown and nape in adults compared to gray coloration of the bill and legs, and white coloration of the crown and nape in chicks (Evans and Knopf 2004), and comparisons of total counts with chick-only counts differed by less than 5% for both years. We did not assign chick counts to individual islands or the Peninsula site, because at that age chicks can swim or walk among the islands or nesting areas during the day.

Nest Monitoring

In 2011 and 2012, we monitored 37 and 35 nests, respectively, to determine nest success rates at contrasting sites in the colony. We searched the islands and Peninsula site for nests (beginning in Apr) in the early stages of incubation, determined by the number of eggs in the nest or staining and texture of the eggs (Evans and Knopf 2004). We marked selected nests using small stakes adjacent to the nest and with a code written on the blunt end of each egg, recorded the location (latitude, longitude, and elevation) using a handheld global positioning system (GPS), and returned to the location at 7–10-day intervals to monitor progress of the nest to determine fate. In subsequent visits to a nest, we recorded the date and whether the nest was still viable. If we observed a hatching (or less than 1-week-old) chick in the nest, we recorded the date, designated the nest as successfully producing a chick, and ceased monitoring the nest. To compare nest success between high-elevation sites near the mainland with low-elevation sites farther from the mainland, we located 17 nests on the Peninsula site (a high-elevation, mainland site) and 20 nests on Eight-acre Island (a low-elevation site approx. 235 m from the nearest mainland) in 2011. We monitored an additional 10 nests on Currie Island (a high-elevation site approx. 127 m from the nearest mainland and 188 m from Eight-acre Island), four nests on the Peninsula site, and 25 nests on Big Island (a low-elevation site approx. 746 m from the nearest mainland) in 2012. We used the latitude and longitude coordinates for each monitored nest to determine the distance to the nearest mainland shoreline (which was 0 m for nests located at the Peninsula site). We did not monitor nests on One-acre Island.

Nest Camera Monitoring

In 2012, we used digital trail cameras to record disturbance, predator presence, and the behaviors of adults and chicks around nests. We placed cameras (Model MFH-DGS-M80, Moultrie, Alabaster, Alabama) near clusters of nests, programmed to take two digital images every 10 minutes if the motion sensor was triggered, which was sufficient to detect any changes in pelican or predator activities. We replaced 8-gigabyte memory cards approximately every 10 days. Each image was digitally stamped with the date and time it was recorded. We deployed cameras on various dates during the early nesting period, and they remained active through 31 August. We used only images captured prior to 1 July to document disturbance, predator presence, and adult and chick behaviors because after that date, few adults were present in the colony and chicks became increasingly mobile and disconnected from their immediate nest locations. Two cameras monitored activities on the Peninsula site from 31 March until all nesting pelicans abandoned the site in late April in response to coyote (*Canis latrans*) predation. We placed six cameras on Big Island between 11 April and 12 May, one camera on One-acre Island on 6 May, three cameras on Currie Island between 6 May and 12 June, and three cameras on Eight-acre Island between 19 May and 25 May.

We categorized disturbance events from the digital images recorded by the nest cameras in seven different categories. When an image captured a specific predator (Fig. 2.3A), we categorized the event as striped skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*), or coyote. If incubating (or brooding) adults or chicks abruptly left the nest locations at the time researchers were known to be visiting the colony (or seen in the image), we categorized the event as human disturbance. If incubating (or brooding) adults or chicks abruptly left the nest locations but no predator or human visit could be verified, we categorized the event as unknown disturbance (Fig. 2.3B). If the image was of routine behaviors (e.g., preening) associated with incubating (or brooding) adults or chicks at the nest locations, we categorized the event as undisturbed (Fig. 2.3C). Finally, in some instances cameras malfunctioned during the recording of the digital image because of lighting, weather, or battery power, and a clear image could not be discerned. We categorized these events as malfunction.

Using the date and time record for each categorized event, we tabulated the number of camera-days for each disturbance category for each island; we assigned a camera-day for an event if that event occurred on that day. For instance, if a coyote was recorded by a camera on a day, then we assigned one coyote disturbance camera-day for the site on which the camera was

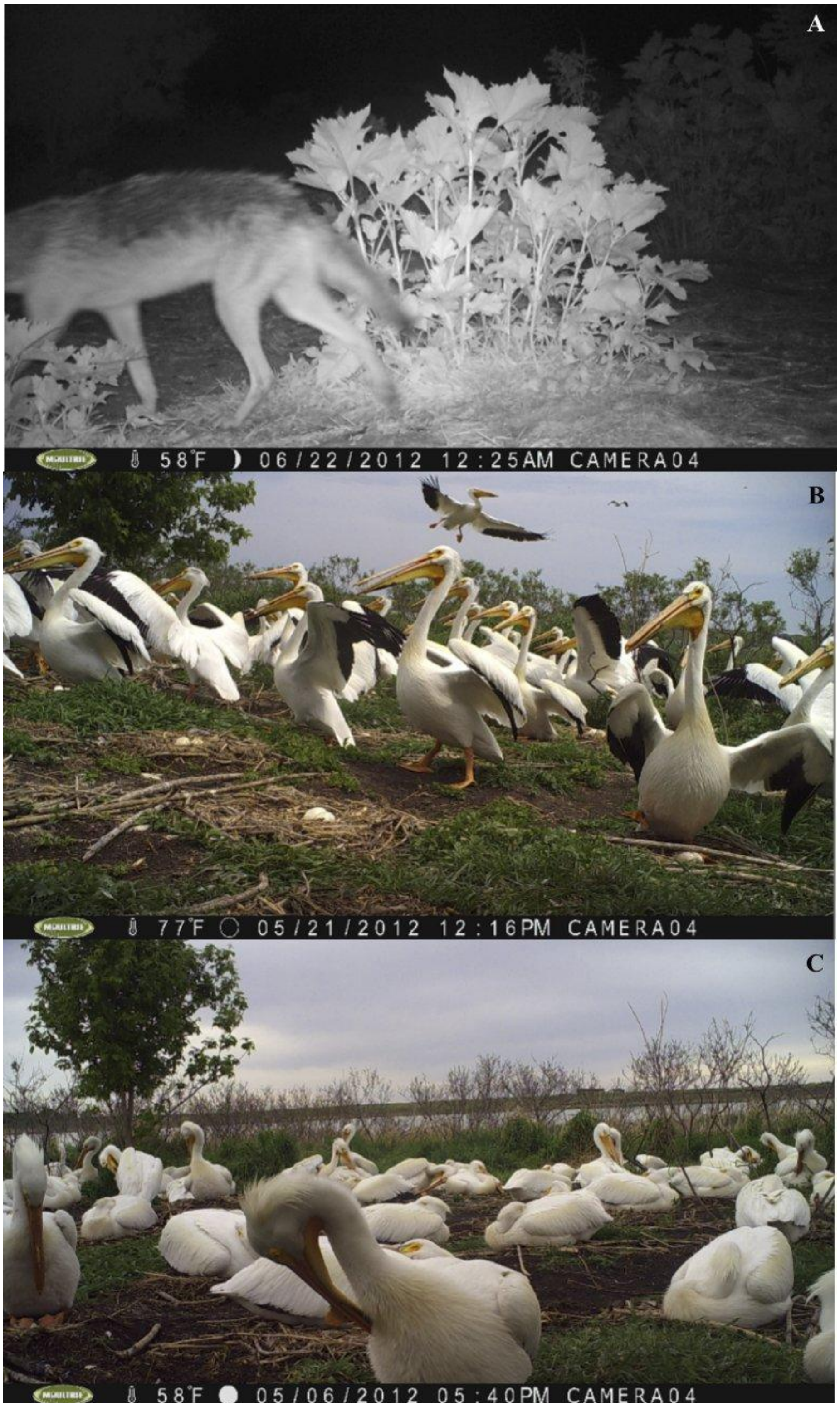

Figure 2.3. Images captured by remote nest cameras at Marsh Lake, Minnesota in 2012 showing coyote (predator) disturbance event (A), unknown disturbance event (B), and undisturbed incubating adult American white pelicans (C).

located. We assigned only one category disturbance for a particular camera-day. When multiple events were recorded on a single day for a particular camera, we prioritized the category disturbance given for the camera-day such that documentation of known predator (i.e., skunk, raccoon, or coyote) events were given higher priority over all other categories of disturbance. Thus, if a skunk event and another event (e.g., undisturbed event, unknown event) were recorded by a camera on a particular day, we assigned a skunk disturbance camera-day for that camera. If multiple predator events occurred on the same day for a particular camera, we assigned the predator disturbance camera-day based on the first predator recorded. Similarly, we assigned unknown disturbance event if undisturbed event or malfunction event also occurred. We assigned a malfunction event even if an undisturbed event occurred as well. Because some nest sites (e.g., Big Island, Eight-acre Island) had more than one camera deployed, multiple different disturbance event camera-days could occur on a single day for some nesting sites.

Statistical Analysis

We used a general linear model to analyze the relationship between April water flow and nest distribution and chick production. We modeled the number (and proportion) of nests on high-elevation sites (Currie Island and Peninsula site) as a function of mean daily discharge in April. We also modeled the number of chicks per nest (computed from the ratio of the annual total chick count and the annual total nest count) as a function of mean daily discharge in April.

We modeled nest success for 2011 and 2012 to compare location effects on the probability that a nest successfully produced a chick. We used Program MARK to compute the daily probability of nest survival from our nest observations in 2011 and 2012 (Mayfield 1975, White and Burnham 1999). We excluded the four nests on the Peninsula site in 2012 from the analysis because all of these nests failed and adults abandoned the site (Table 2.1). We

Table 2.1. Estimated number of American white pelican nests by nest site, near-fledged chicks, and near-fledged chicks per nest at Marsh Lake, Minnesota for 2003 and 2006–2012. Counts of near-fledged chicks were not available for 2003 and 2008.

Year	One-acre Island	Big Island	Peninsula site	Eight-acre Island	Currie Island	All sites	Chicks	Chicks per nest
2003	0	9,040	2,602	5,300	0	16,942		
2006	0	4,424	4,748	5,444	4,780	19,396	11,339	0.58
2007	0	3,537	4,850	4,645	5,719	18,751	9,960	0.53
2008	210	3,720	4,091	3,162	4,286	15,469		
2009	400	5,430	3,701	2,400	5,709	17,640	9,818	0.56
2010	36	1,253	6,282	555	6,029	14,155	7,446	0.53
2011	0	339	9,524	1,140	6,755	17,758	8,931	0.50
2012	333	6,375	0	3,579	5,119	15,406	9,344	0.61

considered 11 models in which daily nest survival was modeled with effects for 1) year, high-elevation versus low-elevation site, and interaction, 2) year and high-elevation versus low-elevation site, 3) year, 4) high-elevation versus low-elevation site, 5) year and distance of the nest to nearest mainland shoreline, 6) year and distance of the island to nearest mainland shoreline, 7) year and nest elevation, 8) distance of the nest to nearest mainland shoreline, 9) distance of the island to the nearest mainland shoreline, 10) nest elevation, and 11) no other effects (i.e., constant daily nest survival rate for all years, locations, and nests). We used the relative Akaike's Information Criterion adjusted for small sample size (ΔAIC_c; Burnham and Anderson 2002) to select the most parsimonious model given the data.

We modeled total nest counts from 1968 to 2012 using a sigmoidal function and an exponential function with year as the independent variable to assess trends in the American white pelican breeding colony size at Marsh Lake. We used maximum likelihood methods to determine the coefficients for each model, determined significance of the model in explaining variation in the number of nests observed in a year using an *F* test, and compared the 2-parameter sigmoid model, in which the $\text{number of nests} = \frac{25 \cdot e^{r \cdot (\text{year-1968})}}{K + \left(25 \cdot e^{r \cdot (\text{year-1968})} - 1\right)}$, with the single-parameter exponential model, in which the $\text{number of nests} = 25 \times e^{r \times (\text{year-1968})}$, using the ΔAIC_c based on least-squares regression (Burnham and Anderson 2002) to determine the most parsimonious model.

We compared disturbance event camera-day totals among sites using a likelihood ratio test. For the disturbance event camera-day totals, we compared the distribution of disturbance event camera-days among nest sites using all events as well as reduced comparisons for known predators (i.e., skunk event camera-days combined with raccoon event camera-days and coyote event camera-days), non-human disturbance (i.e., combined predator events and unknown event camera-days), and both of these reduced comparisons with the malfunction and human event camera-days removed.

We used a general linear model to analyze the relationship between nest density and nest-site area. We modeled the density of nests as a function of nest-site area (during Apr) for the Peninsula site, Currie Island, Eight-acre Island, and Big Island. We conducted statistical analyses using either SAS (SAS Institute, Inc., Cary, North Carolina) or JMP (SAS Institute, Inc.) analysis software. We assumed significance at or below the 0.05 level. This research was conducted in accordance with North Dakota State University Institutional Animal Care and Use Committee (A13057).

Results

Nests and young of American white pelicans varied temporally and spatially at Marsh Lake (Table 2.1). Nest counts indicated between 14,000 and 20,000 breeding pairs have occupied Marsh Lake since 2003. Chick counts indicated between 7,000 and 12,000 chicks were produced annually at Marsh Lake since 2003, with chick production varying from 0.50–0.61 chicks per breeding pair per year.

Nest-Site Distribution and Production

The number and proportion of nests on high-elevation sites were positively related to discharge in the Upper Minnesota River during April. Over 80% of the variation in the number of nests located on the Peninsula site was explained by a linear regression of mean daily discharge in the Upper Minnesota River during April (number of Peninsula site nests = 1,209.5 + 101.7·mean daily discharge in April; $F_{1,6} = 26.9$, $P = 0.002$, $r^2 = 0.82$). Similarly, over 93% of the variation in the number of nests on high-elevation sites (i.e., Currie Island and Peninsula site) was explained by a linear regression of mean daily discharge in the Upper Minnesota River during April (number of Currie Island and Peninsula site nests = 3,961.4 + 165.4·mean daily discharge in April; $F_{1,6} = 93.7$, $P < 0.001$, $r^2 = 0.94$). Finally, the proportion of nests on high-elevation sites increased significantly as mean daily discharge in the Upper Minnesota River during April increased ($F_{1,6} = 36.2$, $P = 0.001$; Fig. 2.4). In contrast, nests on low-elevation sites declined as April flow increased. For instance, the number of nests on Big Island decreased as mean daily discharge in the Upper Minnesota River during April increased (number of nests on Big Island = 7,571.5 – 103.0·mean daily discharge in April; $F_{1,6} = 28.8$, $P = 0.002$, $r^2 = 0.83$).

Chick production was negatively related to discharge in the Upper Minnesota River during April (Fig. 2.5). More than 84% of variation in the colony’s annual reproductive rate (number of chicks produced/nest) was explained by a linear regression of mean daily discharge in the Upper Minnesota River during April ($F_{1,4} = 22.2$, $P = 0.009$; Fig. 2.5).

Nest success was lower on high-elevation sites in close proximity to the mainland. The most parsimonious model in our candidate set assumed nest daily survival rate differed between

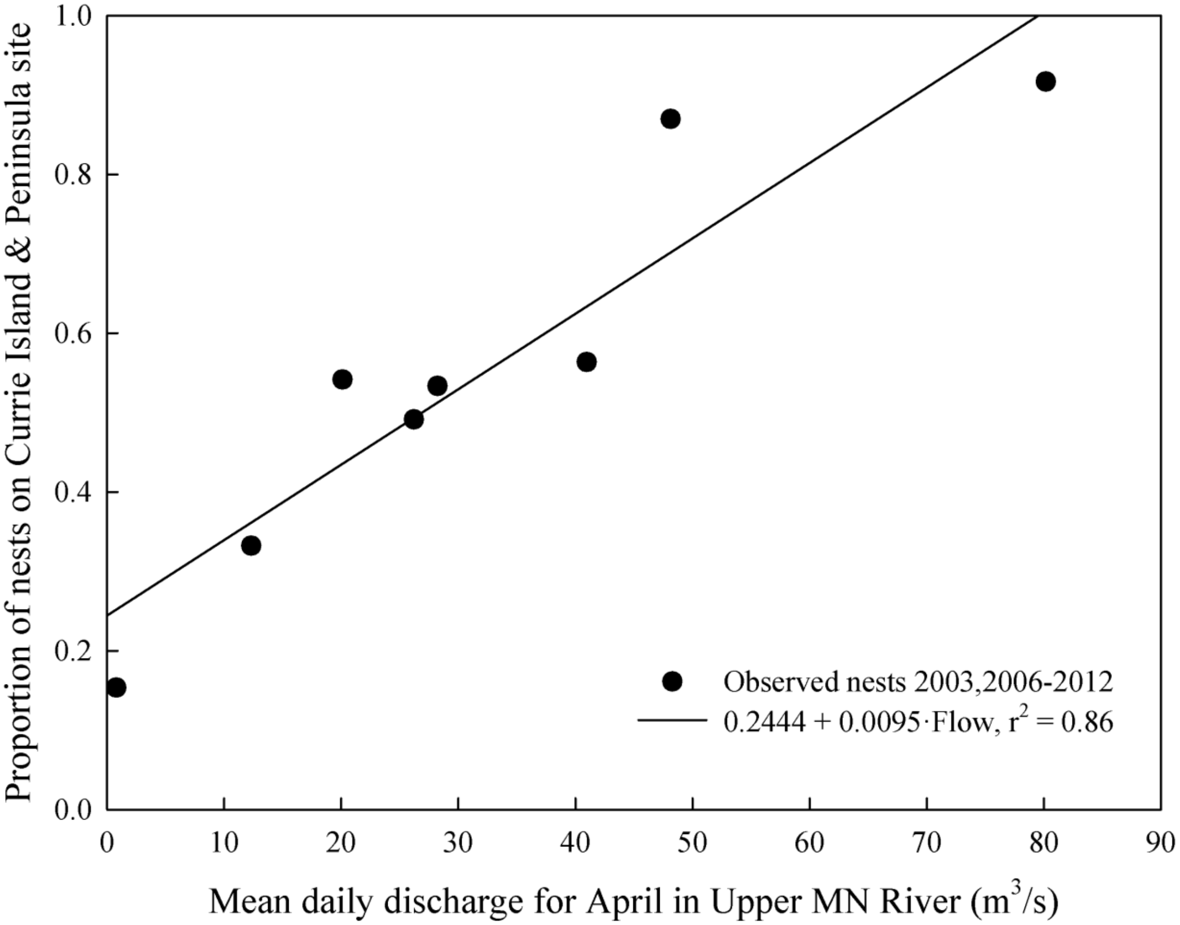

Figure 2.4. Proportion of American white pelican nests located on Currie Island and the Peninsula site (high-elevation sites near the mainland) at Marsh Lake, Minnesota during 2003 and 2006–2012 was positively related to mean daily discharge in April in the Upper Minnesota (MN) River.

high-elevation sites and low-elevation sites, and accounted for over 35% of the evidence given the data (Table 2.2; Fig. 2.6). However, the second-most parsimonious model (accounting for approx. 15% of the evidence given the data; Table 2.2) assumed nest daily survival rate increased with the distance of the nest from mainland shoreline (Fig. 2.6). Models in which the nest daily survival rate varied as a function of nest elevation per se were the least parsimonious models in the candidate set, accounting for less than 2% of the evidence given the data (Table

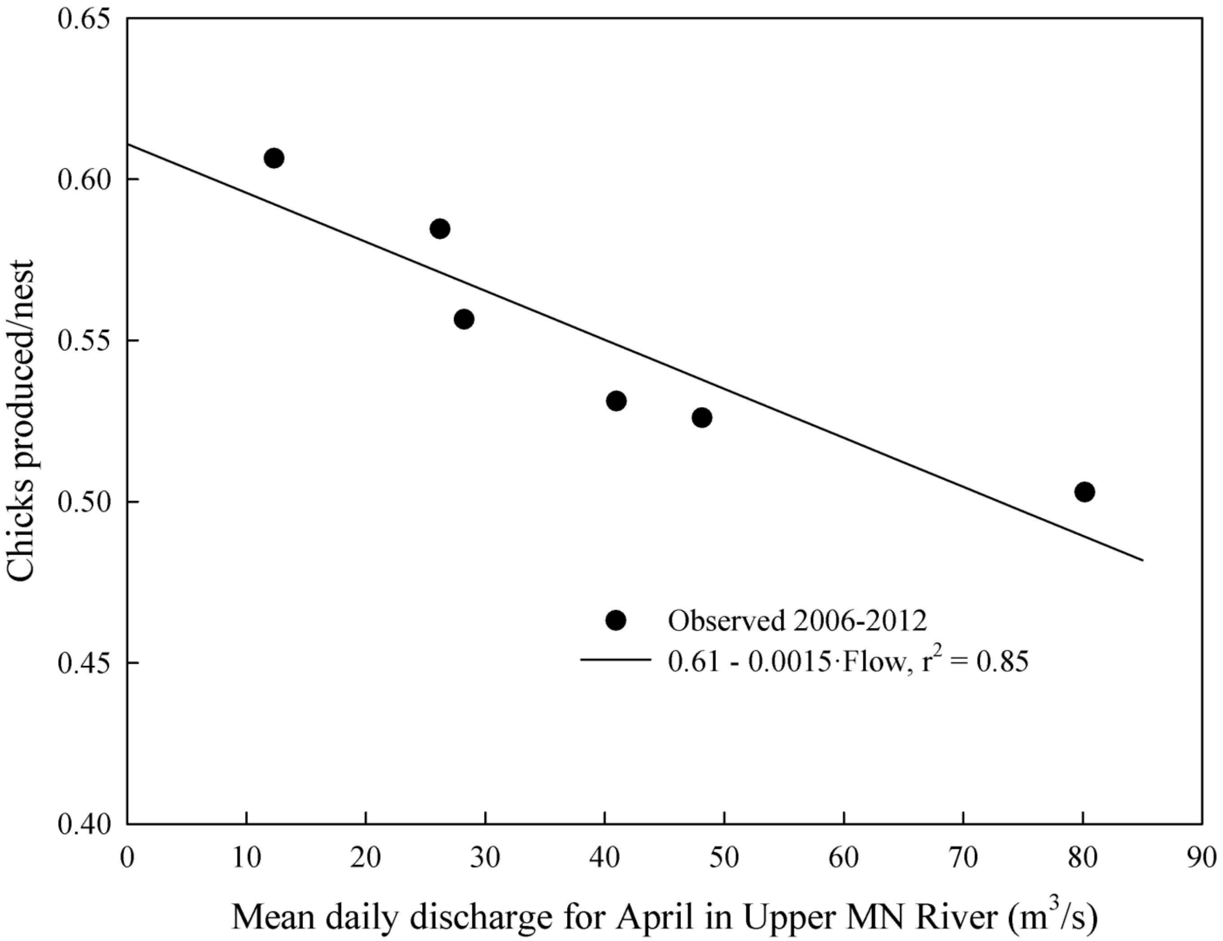

Figure 2.5. The number of near-fledged American white pelican chicks produced per nest at Marsh Lake, Minnesota during 2006–2012 was negatively related to mean daily discharge in April in the Upper Minnesota (MN) River.

2.2). High-elevation sites are nearer to the mainland shoreline, and models in which nest daily survival rate varied with distance from the shoreline (either as mean island distance, individual nest distance, or site category) were more parsimonious than all other models of nest daily survival rate, accounting for more than 94% of the evidence given the data (Table 2.2).

Nest camera monitoring in 2012 indicated high-elevation sites in close proximity to the mainland experienced significantly more disturbance than low-elevation sites away from the mainland. The number of disturbance event camera-days differed among nesting sites ($\chi^2_{24,\,810}$ =

Table 2.2 Candidate models of nest daily survival probability (S), functional form (β_i terms represent parameters), relative Akaike's Information Criterion adjusted for small sample size (ΔAIC_c), normalized Akaike weight (w_i), and model likelihood (i.e., evidence ratio compared to the model with lowest ΔAIC_c) from observations of 37 American white pelican nests in 2011 and 35 nests in 2012 at Marsh Lake, Minnesota. High-elevation site group includes the Peninsula site and Currie Island; low-elevation site group includes Big Island and Eight-acre Island. Island distance to mainland is 0 for the Peninsula site.

Model	Functional form	ΔAIC_c	w_i	Model likelihood
S(High/Low site)	$\text{logit}(S) = \beta_0 + \beta_1 \cdot \text{Site}$	0.00	0.35	1.00
S(Nest distance to mainland)	$\text{logit}(S) = \beta_0 + \beta_1 \cdot \text{Nest distance}$	1.64	0.16	0.44
S(Year + High/Low site)	$\text{logit}(S) = \beta_0 + \beta_1 \cdot \text{Year} + \beta_2 \cdot \text{Site}$	1.99	0.13	0.37
S(Year + Nest distance to mainland)	$\text{logit}(S) = \beta_0 + \beta_1 \cdot \text{Year} + \beta_2 \cdot \text{Nest distance}$	2.25	0.11	0.33
S(Island distance to mainland)	$\text{logit}(S) = \beta_0 + \beta_1 \cdot \text{Island distance}$	3.00	0.08	0.22
S(Year + Island distance to mainland)	$\text{logit}(S) = \beta_0 + \beta_1 \cdot \text{Year} + \beta_2 \cdot \text{Island distance}$	3.42	0.06	0.18
S(Year × High/Low Site)	$\text{logit}(S) = \beta_0 + \beta_1 \cdot \text{Year} + \beta_2 \cdot \text{Site} + \beta_3 \cdot \text{Year-Site}$	3.99	0.05	0.14
S()	$\text{logit}(S) = \beta_0$	4.98	0.03	0.08
S(Year)	$\text{logit}(S) = \beta_0 + \beta_1 \cdot \text{Year}$	6.81	0.01	0.03
S(Nest elevation)	$\text{logit}(S) = \beta_0 + \beta_1 \cdot \text{Nest elevation}$	6.92	0.01	0.03
S(Year + Nest elevation)	$\text{logit}(S) = \beta_0 + \beta_1 \cdot \text{Year} + \beta_2 \cdot \text{Nest elevation}$	8.57	0.00	0.01

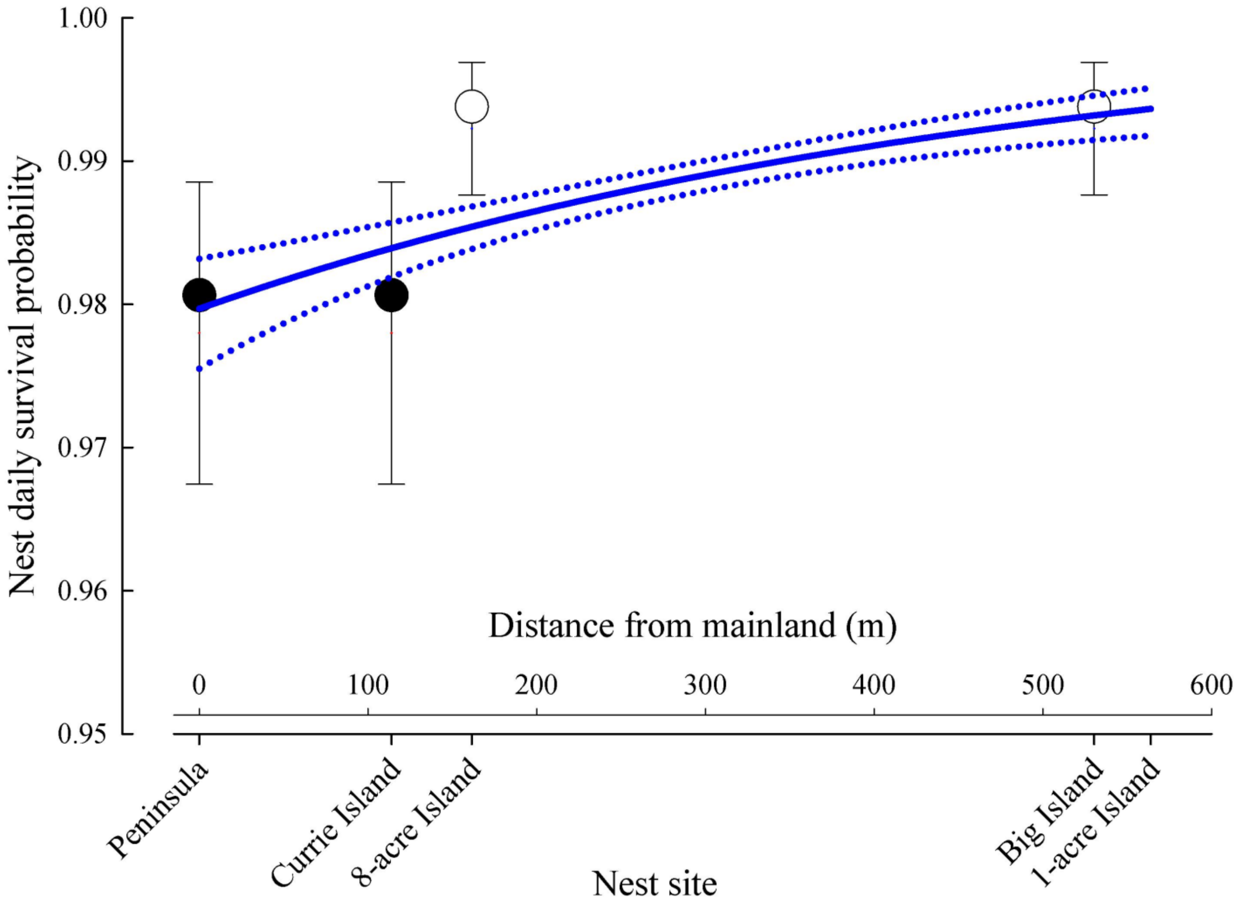

Figure 2.6. American white pelican nest daily survival probability (S) at Marsh Lake, Minnesota during 2011 and 2012 for the highest ranked model in the candidate set assumed differences between the high-elevation, near-mainland sites (i.e., Peninsula site and Currie Island; filled circles with 95% CIs given by the bars) and the low-elevation sites (i.e., Eight-acre and Big islands; open circles with 95% CIs given by the bars). Nest daily survival probability for the second highest ranked model assumed S increased with distance of the nest from the mainland shoreline (solid blue line, with 95% CIs indicated by the dashed blue lines).

157.11, $P < 0.001$; Table 2.3) because there were fewer disturbance event camera-days at low-elevation sites farther from the mainland (e.g., One-acre and Big islands). Furthermore, we found differences in disturbances between the Peninsula site, Currie Island, Eight-acre Island, Big Island, and One-acre Island (Table 2.3). These included reduced comparisons for known predators ($\chi^2_{16,\,810} = 150.04$, $P < 0.001$), non-human disturbance ($\chi^2_{12,\,810} = 106.16$, $P < 0.001$), known predators with malfunction and human event camera-days removed ($\chi^2_{8,\,629} = 112.81$, $P <$

Table 2.3. Disturbance event camera-days by nesting site for observations of American white pelican nests at Marsh Lake, Minnesota in 2012. Combined categories used in reduced contingency analyses are indicated with footnotes.

	Disturbance event									
Site	Human	Coyote	Raccoon	Skunk	Unknown	Malfunction	Undisturbed	Predator[a]	Non-human[b]	Total
Peninsula site	8	1	1	0	24	0	44	2	26	78
Currie Island	11	2	8	13	9	31	78	23	32	152
High-elevation[c]	19	3	9	13	33	31	122	25	58	230
Big Island	25	0	0	0	5	38	186	0	5	254
One-acre Island	12	0	0	0	5	0	48	0	5	65
Eight-acre Island	20	0	6	16	40	36	143	22	62	261
Low-elevation[d]	57	0	6	16	50	74	377	22	72	580
Total	76	3	15	29	83	105	499	47	130	810

[a] Coyote + Raccoon + Skunk (and not included in Total column).

[b] Predator + Unknown (and not included in the Total column).

[c] Peninsula site + Currie Island (and not included in the Total row).

[d] Big Island + One-acre Island + Eight-acre Island (and not included in the Total row).

0.001), non-human disturbance with malfunction and human event camera-days removed ($\chi^2_{4,\,629}$ = 69.85, $P < 0.001$), and sites combined as high-elevation (Peninsula site and Currie Island) or low-elevation (One-acre, Big, and Eight-acre islands) with human event camera-days removed ($\chi^2_{3,\,734}$ = 23.16, $P < 0.001$; Table 2.3). Only one low-elevation site (Eight-acre Island, which is located between the Peninsula site and Currie Island; Fig. 2.1) experienced known predator event camera-days.

Pre-2003 Nest Counts

We obtained nest count estimates at the Marsh Lake colony prior to 2003 from the literature, personal communications, and unpublished data. Nest counts increased from a low of 25 in 1968 to a high of 6,000 in 2001 (Table 2.4). All counts were from ground surveys in the colony.

Since 1968, nest numbers (based on pre-2003 ground counts and post-2003 counts from aerial imagery) at Marsh Lake have increased, but since 2000 nest numbers have varied around a plateau. The 2-parameter sigmoid model (with $K = 18725.66 \pm 1476.56$ and $r = 0.215 \pm 0.010$) explained over 90% of the variation in historical nest numbers ($F_{1,\,20} = 133.51$, $P < 0.001$, $r^2 = 0.93$; Fig. 2.7). The single-parameter exponential model (with $r = 0.156 \pm 0.002$) explained only 63% of the variation in nest number ($F_{1,\,20} = 36.38$, $P < 0.001$, $r^2 = 0.63$). Given the data, the sigmoid model was more parsimonious (i.e., $\Delta\text{AIC}_c = 0$) than the exponential model (ΔAIC_c = 33.4).

Number of nests and nest density were negatively related to nest-site area at the Peninsula site and Currie Island. Estimated area (in ha) available for nesting at the site during April explained over 75% of the variation in the number of nests (number of nests = 13,045.9 – 2,803.0·estimated area; $F_{1,\,6} = 19.6$, $P = 0.005$, $r^2 = 0.77$) and nest density for the Peninsula site

Table 2.4. American white pelican nest count estimates reported from ground surveys conducted at Marsh Lake, Minnesota prior to 2003.

Year	Number of nests	Source
1968	25	Breckenridge (1968)
1972	150	Sloan (1982)
1974	75	A. H. Grewe, Jr. and J. C. Dorio, unpublished data
1976	276	Orr (1980)
1977	349	Orr (1980)
1978	465	Orr (1980)
1979	500	Sloan (1982)
1980	961	Sidle et al. (1985)
1983	1,450	Schladweiler (1984)
1984	1,465	A. H. Grewe, Jr., personal communication
1992	5,000	A. H. Grewe, Jr., personal communication
1996	5,000	Braud (1997)
2001	6,000	King and Anderson (2005)

($F_{1,6} = 19.4$, $P = 0.005$; Fig. 2.8A) and over 80% of the variation in the number of nests (number of nests = 9,742.1 – 631.9·estimated area; $F_{1,6} = 26.2$, $P = 0.002$, $r^2 = 0.81$) and nest density for Currie Island ($F_{1,6} = 47.4$, $P < 0.001$; Fig. 2.8B). However, the number of nests was positively related to area available at both Eight-acre Island (number of nests = −1,113.3 + 1,436.1·estimated area; $F_{1,6} = 5.0$, $P = 0.067$, $r^2 = 0.46$) and Big Island (number of nests = −2,780.1 + 1,929.8·estimated area; $F_{1,6} = 15.1$, $P = 0.008$, $r^2 = 0.72$), and the estimated area available in April did not explain the variation in nest density at Eight-acre Island ($F_{1,6} = 0.4$, $P = 0.557$, $r^2 = 0.06$; Fig. 2.8C) nor Big Island ($F_{1,6} = 2.4$, $P = 0.170$, $r^2 = 0.29$; Fig. 2.8D).

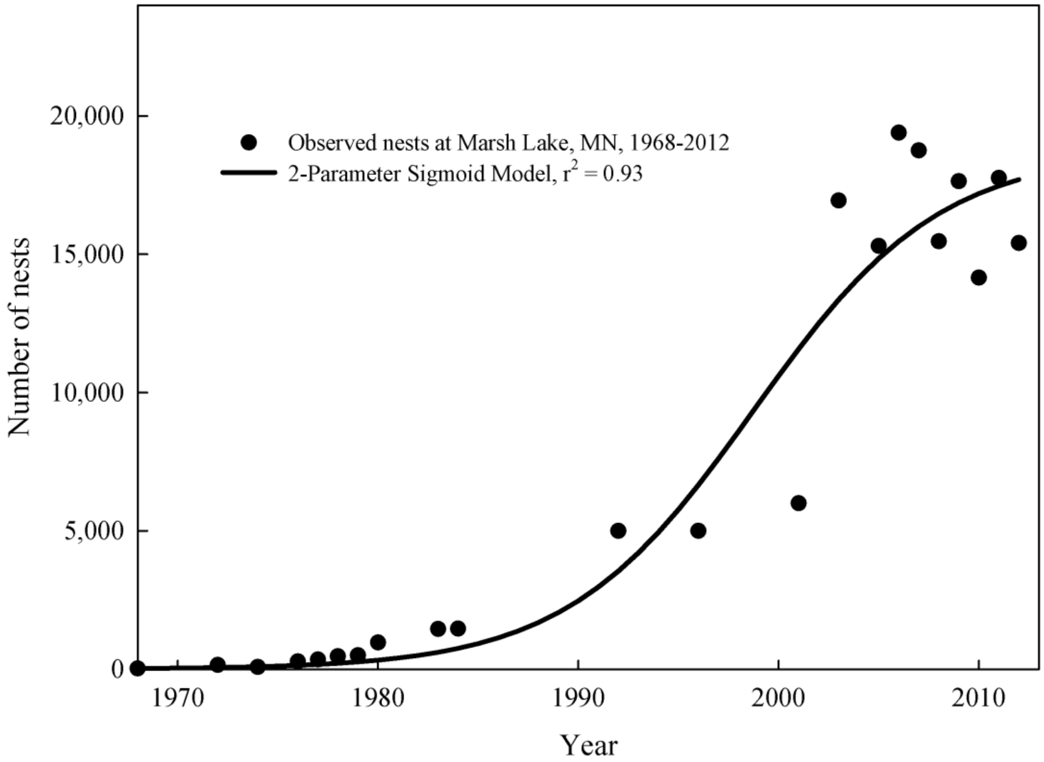

Figure 2.7. The number of annual American white pelican nests at Marsh Lake, Minnesota has increased to a plateau for 1968–2012, with a sigmoid model explaining more than 90% of the annual variation in the number of nests observed.

Discussion

Many factors affect nest-site selection and production in colonial nesting birds, and the distribution of American white pelican nests at Marsh Lake varies annually. Nest-site selection may vary with water level, available nesting space, vegetation, risk of depredation, or individual habitat preferences. However, our observations indicate that the majority of the variation in nest-site selection is explained by April flows in the Upper Minnesota River. Our nest counts may be biased because early nests that failed prior to the census, late nests initiated after the census, and nests obscured from view in the images would not be counted. However, we maintained consistent census methods for eight years, and during this period the relative proportion of nests located on sites near the mainland increases with increasing April flows (Fig. 2.4). Higher spring

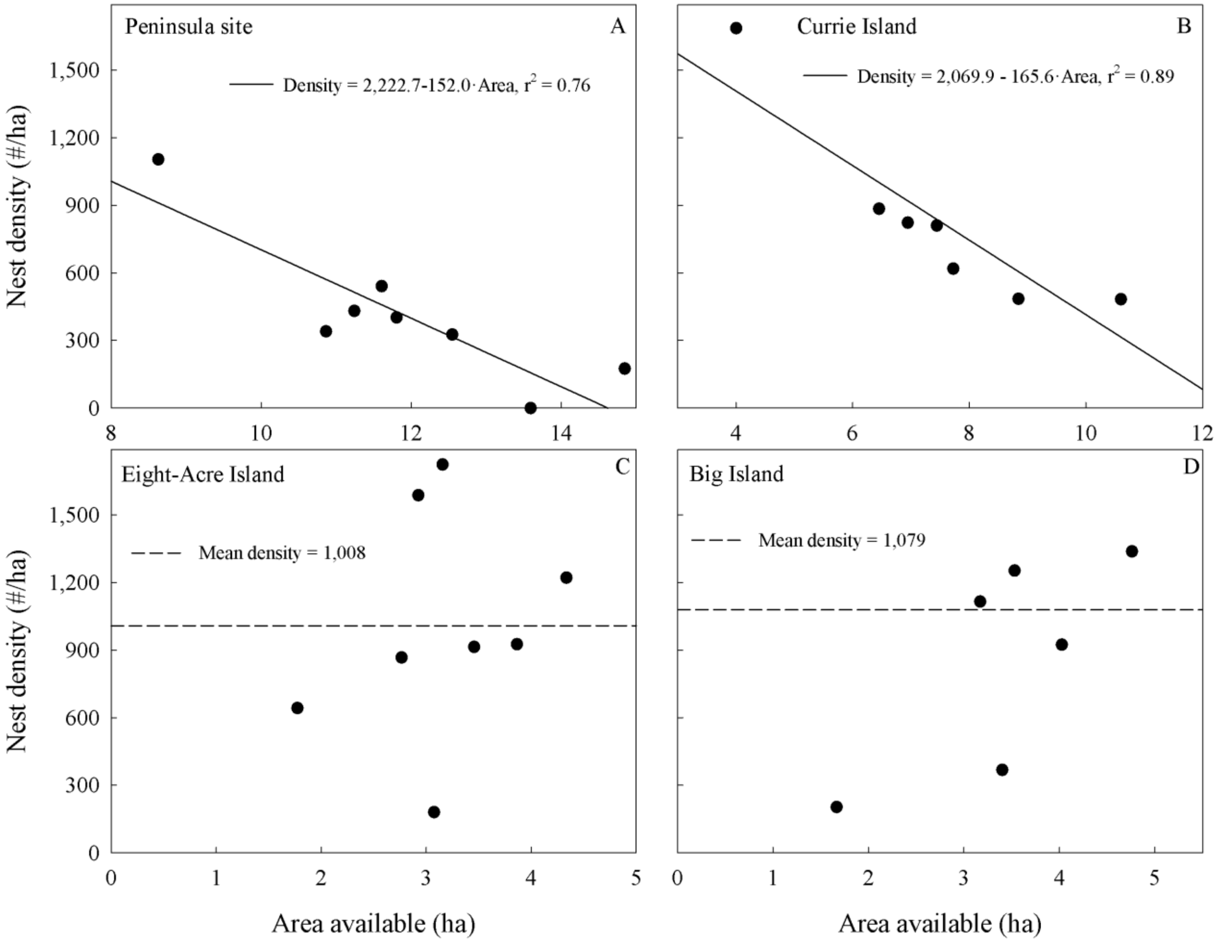

Figure 2.8. Nest density for American white pelicans at Marsh Lake, Minnesota during 2003 and 2006–2012 was negatively related to area available at the high-elevation, near-mainland Peninsula site (A) and Currie Island (B) but was not related to area available for nesting at the low-elevation Eight-acre Island (C) and Big Island (D), which are located farther from the mainland.

flow inundates parts or all of the low-elevation, insular nesting habitat and pelicans then select higher-elevation sites closer (or connected) to the mainland. These data support the hypothesis that American white pelicans prefer islands distant from the mainland for nesting (Vermeer 1970, Evans and Knopf 2004).

Although high-elevation sites offer protection from flooding, nests on these sites were less productive. We observed lower nest daily survival rates from the high-elevation sites in two years at Marsh Lake (Table 2.2, Fig. 2.6). At Marsh Lake, the high-elevation nesting areas (e.g., the Peninsula site and Currie Island) safe from flooding exhibited nest success of approximately 60%, whereas nest success at two low-elevation sites (Eight-acre Island and Big Island) exceeded 80% (Table 2.2, Fig. 2.6). Furthermore, cameras used to monitor nesting activity indicate rates of all disturbances, but especially predator disturbance, are significantly higher on the near-mainland, high-elevation nesting sites than on the low-elevation islands (Table 2.3). In fact, the only predator event camera-days observed on a low-elevation site occurred at Eight-acre Island, which is located between and near the Peninsula site and Currie Island (Fig. 2.1) where predator event camera-days were frequently observed (Table 2.3). Based on these observations, we conclude that nests nearer the mainland (which are high-elevation sites at Marsh Lake) experience lower rates of success because of depredation, supporting hypotheses that distant islands offer protection from predators (Vermeer 1970, Evans and Knopf 2004).

Because the number of pelicans nesting at Marsh Lake appears to have plateaued, April flows in the Upper Minnesota River affect fledgling production. Modeling growth in nesting (using pre-2003 nest counts and recent census counts from aerial photographs) indicates that the American white pelican colony at Marsh Lake supports approximately 18,725 nests annually (Fig. 2.7). April river flows upstream of Marsh Lake determine the proportion of those nests on high-elevation sites (closer to the mainland) with lower nest success versus low-elevation sites (farther from the mainland) with higher nest success. When flows are high, more nests are located on high-elevation, near-mainland sites and production declines. Indeed, April river flows are negatively related to colony productivity (Fig. 2.5).

The availability of nesting habitat on preferred sites may be limiting the population at Marsh Lake. The number of nests on the low-elevation sites away from the mainland (Eight-acre and Big islands) is positively related to area available (i.e., area of the island above water), a pattern observed in other colonial nesting bird populations in which there are density-dependent dynamics affecting reproduction (Sherley *et al*. 2014). At Marsh Lake, nest density on Eight-acre and Big islands was not related to area available (Fig. 2.8C and 2.8D), similar to patterns observed in little terns (*Sternula albifrons*) because of habitat preferences for small islands (Eason *et al*. 2012). We hypothesize that the mean nest densities observed on Big and Eight-acre islands (approx. 1,000 nests per hectare; Fig. 2.8C and 2.8D) may represent maximum nesting densities for American white pelicans. Nest densities at the Peninsula site and Currie Island only approached these levels (Fig. 2.8A and 2.8B) in 2011, when upstream flows in the Upper Minnesota River were highest for the survey period and therefore the least amount of total area was above the water level in Marsh Lake.

Limitations due to nest density and area available on preferred nesting sites could thereby restrict reproductive output and future growth of the Marsh Lake pelican colony. In waterfowl, insular nesting habitat provides protection from mammalian nest predators if the islands are sufficiently isolated to prevent access by mainland predators (Zoellick *et al*. 2004). Our observations from nest cameras and nest survival rates support a similar hypothesis for American white pelican nesting at Marsh Lake. In other colony-nesting birds, the benefits of island nesting (Koczur *et al*. 2014, Anteau *et al*. 2014) or nesting farther from mainland areas (Skorka *et al*. 2014) are consistent with our findings for American white pelicans at Marsh Lake.

These data show that water management in the Upper Minnesota River basin likely affects nesting and production in the American white pelican colony at Marsh Lake. Currently, water levels in Marsh Lake are positively related to April flow in the Upper Minnesota River. Recent evidence indicates American white pelicans are shifting the timing of nesting earlier at

Chase Lake, North Dakota (Sovada *et al*. 2014). If a similar pattern occurs at Marsh Lake, we would predict that the positive relationship between production and April flow in the Upper Minnesota River might shift such that late-March or early-April flow better predicts production. However, flow in the Upper Minnesota River would remain the primary factor influencing production in the Marsh Lake colony. The proposed Marsh Lake Ecosystem Restoration Project (USACE 2011) will attempt to return the lake to conditions experienced prior to impoundment (i.e., a shallow, vegetated lake), including the water-level regimes. This will be accomplished by installing a water control structure at the Marsh Lake dam that will allow for active management of lake levels, including periodic winter and growing-season drawdowns intended to enhance growth of aquatic vegetation and native fish populations while improving water clarity (USACE 2011), rather than the current situation in which lake levels are principally determined by upstream flow. Based on our quantification of the relationship between nest distribution (and productivity) and April discharge in the Upper Minnesota River (and therefore water level elevation in Marsh Lake under current conditions), managers can estimate the effects of different water-level scenarios under the proposed management plan on American white pelican production. Although project planners recognized the need to maintain adequate water levels during the breeding season to ensure that pelican nesting islands remain isolated from the mainland and potential mammalian predators (USACE 2011), they were unable to estimate how different water-level scenarios would alter chick production in the colony. Our findings enable managers to quantify expected production under the plan, and therefore assess the effects of other outcomes of the plan.

If other outcomes of the Marsh Lake Ecosystem Restoration plan alter human disturbance or predator activity on the islands, our findings indicate changes in production will follow. For instance, another goal of the plan is to increase public recreational opportunities on the lake. An increase in boating activity at lakes used for foraging by American white pelicans breeding in Canada did not affect foraging success or behavior (Gaudet and Somers 2014). However, human disturbance (Johnson and Sloan 1976, Boellstorff *et al*. 1988) and low-flying aircraft (Bunnell *et al*. 1981) can disrupt pelican nesting, and nesting colonies are considered sensitive to human activity (Evans and Knopf 2004). Our findings indicate the low-elevation sites away from the mainland (i.e., Eight-acre, Big, and One-acre islands) are most preferred for nesting and contribute differentially to production than other nesting areas, which is practical guidance for managers regulating recreation at Marsh Lake. For instance, Carney and Sydeman (1999) recommended a buffer of 100 m to 600 m between human activities and pelican nests. If a 600 m buffer was adopted at Marsh Lake, however, it would restrict recreation in Marsh Lake to areas upstream and downstream of Big Island and preclude movement between the upper and lower zones from early April to early July.

Effective adaptive management requires the ability to make predictions of expected outcomes to which observed outcomes can be compared. Our findings provide the means to make predictions of American white pelican production at Marsh Lake based on spring water levels. With potential lake-level management capability, maintaining lower lake levels during typical spring flooding would allow pelicans to select nest sites on preferred low-elevation islands farther from the mainland, thereby reducing mammalian predation and enhancing pelican production on the lake. American white pelicans nest at several reservoir or riverine sites (King and Anderson 2005), including sites where managers have some control over flow or water levels (Findholt and Anderson 1995, Moreno-Matiella and Anderson 2005, Adkins *et al*. 2014). It is not known if American white pelicans will renest after early nest failure (Evans and Knopf

2004), so protection from nest loss early in the season could be critical. Furthermore, many other colony-nesting birds (including species with threatened or endangered status) use riverine or reservoir habitat for nesting (Stahlecker 2009, Anteau *et al*. 2012, Hunt *et al*. 2013) where water levels can be managed. As such, our study demonstrates potentially broad applications for models of productivity, nesting dynamics, discharge, and water levels as a tool for resource managers working with colonial waterbirds. Indeed, nest success of piping plovers (*Charadrius melodus*) and least terns (*Sternula antillarum*) has been linked to discharge in the Missouri River (Anteau *et al*. 2012, Buenau *et al*. 2014). Colonial nesting birds are also susceptible to disease outbreaks (Sovada *et al*. 2008, Johnson *et al*. 2010), exposure to contaminants (Boellstorff *et al*. 1985, Pietz *et al*. 2008) or vulnerability to human disturbance (Johnson and Sloan 1976, Boellstorff *et al*. 1988), and modeling how water-level changes relate to these factors could prove useful for future research.

Management Implications

Nest distribution and productivity of American white pelicans can be quantified by spring flow and water levels in the Marsh Lake system. Our findings provide a new method for resource managers to evaluate proposed changes for water management in the Upper Minnesota River. In addition, our study provides a framework for modeling nesting dynamics and productivity for other breeding waterbirds using water level or discharge data.

Acknowledgments

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GROWTH AND DEVELOPMENT OF AMERICAN WHITE PELICAN (*PELECANUS ERYTHRORHYNCHOS*) CHICKS AT MARSH LAKE, MINNESOTA[2]

Abstract

Size at hatch and growth rates of American White Pelican (*Pelecanus erythrorhynchos*) chicks were examined at Mash Lake, Minnesota during 2010–2012. On the day of hatch, the mass and lengths of tarsus, wing and culmen were recorded for the oldest chick in 2-egg nests. No difference was detected in skeletal size at hatch during 2010–2012, but mass of chicks was 11% lower in 2010 than in 2011. Growth rates for mass and wing did not differ between 2011 and 2012, but over 40% of the variation in absolute and instantaneous (relative) growth rates of tarsus was explained by year, with higher rates in 2011; in 2011 nest initiations were started later than other years. Little variation in size at hatching or growth rates were detected between years, but significant variation in size at hatching and growth rates were detected within season depending on the timing of hatch. No difference was detected in initial mass throughout the nesting season, but initial tarsus and wing length were shorter in chicks hatched later in the season in 2012. However, absolute and instantaneous growth rates for mass, tarsus, and wing were faster for late-hatched chicks in 2012, potentially allowing late-hatched chicks to fledge at an earlier age.

Introduction

Colonially-nesting birds synchronize nesting in space or time to enhance reproductive success (Danchin and Wagner 1997; Jovani and Grimm 2008). However the causal links

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[2] The material in this chapter was co-authored by Jon J. DiMatteo and Mark E. Clark for submission to *Waterbirds*. Jon J. DiMatteo was the principal investigator responsible for project design, data collection and analysis, description of results, and development of conclusions. Jon J. DiMatteo also drafted and revised all versions of this chapter. Mark E. Clark served as proofreader and corroborated the math in the statistical analysis conducted by Jon J. DiMatteo.

between breeding synchrony and recruitment are not well understood. Chick size, growth and survival vary with the timing of nesting in many colonially-nesting birds (Catry *et al*. 1998; Arnold *et al*. 2004; Ritz *et al*. 2005; Hipfner *et al*. 2010). Generally, chicks that hatch earlier exhibit greater survival rates compared to chicks that hatch later (Arnold *et al*. 2006; Harris *et al*. 2007; Minias *et al*. 2013; Saunders *et al*. 2014), but there are exceptions (e.g., Braasch *et al*. 2009).

It remains unclear how size at hatch, condition, and growth relate to chick survival in colonially-nesting species. Mass gain in chicks related to timing of nest initiations can lead to differential survival associated with timing of nest initiations, but egg and parental quality might interact with these timing effects (Arnold *et al*. 2006). Factors such as temperature that affect chick thermoregulation may be correlated with timing of nesting and affect survival indirectly, as seen in the Great Tit (*Parus major*) (Greño *et al*. 2008). Recent findings also show that late-season chicks of some species might exhibit faster growth to compensate for the shorter development window (Benowitz-Fredericks and Kitaysky 2005; Hirose *et al*. 2012). However this rapid growth may come at the cost of elevated metabolic oxidative stress (Stier *et al*. 2014), potential later-life behavioral differences with fitness consequences (Krause and Naguib 2011), or the inability to withstand bouts of food restriction that can affect survival (Benowitz-Fredericks and Kitaysky 2005).

In this study, we examined variation in size at hatching, condition and growth of American White Pelican (*Pelecanus erythrorhynchos*) chicks within (i.e., relative to nest initiation dates) and between breeding seasons. The American White Pelican (henceforth pelican) nests colonially, clutches are typically two eggs (range 1-4), and nest initiations can extend over a period of 30–60 days (Evans and Knopf 2004; Sovada *et al*. 2013). Variation in the growth of chicks has not been quantified (Evans and Knopf 2004). We examined temporal variation in the size, condition and growth of the first chick to hatch in individual nests with a 2-egg clutch. We assume this reasonably represents reproductive investment in pelicans because the second-hatched chick often receives less food, suffers from agonistic interactions with the older chick and experiences greater mortality, including siblicide (Evans and Knopf 2004; Sovada *et al*. 2013). We characterized multiple aspects of initial size and size as the chick ages over three breeding seasons and within a breeding season for individual offspring.

Methods

Study Area

We monitored pelicans nesting on several islands and a peninsula in Marsh Lake at Lac qui Parle Wildlife Management Area (WMA) in southwestern Minnesota (45^{o} 11’ N, 096^{o} 09’ W) from 2010–2012. Lac qui Parle WMA is a 12,545-ha area along the Upper Minnesota River in Chippewa, Swift, Big Stone and Lac qui Parle counties, Minnesota managed by the Minnesota Department of Natural Resources (MN DNR) for waterbirds and other resources (MN DNR 1997). Marsh Lake is an approximately 6.5 km long and 1.5 km wide floodplain lake at the confluence of the Pomm de Terre and Minnesota rivers (further impounded with the construction of a dam in the 1930s [USACE 2011]) within the Lac qui Parle WMA. Twenty-five pairs of pelicans were observed nesting at Marsh Lake in 1968 (Breckenridge 1968), numbers of nesting pairs increased in subsequent years until year 2000, and have since averaged 18,725 nesting pairs (DiMatteo *et al*. 2015). The phenology and number of pelicans nesting at Marsh Lake has been monitored annually since 2004 (DiMatteo *et al*. 2015).

Initial Chick Size

We monitored size at hatch in pelican chicks during 2010–2012. Each year during the week in which hatching peaked, we measured mass (± 1.0 g), tarsometatarsus length (henceforth tarsus, ± 0.1 mm), culmen length (± 0.1 mm; measured at the mid-line of the bill from the posterior exposed edge to the anterior tip) and wing length (henceforth wing, ± 1.0 mm) by measuring the folded right wing from the carpal joint to the tip of the digits (i.e., the approximate length of the carpometacarpus, phalanx one and phalanx two). Mass measurements were obtained with a spring scale, and length measurements with a digital vernier caliper. Chicks were selected from nests containing a single chick and a single unhatched egg where adjacent nests also contained a single chick and a single unhatched egg (indicating a synchronous group of nests in which the first egg hatched within the last 24 hours). We also quantified condition of chicks at hatch with the residuals (along the mass axis) of an orthogonal regression of mass and tarsus length (Green 2001).

Between-breeding Season Chick Growth Variation

In 2011 and 2012 we monitored chick growth by taking subsequent measurements from the chicks sampled for the initial-size monitoring, which is described above. Mass was measured with a spring scale for chicks < 1,000 g and a digital scale when > 1,000 g. Our goal was to measure chicks every 7–10 days. To facilitate sampling the same chicks, we marked them with color-coded nape tags as described by Arnold *et al*. (2011). When chicks were large enough, they were marked with a federal legband on the left leg and a coded patagial tag on the left wing.

Within-breeding Season Chick Growth Variation

In 2012 we also monitored within-breeding season variation in size at hatch and chick growth. We monitored chicks from three respective cohorts: early (hatched during the first week in which hatching occurred in the colony), middle (hatched during the week when hatching peaked in the colony) and late (hatched when hatching began to wane at the colony). Sampling and data collection was similar to that described above; on the day of hatch and at 7–10 day intervals we measured the oldest chick from nests with a 2-egg clutch.

Statistical Analyses

We fit individual curves to size-at-age measurements to quantify growth in pelican chicks. We used the Gompertz growth equation (Ricklefs 1967; 1969) in which size (y, in g for mass, mm for tarsus length and mm for wing length) varies with age (x, in days from hatching) according to $\mathrm{y(x)} = A_0 \cdot \exp\left(\exp\,(b_0) \cdot \frac{\exp\,(b_1 \cdot \mathrm{x} - 1)}{b_1}\right)$, with initial size given by A_0 (in g for mass, mm for tarsus length and mm for wing length), the instantaneous (relative) growth rate at age 0 (in day^{-1}) given by b_0 and slope of the logarithm of the instantaneous growth rate as a linear function of age (in day^{-1}) given by b_1 to model growth in size of individual chicks in which there were size measurements for at least three occasions. From the parameters of the Gompertz growth models, we calculated the absolute growth rate (in g/day for mass, mm/day for tarsus length, or mm/day for wing length) for one-day-old chicks as $A_0 \cdot \exp\,(b_0)$, and we calculated the average instantaneous growth rate (in day^{-1}) from hatching to age five days.

Finally, we combined size measurements for chicks with at least three measurements from middle cohorts in 2011 and all three cohorts from 2012 and modeled size at age to gain insight into the overall growth patterns in body size for pelican chicks. We modeled size (i.e., mass, tarsus length, wing length and culmen length) at age using two models in which size reaches an asymptotic value and one model in which size does not reach an asymptotic value to determine if our observations of pelican chick size exhibited asymptotic growth, and if so at what ages asymptotic levels occur. For the asymptotic growth models, we used the 3-parameter

Gompertz model previously described, and a more general 4-parameter model in which size (y, in g for mass, mm for tarsus length, and mm for wing length) varies with age (x, in days from hatching) according to $\mathrm{y(x)} = A_f - (A_f - A_0) \cdot \exp(-k \cdot \mathrm{x}^p)$, with A_f indicating asymptotic size, A_0 indicating initial size, and k and p growth rate parameters (Janoschek 1957; Gille *et al.* 1999). For the non-asymptotic model we assumed size changed as a linear function of age.

We also developed a linear model of age using culmen length to develop a surrogate means of estimating chick age from a single body size measurement. We combined culmen length measurements at known age for middle cohort chicks observed in 2011 and chicks from all three cohorts in 2012 to develop the model. It was previously noted that culmen length changed linearly with age for chicks up to 30 days post hatching (Lingle and Sloan 1979). We developed a regression of age (days post hatching) and culmen length (in mm) from our observations of size as an alternative to the Lingle and Sloan (1979) model for predicting chick age using culmen length.

We used general linear models to determine effects of year and season on chick size at hatching and chick growth. We compared measures of size at hatching and condition across years using analysis of variance (ANOVA). We also compared growth parameters for individual chicks from 2011 and 2012 using ANOVA. We compared variation in size at hatching and chick growth (from individual growth parameters) within the 2012 season using linear regression with Julian date of hatching and ANOVA for cohort (early versus middle versus late). We also checked for pairwise correlations among measures of size at hatching as well as estimates of growth rates using Pearson product moment (ρ) and a t-test. We used maximum likelihood methods to determine the coefficients for the asymptotic and non-asymptotic growth models, determined significance of the model in explaining variation in size at age using an F test, and compared the three models using the relative Akaike's Information Criterion adjusted for small sample size (ΔAIC_c) based on least-squares regression to determine the most parsimonious model for each measure of size (Burnham and Anderson 2002) assuming sample size equal to the number of individuals measured (rather than the total number of measurements for a particular measure of size). We assumed statistical significance at the $\alpha = 0.05$ level. All statistical analyses were completed using SAS software (SAS Institute 2001) or JMP software (SAS Institute 2012).

Results

Phenology

Phenology of pelican nesting varied from 2010–2012. In 2010 pelicans initiated nesting after the second week of April, and the first chicks began hatching approximately 12 May. Peak chick hatching occurred in the last week of May (when we measured and marked 25 newly hatched chicks on 26 May), and the last chicks were hatching in the last week of June in 2010. Nesting phenology in 2011 was similar to that in 2010, with the first nests initiated early April, peak nesting at the end of April and the final nests initiated in the last weeks of May. Chicks began hatching in the second week of May, peaked by the last week of May (when we measured and marked 25 newly hatched chicks on 26 May) and the last chicks were hatching by the end of June in 2011. In 2012 pelican nesting began earlier than in 2010 and 2011, with the first nests initiated at the start of April, nest initiations peaked by mid April and few nests were initiated after the second week of May. In 2012 the first chicks hatched in the final week of April (and we measured and marked five newly hatched chicks on 26 April and 25 on 30 April), hatching peaked in mid-May (when we measured and marked 30 newly hatched chicks on 14 May), and the last chicks were hatching in early June (when we measured and marked 30 newly hatched chicks on 2 June).

Between-breeding Season Variation in Initial Size and Growth

Chicks produced in 2010 weighed less than chicks from 2011, but skeletal size did not differ by year. For chicks hatched during the peak period of hatching, mass at hatching differed by year ($F_{2,\,77} = 3.60$, $P = 0.032$, $r^2 = 0.09$ with mean ± standard error of 109.4 ± 3.5 g in 2010, versus 122.8 ± 3.5 g in 2011 and 115.8 ± 3.2 g in 2012; Fig. 3.1). Tukey's HSD comparison of the means indicated the mean for 2010 was significantly lower than the mean for 2011. In contrast, tarsus length ($F_{2,\,77} = 1.64$, $P = 0.201$, $r^2 = 0.04$ with mean ± standard error of 21.1 ± 0.2 mm in 2010, 21.0 ± 0.2 mm in 2011 and 20.5 ± 0.2 mm in 2012), culmen length ($F_{2,\,77} = 0.09$, $P = 0.911$, $r^2 < 0.01$ with mean ± standard error of 21.4 ± 0.3 mm in 2010, 21.2 ± 0.3 mm in 2011 and 21.2 ± 0.2 mm in 2012) and wing length ($F_{2,\,77} = 2.79$, $P = 0.067$, $r^2 = 0.07$ with mean ± standard error of 20.6 ± 0.2 mm in 2010, 21.3 ± 0.2 mm in 2011 and 20.9 ± 0.2 mm in 2012) at hatching did not differ between years (Fig. 3.1). Pairwise comparisons indicated all measures of size at hatching were positively correlated, with $\rho^2 > 0.40$ and $P < 0.002$ for chicks from the middle cohorts for 2010–2012.

Mass residuals (i.e., condition) from the tarsus-mass regression were lower in 2010. The orthogonal regression of tarsus length by mass indicated tarsus length and mass at hatching were positively correlated (tarsus length = 12.50 + 0.07·mass; n = 140, $\rho^2 = 0.56$, $P < 0.001$; with the regression determined by observations of middle cohort one-day-old chicks from 2010 and 2011, and early, middle and late cohort one-day-old chicks from 2012). Residuals along the mass axis were lower in 2010 (-5.9 ± 1.3 g) compared to 2011 (1.5 ± 1.3 g) and 2012 (1.0 ± 1.2 g; $F_{2,\,77}$ =

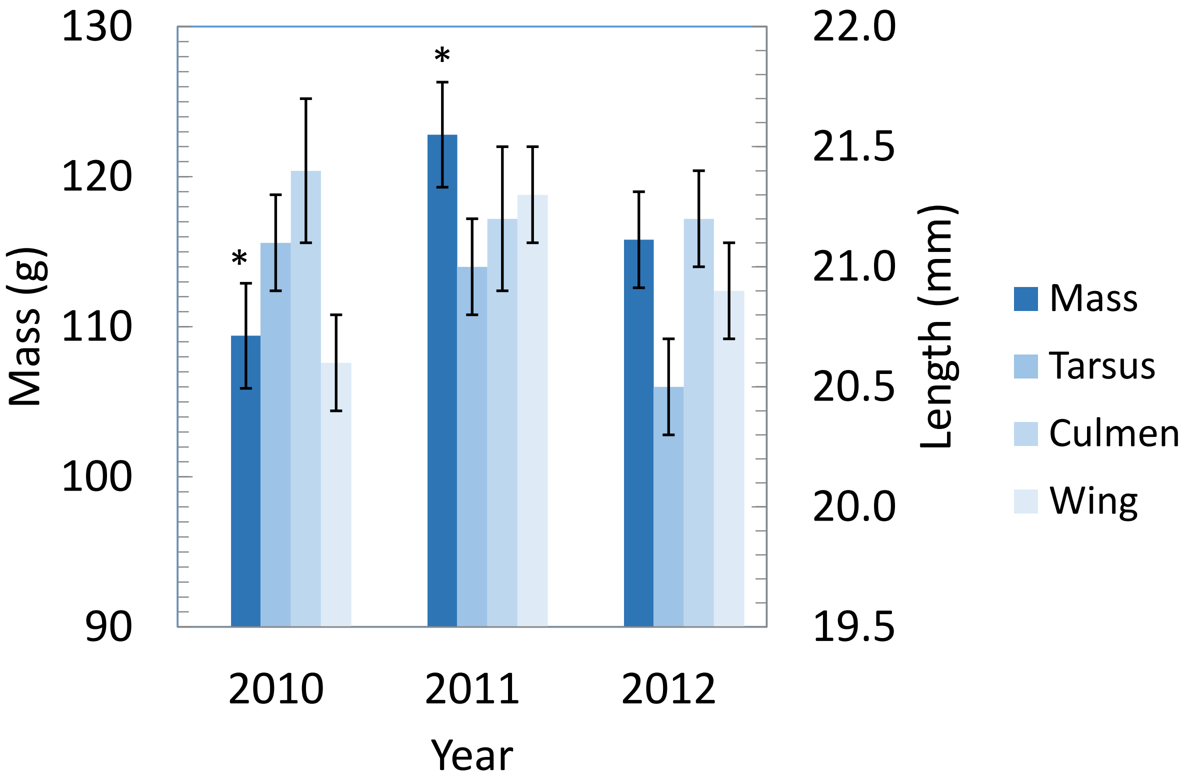

Figure 3.1. Mean initial mass (g), tarsus length (mm), culmen length (mm) and wing length (mm) for American White Pelican (*Pelecanus erythrorhynchos*) chicks hatched during the peak period of hatching at Marsh Lake, Minnesota, 2010-2012 (* = significant difference).

9.93, $P < 0.001$, $r^2 = 0.21$; comparison with middle cohort chicks only), indicating chicks hatched at lower mass relative to their skeletal size in 2010.

Absolute and instantaneous (relative) growth rates of mass and wing length for chicks encountered and measured three or more times did not differ between 2011 and 2012, but absolute and instantaneous growth rates of tarsus were faster for chicks hatched in 2011 versus 2012. We captured eight chicks from 2011 and 14 chicks from the 2012 (middle) cohort on three or more occasions to estimate growth rates from size measurements. However we did not include one of the chicks from 2011 in the growth rate comparisons because a mass loss of more than 700 g was observed between the second and third captures (at ages 18 days and 38 days, respectively), and the chick exhibited lethargy and lack of coordination on the third encounter.

Variation in absolute growth of mass was not explained by year ($F_{1,\,19} = 0.02$, $P = 0.902$, $r^2 < 0.01$ with mean ± standard error of 30.7 ± 3.3 g/day in 2011 and 30.2 ± 2.3 g/day in 2012; Fig. 3.2). Similarly, variation in the growth of wing length was not explained by year ($F_{1,\,19} = 1.06$, $P = 0.317$, $r^2 = 0.05$ with mean ± standard error of 1.7 ± 0.2 mm/day in 2011 and 1.5 ± 0.1 mm/day in 2012; Fig. 3.2). However more than 40% of the variation in the absolute growth rate of tarsus was due to year ($F_{1,\,19} = 13.48$, $P = 0.002$, $r^2 = 0.41$), with growth rates observed in 2011 (3.1 ± 0.2 mm/day) significantly faster than those observed in 2012 (2.0 ± 0.2 mm/day; Fig. 3.2). Instantaneous growth rates exhibited a similar pattern. Year did not explain significant variation in the instantaneous rates for mass ($F_{1,\,19} = 0.15$, $P = 0.702$, $r^2 < 0.01$ with mean ± standard error of 0.227 ± 0.013 day^{-1} in 2011 and 0.233 ± 0.009 day^{-1} in 2012) or wing length ($F_{1,\,19} = 0.95$, $P = 0.341$, $r^2 = 0.05$ with mean ± standard error of 0.078 ± 0.006 day^{-1} in 2011 and 0.071 ± 0.004 day^{-1} in 2012), but explained 42% of the variation in instantaneous rate of growth of tarsus ($F_{1,\,19} = 13.67$, $P = 0.002$, $r^2 = 0.42$ with mean ± standard error of 0.126 ± 0.007 day^{-1} in 2011 and 0.092 ± 0.005 day^{-1} in 2012).

Growth rates for the 2011 and 2012 (middle) cohorts were positively correlated, with $\rho > 0.47$ and $P < 0.03$ for all pairwise comparisons (e.g., absolute rate of growth in tarsus was positively correlated with the instantaneous rate of growth in wing length with $\rho = 0.80$, $P < 0.001$). In addition, mass at hatching was positively correlated with the instantaneous rate of growth in tarsus ($\rho = 0.46$, $P = 0.038$) and the instantaneous rate of growth in wing ($\rho = 0.68$, $P < 0.001$). Tarsus length at hatching was positively correlated with the instantaneous rate of growth in wing ($\rho = 0.56$, $P = 0.009$). Wing length at hatching was positively correlated with the instantaneous rate of growth in mass ($\rho = 0.47$, $P = 0.031$) and the instantaneous rate of growth in wing ($\rho = 0.60$, $P = 0.004$).

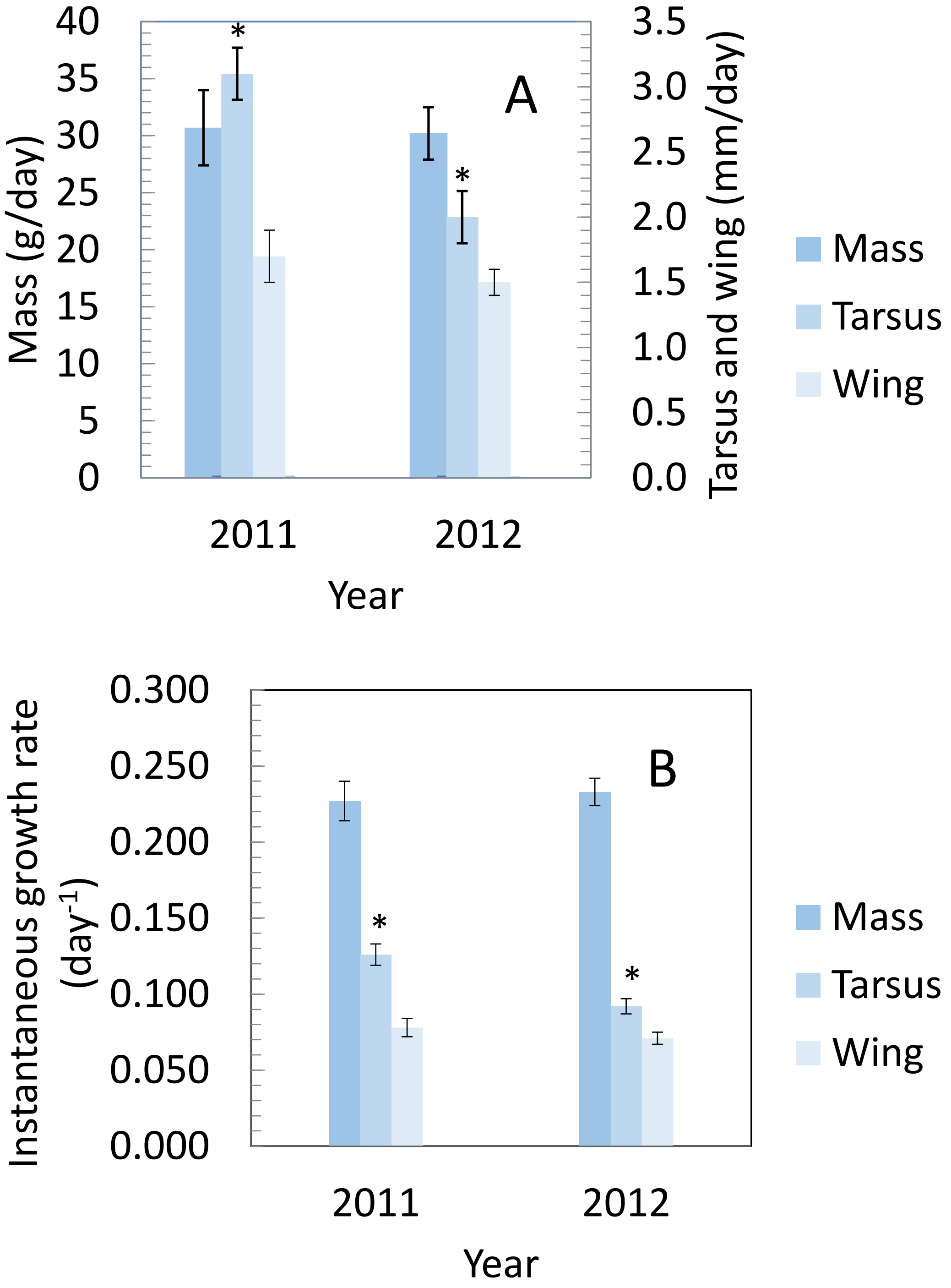

Figure 3.2. Absolute growth rate for mass (g/day), wing (mm/day), and tarsus (mm/day; A), and instantaneous growth rate (day-1) for mass, wing, and tarsus (B) for American White Pelican (*Pelecanus erythrorhynchos*) chicks hatched during the peak of hatching at Marsh Lake, Minnesota, 2011–2012 (* = significant difference).

Within-breeding Season Variation in Initial Size and Growth

Chicks hatched later in the season had smaller skeletal size in 2012. Mass at hatching did not differ among early, middle and late cohort chicks in 2012 ($F_{2,\,89} = 0.14$, $P = 0.871$, $r^2 < 0.01$ with mean ± standard error of 117.9 ± 2.9 g for the early cohort, versus 115.8 ± 2.9 g for the middle cohort and 116.6 ± 2.9 g for the late cohort; Fig. 3.3). However cohort explained a significant amount of variation in tarsus length ($F_{2,\,89} = 20.68$, $P < 0.001$, $r^2 = 0.32$) and wing length at hatching in 2012 ($F_{2,\,89} = 5.42$, $P = 0.006$, $r^2 = 0.11$; Fig. 3.3). Both tarsus length (mean ± standard error of 21.5 ± 0.2 mm for the early cohort, versus 20.5 ± 0.2 mm for the middle cohort and 19.7 ± 0.2 mm for the late cohort, with all means significantly different by Tukey's HSD) and wing length (mean ± standard error of 21.5 ± 0.2 mm for the early cohort, versus 20.9 ± 0.2 mm for the middle cohort and 20.7 ± 0.2 mm for the late cohort, with the early cohort differing significantly from the middle and late cohorts by Tukey's HSD) declined in later hatching cohorts (Fig. 3.3). Culmen length at hatching did not differ among cohorts in 2012 ($F_{2,\,89} = 0.54$, $P = 0.586$, $r^2 = 0.01$ with mean ± standard error of 21.5 ± 0.2 mm for the early cohort, versus 21.2 ± 0.2 mm for the middle cohort and 21.3 ± 0.2 mm for the late cohort; Fig. 3.3). Pairwise comparisons indicated all measures of size at hatching were positively correlated, with $\rho > 0.26$ and $P < 0.016$ for chicks from the 2012 cohorts.

Absolute growth rates of mass, tarsus length and wing length for chicks encountered and measured three or more times varied among cohorts. In 2012 we captured 26 chicks from the early cohort, 14 chicks from the middle cohort and 14 chicks from the late cohort on three or more occasions to estimate growth rates from size measurements. Variation in absolute growth rates explained by cohort ranged from 10–13%, with absolute growth rates of mass ($F_{2,\,53} = 3.86$, $P = 0.028$, $r^2 = 0.13$ with mean ± standard error of 35.1 ± 1.6 g/day for the early cohort, 30.2 ±

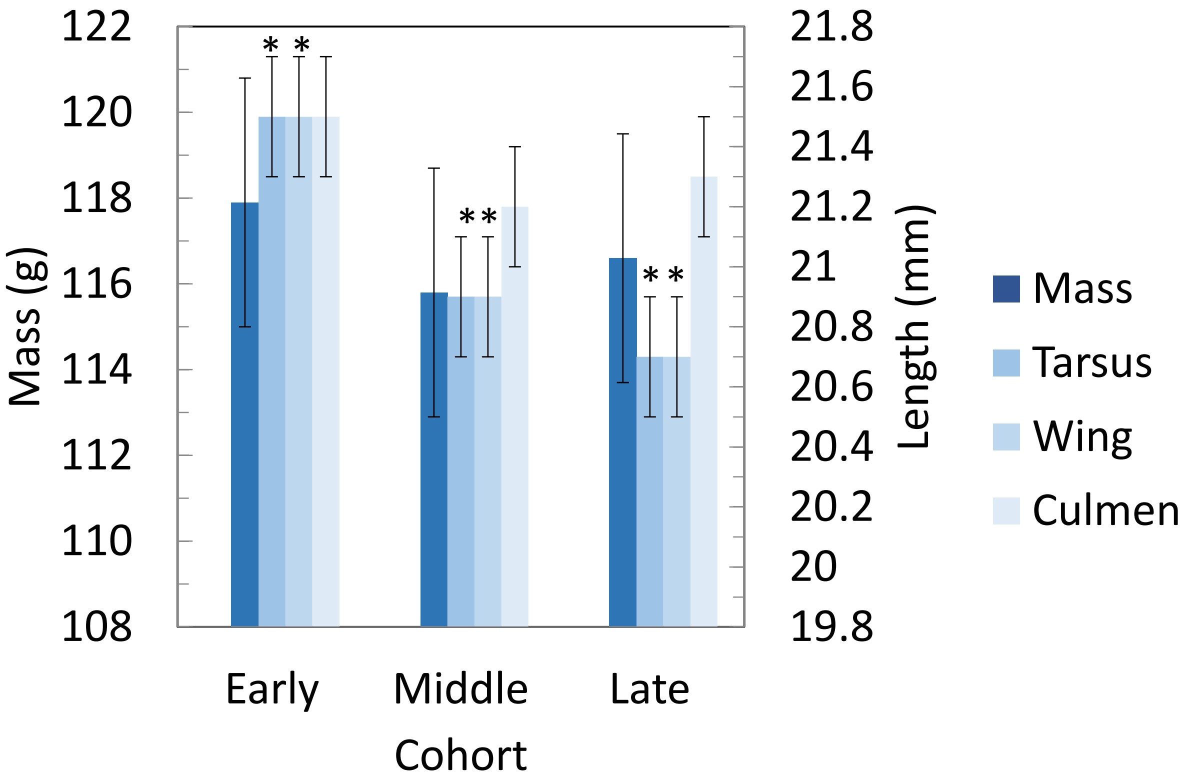

Figure 3.3. Mean initial mass (g), tarsus length (mm), culmen length (mm) and wing length (mm) for American White Pelican (*Pelecanus erythrorhynchos*) chicks hatched from early, middle, and late cohorts at Marsh Lake, Minnesota, 2012 (* = significant difference).

2.2 g/day for the middle cohort and 39.0 ± 2.2 g/day for the late cohort) and tarsus length ($F_{2,\,53}$ = 3.45, P = 0.039, r^2 = 0.12 with mean ± standard error of 2.4 ± 0.1 mm/day for the early cohort, 2.0 ± 0.1 mm/day for the middle cohort and 2.5 ± 0.1 mm/day for the late cohort) significantly higher in the late cohort. However absolute growth rate of wing length did not differ among the cohorts in 2012 ($F_{2,\,53}$ = 2.86, P = 0.066, r^2 = 0.10 with mean ± standard error of 1.52 ± 0.1 mm/day for the early cohort, 1.51 ± 0.1 mm/day for the middle cohort and 1.81 ± 0.1 mm/day for the late cohort).

Instantaneous growth rates of mass, tarsus length and wing length for chicks encountered and measured three or more times also varied among cohorts, with late cohorts having the fastest growth rates. Variation in instantaneous growth rates explained by cohort ranged from 12–23%.

Instantaneous growth rates of mass ($F_{2, 53} = 7.48$, $P = 0.001$, $r^2 = 0.23$ with mean ± standard error of 0.26 ± 0.001 day^{-1} for the early cohort, 0.23 ± 0.001 day^{-1} for the middle cohort and 0.28 ± 0.001 day^{-1} for the late cohort), tarsus length ($F_{2, 53} = 6.00$, $P = 0.005$, $r^2 = 0.19$ with mean ± standard error of 0.10 ± 0.003 day^{-1} for the early cohort, 0.09 ± 0.005 day^{-1} for the middle cohort and 0.11 ± 0.005 day^{-1} for the late cohort) and wing length ($F_{2, 53} = 3.35$, $P = 0.043$, $r^2 = 0.12$ with mean ± standard error of 0.07 ± 0.003 day^{-1} for the early cohort, 0.07 ± 0.004 day^{-1} for the middle cohort and 0.08 ± 0.004 day^{-1} for the late cohort) differed significantly among the cohorts in 2012. Growth rates for mass and tarsus length were significantly faster for the late cohort compared to the middle cohort (Tukey's HSD). Instantaneous growth rates of wing length were not different by the Tukey test, but pairwise comparison with the t-test indicated the growth rate for the late cohort was significantly faster than the other cohorts.

All of the growth rates for the 2012 cohorts were positively correlated with the other measures of growth. Pairwise comparisons indicated the growth rates were positively correlated, with $\rho > 0.56$ and $P < 0.001$ for all comparisons (e.g., absolute rate of growth in mass was positively correlated with the instantaneous rate of growth in tarsus length with $\rho = 0.67$, $P < 0.001$). In addition, mass at hatching was positively correlated (with $\rho > 0.40$ and $P < 0.003$) with the instantaneous rate of growth in tarsus ($\rho = 0.44$, $P = 0.001$) and the instantaneous rate of growth in wing ($\rho = 0.40$, $P = 0.003$). Tarsus length at hatching was not correlated (with $\rho < 0.19$ and $P > 0.17$) with instantaneous growth rates of mass, tarsus or wing. Wing length at hatching was positively correlated with the instantaneous growth in tarsus ($\rho = 0.34$, $P = 0.013$).

Increases in mass, tarsus length and wing length for chicks encountered and measured three or more times exhibited asymptotic growth; however, models of asymptotic growth in culmen length were not supported. We obtained 204 observations (for each size measurement) from 62 individuals (eight from the middle cohort in 2011; 54 from all cohorts in 2012) with measurements at three or more ages. Ages ranged from 1–88 days post hatching, however 203 of the 204 observed ages were less than 40 days post hatching and a singular observation at age 88 days post hatching. Asymptotic models for mass (Gompertz), tarsus (Janoschek), and wing (Janoschek) length at age had more than 95% of the evidence given the data compared to linear models (which all had $\Delta \mathrm{AIC}_c > 25$) for these measures of size (Table 3.1). The most parsimonious models for size at age indicated pelicans have attained 95% of asymptotic mass, 99% of asymptotic tarsus length and 78% of asymptotic wing length at 40 days past hatching (Fig. 3.4). In contrast the 4-parameter asymptotic model for culmen length (Janoschek) carried only 56% of evidence given the data compared to approximately 43% for a linear model, and these models differed by less than 0.5 in AIC_c value (Table 3.1). We repeated these analyses with the age 88 days past hatching observation excluded, but the results did not qualitatively differ (i.e., asymptotic models for mass, tarsus and wing length were the most parsimonious models in the set, with more than 75% of asymptotic size attained by age 40 days past hatching but the 4-parameter asymptotic model for culmen length was approximately equally ranked with the linear model). In fact, the linear regression of culmen length from age explained over 95% of the variation observed (Age = 0.3 · Culmen length - 5.2; $F_{1,\,281} = 6952.0$, $P < 0.001$, $r^2 = 0.96$; Fig. 3.4).

Discussion

Pelican chicks during peak hatching at Marsh Lake exhibited little annual variation in initial size during 2010–2012. While initial mass was lower in 2010, no difference in skeletal size was detected among years. In addition, there was minimal annual variation in growth rates

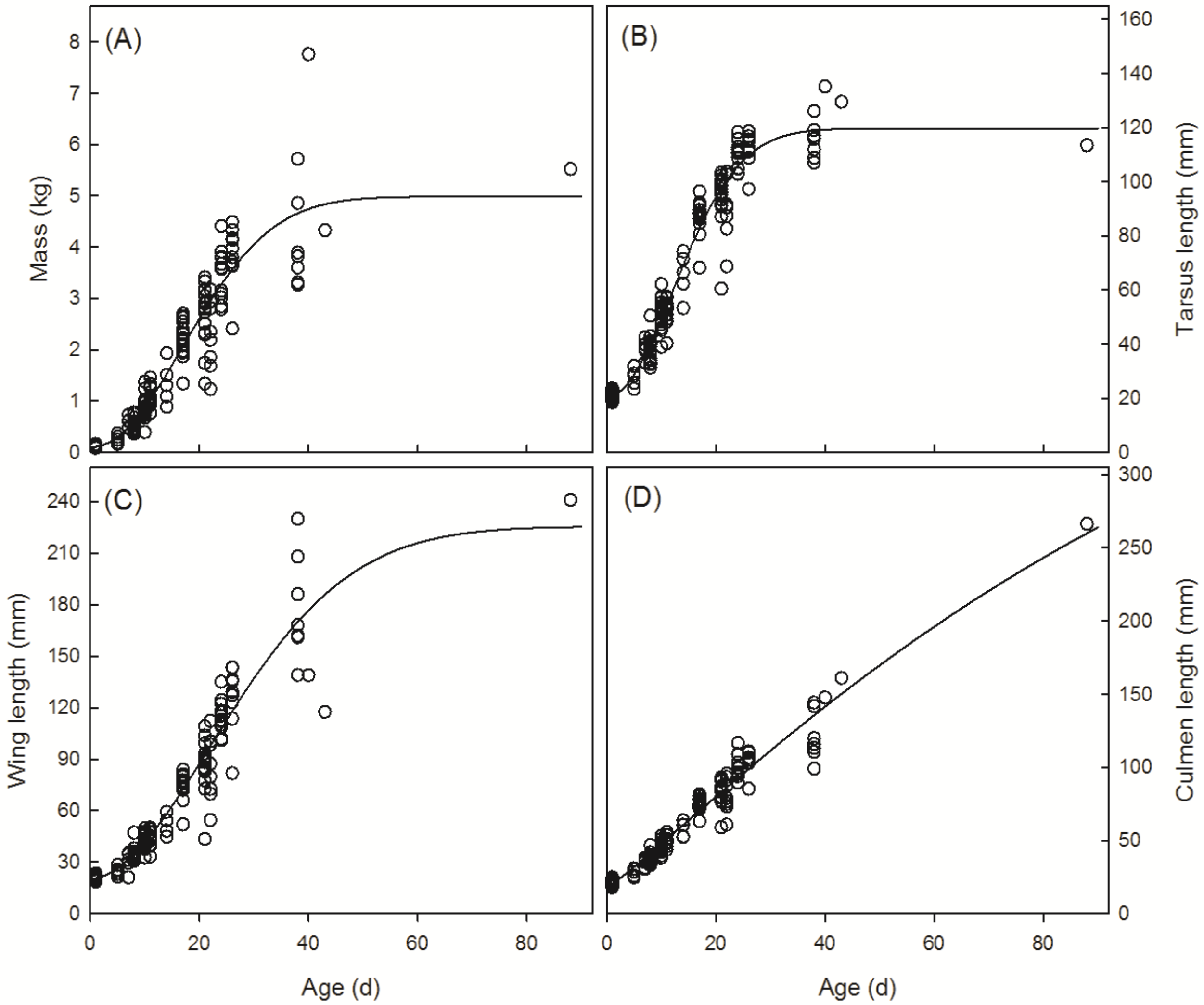

Figure 3.4. Size at age (days post-hatching) as indicated by (A) mass (kg), (B) tarsus length (mm), (C) wing length (mm) and (D) culmen length (mm) for American White Pelican chicks with three or more observations at Marsh Lake, Minnesota, 2011-2012. Open circles indicate observed values and the lines indicate an asymptotic model fit to the data.

between 2011 and 2012. Absolute and instantaneous growth rates for tarsus were faster in 2011, but no differences were detected in mass or wing growth.

Although little variation was seen in initial size and growth between years, significant variation was detected in both initial size and growth among early, middle, and late cohorts in 2012. No difference in initial mass was detected among cohorts, but both initial tarsus length and initial wing length were shorter in later hatched chicks. Absolute and instantaneous growth rates,

Table 3.1. Measurement, candidate growth model, relative Akaike's Information Criterion adjusted for small sample size (ΔAICc), normalized Akaike weight (wi), and model likelihood from observations of 62 American White Pelican (*Pelecanus erythrorhynchos*) chicks measured three or more times in 2011 and 2012 at Marsh Lake, Minnesota.

Measurement	Model	ΔAIC_c	w_i	Model Likelihood
Mass	Gompertz	0.00	0.78	1.00
	Janoschek	2.55	0.22	0.28
	Linear	38.35	3.68	0.00
	Constant	283.62	2.02	0.00
	Exponential	688.53	2.40	0.00
Tarsus	Janoschek	0.00	1.00	1.00
	Gompertz	15.82	0.00	0.00
	Linear	110.37	1.08	0.00
	Constant	208.78	4.62	0.00
	Exponential	384.75	2.83	0.00
Wing	Janoschek	0.00	0.73	1.00
	Gompertz	2.01	0.27	0.37
	Linear	26.60	1.22	0.00
	Constant	154.61	1.96	0.00
	Exponential	342.25	3.52	0.00
Culmen	Janoschek	0.00	0.56	1.00
	Linear	0.50	0.44	0.78
	Gompertz	10.13	0.00	0.00
	Constant	195.69	1.80	0.00
	Exponential	356.89	1.79	0.00

however, were faster for mass and tarsus in later hatched chicks, as was instantaneous growth rate for wing.

Mass and tarsus length plateau by 50 days post-hatching, but wing length does not (Fig. 3.4). Wing growth continues after fledging in the Brown Pelican (*Pelecanus occidentalis*) (Schreiber 1976) and other birds (Ricklefs 1984; Weidinger 1997; Reed *et al.* 1999). Plateau in wing length at a younger age may be constrained by a decrease in feather quality as growth rates increase (Rohwer and Rohwer 2013).

Initial size and growth of culmen did not vary between years or among cohorts within a season, and we provide a model for predicting age based on culmen length. Lingle and Sloan (1979) also provided a model for predicting age based on culmen length, but their model used post-nare culmen length while we opted to use exposed culmen length. Lingle and Sloan (1979) reported linear growth in the culmen to 30 days post-hatching. However, we found linear growth in the culmen through at least 40 days. Schreiber (1976) reported linear culmen growth in Brown Pelicans through fledging, with females attaining adult culmen length around the time of fledging, whereas males continued to grow culmen after fledging. We observed a chick at 88 days post-hatching exhibiting linear growth in the culmen (Fig. 3.4), which suggests pelicans exhibit a similar pattern of linear culmen growth through fledging.

The variation in initial size and growth rates among cohorts hatched at different times within the breeding season contrasts with the consistency in these traits between years. Evans and McMahon (1987) found similar growth rates for first-hatched chicks from different subcolonies with different hatching dates within the season at breeding colonies in the Interlake region of Manitoba, Canada, which differs from our observations of generally increasing growth rates for cohorts hatched later in the season. The differences in within season growth patterns for the Marsh Lake colony compared to the Manitoba colonies could be due to a number of factors including food availability, parental care or the latitudinal differences in length of the growing season (which is longer at Marsh Lake). Indeed we observed chick cohorts that hatched over a wider range of dates (and therefore wider range in the age differences among cohorts) compared to the cohorts observed by Evans and McMahon (1987). Elevated growth rates in colonial waterbird chicks hatched later in the season may enable late chicks to catch up with early chicks and achieve survival benefits from fledging synchrony (Benowitz-Fredericks and Kitaysky 2005; Hirose *et al.* 2012; Jakubas and Wojczulanis-Jakubas 2014), We found that late chicks hatch at smaller skeletal size (but similar mass) than early chicks. This could also facilitate catch-up with the early chicks if their asymptotic size is also smaller. We provide the first data on annual variation in initial size and growth of pelican chicks, which indicated between-year variation was less than within-year variation in chick size and growth. Although we did observe faster growth rates in the tarsus of chicks in 2011 (the only annual difference observed), nesting occurred later in 2011 than in 2012. Hence the faster tarsal growth rates for the year in which nesting was later is consistent with the pattern for growth rates within season.

Fledging synchrony is an adaptive behavior in other colonial waterbirds. Colonial seabirds face increased predation risk at the time of fledging because marine predators wait offshore for fledglings to land on the water when they leave the colony (Penney and Lowry 1967). By leaving en masse fledgling mortality risk is lower because predators are overwhelmed (Penney and Lowry 1967; David *et al.* 2003; Makhado *et al.* 2006; Makhado *et al.* 2013). Although pelicans do not face concentrations of aquatic predators at fledging from Marsh Lake, pre-fledged chicks do face terrestrial predators (DiMatteo *et al.* 2015), and the effects of predator swamping on land would decrease as crèche (pod) sizes decrease.

The mechanisms regulating within-season variation in growth can vary diametrically among species. For instance in waterfowl, late-season declines in the availability and quality of food resources typically result in slower growth rates (and smaller asymptotic sizes) for ducklings that hatch later in the season than ducklings that hatch early in the season (Cooch *et al.* 1991; Sedinger and Flint 1991; Lindholm *et al.* 1994; Dawson and Clark 2000). In contrast, Kasprzykowski *et al*. (2014) reported faster mass and tarsus growth in Eurasian Bittern (*Botaurus stellaris*) chicks hatched later in the season from nests near food-rich fishponds. Moreover parental care could compensate for within-season changes in the quality or availability of food. Takahashi *et al*. (2003) report parental allocation of resources obtained during foraging is more important than foraging effort in determining offspring growth rates in Adélie Penguins

(*Pygoscelis adeliae*). Variation in chick growth rates could be due to differences in efficiency or pre-hatching maternal investments independent of food resources or post-hatching parental care (Benowitz-Fredericks and Kitaysky 2005; Hirose *et al.* 2012). Thermoregulation also may be less costly in pelican chicks hatched later in the season (Sovada *et al.* 2014), making growth more efficient. Any of these factors could represent mechanisms by which pelican chicks hatched later in the season at Marsh Lake achieve faster growth rates chicks hatched early in the season.

One constraint faced by chicks at Marsh Lake is the need to migrate out of the region before surface waters freeze in the late fall. Pelicans incubate eggs for approximately 30 days (Knopf 1979), and chicks fledge at least 70 days post-hatching (O'Malley and Evans 1982). After fledging, chicks wait at least seven days before leaving the colony (O'Malley and Evans 1982). Thus pelican chicks require a minimum of 107 days to develop from embryo to fledging. With a frost-free period as short as 120 days in the region (NRCS 2000), faster growth rates of late chicks at Marsh Lake allows for successful fledging in a reduced period of time. More rapid growth by late chicks may be necessary at Marsh Lake for sufficient recruitment to maintain the current colony size (Evans and Knopf 2004), which is now one of the largest in North America. To understand what mechanisms regulate seasonal variation in pelican chicks, information on seasonal variation in 1) food resources, 2) parental foraging behavior, 3) parental provisioning, 4) egg investments and 5) chick physiology is needed.

Acknowledgments

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DEMOGRAPHIC CHARACTERISTICS OF AMERICAN WHITE PELICANS (*PELECANUS ERYTHRORHYNCHOS*) BREEDING AT MARSH LAKE, MINNESOTA[3]

Abstract

Population dynamics and the demographic factors that influence them are poorly understood for the American white pelican (*Pelecanus erythrorhynchos*), a large, long-lived, colonial-nesting waterbird that undertakes long migrations. We investigated nest initiation, survival, and age of maturation for American white pelicans nesting at Marsh Lake, Minnesota. Timing of nest initiation at Marsh Lake was not related to age or body condition of adults. However, nests were initiated significantly earlier on a more isolated island with higher nest success than other areas used for nesting. Adult annual survival was similar to that reported for other American white pelican populations. We estimated age of maturation for American white pelicans nesting at Marsh Lake, and found that pelicans are unlikely to begin nesting until they are at least five years old.

Introduction

Understanding how age is related to life history traits is a key to understanding how population size changes over time (Sæther *et al*. 2013). In migratory birds the timing of nesting can have significant consequences on recruitment. In a number of avian species older individuals initiate nesting earlier than younger individuals (Bulluck *et al*. 2013; Claassen *et al*. 2014; Devries *et al*. 2008; Haymes and Blokpoel 1980; Hipfner *et al*. 2010; Massey and Fancher 1989; Nisbet *et al*. 1984; Wendeln *et al*. 2000). Clutch and egg size are typically greater in early-

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[3] The material in this chapter was co-authored by Jon J. DiMatteo and Mark E. Clark for submission to *Canadian Journal of Zoology*. Jon J. DiMatteo was the principal investigator responsible for project design, data collection and analysis, description of results, and development of conclusions. Jon J. DiMatteo also drafted and revised all versions of this chapter. Mark E. Clark served as proofreader and corroborated the math in the statistical analysis conducted by Jon J. DiMatteo.

nesting individuals (Blomberg *et al*. 2014; Cotter *et al*. 2013; Gladbach *et al*. 2010; Krapu *et al*. 2002; Tsuboi and Ashizawa 2011). Age at maturation is less documented in birds, but is related to nest initiation date in common terns (Sterna hirunda) (Becker *et al*. 2008). Within an individual nesting colony of American white pelicans (*Pelecanus erythrorhynchos* [henceforth pelican]), groups of closely-nesting individuals hatch synchronously, but different groups with separation from each other, hatch asynchronously (O'Malley and Evans 1980). O’Malley and Evans (1980) and Orr (1980) conjectured that the asynchrony of the groups was related to age of the adults (with groups of nests of older individuals hatching earlier than groups of nests of younger individuals). Clutch size (two eggs) varies little in pelicans (Evans and Knopf 2004). Individuals can be long-lived (e.g., over 15 years) (Evans and Knopf 2004; Ryder 1981), but age at first reproduction has only been anecdotally reported (Chapman and Chapman 1990; Sloan 1982). We examined relationships among age, size, and condition on the timing of nesting and age at maturation in a large breeding colony of pelicans to provide information on age-related reproductive characteristics. In particular we determined if the timing of nest initiation was correlated with age of the adult, which would be expected if O’Malley and Evans’ (1980) and Orr’s (1980) hypothesis is correct.

Materials and Methods

We monitored pelicans nesting on Marsh Lake at Lac qui Parle Wildlife Management Area (WMA) (N 45^{o} 11’, W 096^{o} 09’) in southwestern Minnesota from early May to late June each year from 2011-2015. Lac qui Parle WMA is a 12,545-ha area along the Upper Minnesota River in Chippewa, Swift, Big Stone, and Lac qui Parle counties, Minnesota managed by the Minnesota Department of Natural Resources for waterbirds and other resources (Minnesota Department of Natural Resources (MN DNR) 1997). Marsh Lake is an approximately 6.5 km long and 1.5 km wide floodplain lake at the confluence of the Pomm de Terre and Minnesota rivers within the Lac qui Parle WMA. Twenty-five pairs of pelicans were reported nesting at Marsh Lake in 1968 (Breckenridge 1968), with increases in numbers through 2000, and numbers have since averaged 18,725 nesting pairs (DiMatteo *et al*. 2015). The abundance of pelican nests and the abundance of late-stage (i.e., near fledging) chicks at Marsh Lake has been monitored nearly annually since 2004 (DiMatteo *et al*. 2015). Pelican nesting is concentrated on several islands (Big Island, Currie Island, Eight-acre Island and One-acre Island) and a peninsula on Marsh Lake, with islands more distant from the mainland (i.e., 746 m to Big Island and 650 m to One-acre Island) preferred over islands closer to the mainland (i.e., 127 m to Currie Island and 235 m to Eight-acre Island) or the peninsula for nesting (DiMatteo *et al*. 2015). Large numbers (typically more than 1,000) of late-stage chicks have been banded annually at the colony since 1972 (except 1997 and 2013), with more than 54,000 banded through 2015 (Fig. 4.1).

The clutch size of American white pelicans is typically two eggs. We measured size, days of incubation and change in mass of both eggs from two-egg clutches of pelicans nesting at Marsh Lake, Minnesota from 2011-2012 and 2014-2015. We measured mass (± 0.01 g), length (± 0.1 mm) and breadth (± 0.1 mm) of freshly laid (i.e., within 24 hours of laying) eggs. We also collected a subset of freshly laid eggs for which we obtained measurements for mass (± 0.001 g), length (± 0.1 mm), breadth (± 0.1 mm) and volume (± 1.0 ml) in the lab within five hours of collection. We measured volume by the difference of the mass of the egg in air and the mass of the egg in water (Evans 1969), but obtained a separate estimate of volume based on displacement for a subset of the eggs. For a subset of nests in 2012, we also monitored change in mass through incubation for eggs for which the laying date was known by obtaining mass measurements on multiple occasions.

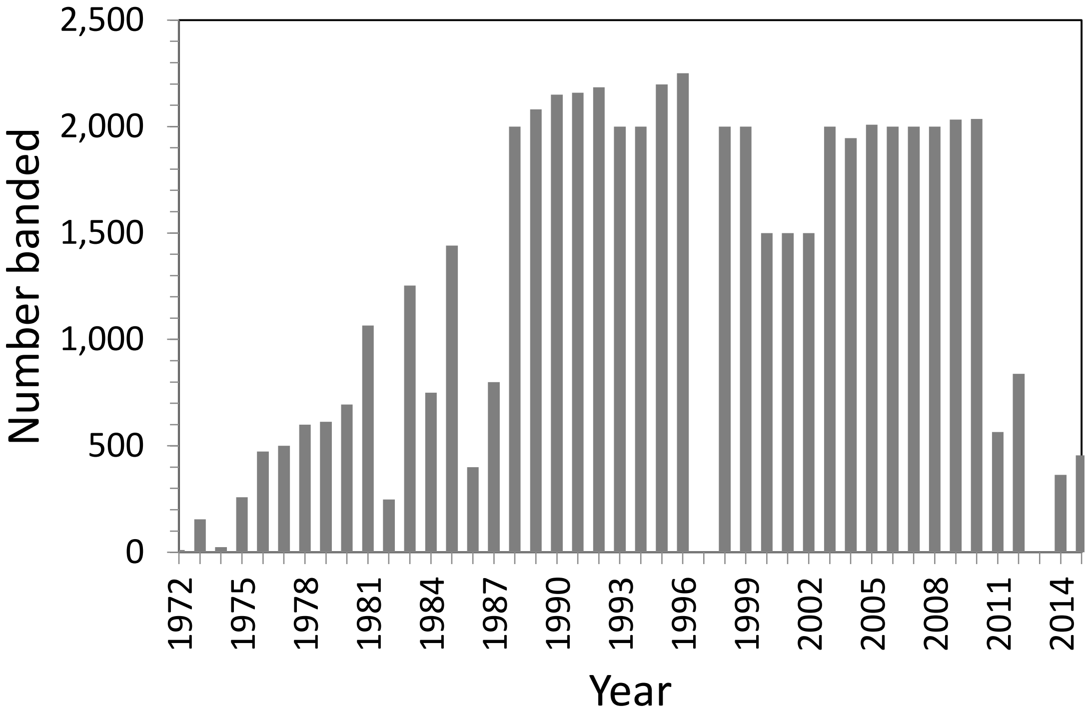

Figure 4.1. American white pelican chicks banded at Marsh Lake, 1972-2015. Bands deployed under authorization of Federal Bird Banding Permit 05838 in 1987; all other years under Permit 08077.

In 2015 we captured adult pelicans at their nests to examine relationships among adult characteristics (e.g., age, condition) and nest-initiation date. We identified individual nests and measured egg size (mass, length and breadth) as described earlier, and used the measurements to estimate initiation date of the nest. We captured one adult at each nest with a modified leg-hold trap (King and Werner 2001). At capture, we recorded mass (± 0.01 kg), length of the tarsometatarsus (henceforth tarsus) (± 0.1 mm), minimum thickness of the tarsus (± 0.1 mm), wing chord length (± 1.0 mm) and culmen length (± 1.0 mm) of the adult. We collected two feathers to supply genetic material to determine sex and released the individual. We used the culmen length measurement as a secondary means for assessing sex (Dorr *et al*. 2005). We quantified condition of the adults at capture by using the residual (along the mass axis) of an orthogonal regression of mass and tarsus length (Green 2001). We determined age (in years) and natal colony for those individuals that had been previously banded as near-fledged chicks. We monitored the nest to determine if the captured individual abandoned the nest or (if it did not abandon) to determine fate of the eggs (hatched versus did not hatch).

We estimated the nest initiation date from measurements of egg size. For nests in 2015 for which initiation day (i.e., the Julian day on which the first egg of the nest was laid) was unknown, we estimated the number of days an egg had been incubated using three different methods: 1) a formula from O’Malley and Evans (1980), 2) a modification of the formula from O’Malley and Evans (1980) and 3) a regression of mass loss following Westerskov (1950). O’Malley and Evans (1980) estimated days of incubation from change in specific gravity (SG, $g \cdot ml^{-1}$), which they estimated by $SG = \frac{M}{0.0005 \cdot L \cdot B^2}$ (where M is egg mass in g, L is egg length in mm and B is egg breadth in mm), as days of incubation $= \frac{1.1023 - SG}{0.0036}$. We modified the O’Malley and Evans (1980) formula by estimating specific gravity from the quotient of mass and a power function for egg volume (V, ml) in which $V = k \cdot L^{a} \cdot B^{b}$ (where L is egg length in mm and B is egg breadth in mm) and k, a and b are constants determined from volume measurements of eggs collected from the Marsh Lake colony. We then estimated the days of incubation by using the O’Malley and Evans (1980) formula with our estimate of specific gravity. Finally we developed an orthogonal regression of days of incubation from mass for known-age eggs measured in the Marsh Lake colony to estimate days of incubation for eggs of unknown age. In this regression, we assumed the log-transformed difference in mass at a specific age (M_{days}, g) and mass when the egg was laid (M_0, g; which was also known) declined at a constant instantaneous rate (r, $g \cdot g^{-1} \cdot d^{-1}$) according to a linear relationship such that $log(M_{days}) - log(M_0) = A + r \cdot days$ (with constant A and days giving the number of days of incubation). For eggs of unknown age, we estimated the fresh mass (i.e., mass when the egg was laid) from a power function for egg mass

(M_0, g) in which $M_0 = k_m \cdot L^c \cdot B^d$ (where L is egg length in mm and B is egg breadth in mm) and km, c and d are constants determined from measurements of eggs obtained within 24 hours of laying from the Marsh Lake colony, then used this estimate and the mass measurement to estimate the days of incubation from the orthogonal regression. If the estimated number of days of incubation (based on any of the three methods) for an egg was less than zero, we assumed the actual value was zero for that method of estimation. For all three methods of estimating days of incubation, we selected the maximum estimate (rounded down to the nearest integer) from both eggs in the nest to determine the estimate of nest initiation day (calculated as the difference between the Julian day of measurement and the days of incubation estimate). We checked correlation among our three methods for estimating nest initiation date using the Pearson product moment (ρ) and a t-test.

We analyzed return rates for known-age birds captured from the number of individuals in the original banded sample, or release cohort ($\mathrm{Returns}_i$), to assess age of first breeding in the colony. We modeled captures for a release cohort with two different models. In the first model, $\mathrm{Returns}_i$ are given by the product of number of individuals in the release cohort (R_i) and a probabilistic function of age at maturation (mat, in years), capture probability (p_c), juvenile survival (S_j) and adult annual survival (S_a) such that $\mathrm{Returns_i} = \mathrm{R_i} \cdot \frac{1}{\left(1+e^{-(\mathrm{i}-\mathrm{mat})}\right)} \cdot \mathrm{p_c} \cdot \mathrm{S_j} \cdot \mathrm{S_a^{i-1}}$ where i is age in years. In this model, probability of maturation is logistic with age at maturation representing the age (in years) at which there is a 50% probability an individual is sexually mature, juvenile survival (post-fledging) is assumed constant across cohorts (years) and adult survival is assumed constant across years. In the second model, $\mathrm{Returns}_i$ are given by the product of number of individuals in the release cohort (R_i), capture probability (p_c), juvenile survival (S^j) and adult annual survival (S_a) such that $\mathrm{Returns_i} = \mathrm{R_i} \cdot \mathrm{p_c} \cdot \mathrm{S_j} \cdot \mathrm{S_a^{i-1}}$ where i is age in years. The second model is therefore a nested simplification of the first model, with all age – 1 + individuals assumed to be sexually mature. We fit both models for expected captures to our observed captures, to provide estimates for age at maturation, adult annual survival and the product of capture probability and juvenile survival (because both p_c and S_j cannot be estimated without additional information).

We compared nest initiation date to age, sex, condition and location using general linear models, and used maximum likelihood methods to estimate parameters for models of egg volume, fresh mass and expected captures. In models for egg size, we checked for effects of year if measurements were collected for eggs laid in the colony in different years. We also checked for correlations among size measurements of adult pelicans by using Pearson product-moment and a χ^2 test. We determined significance of general linear models in explaining variation using an F or t test. We compared sex ratios among captures and capture locations using a Likelihood Ratio test. We assessed goodness of fit of the models for captures using a χ^2 test. We used a likelihood ratio test and the relative Akaike's Information Criterion adjusted for small sample size (ΔAICc) to determine which capture model best fit the data (Burnham and Anderson 2002; Lebreton *et al*. 1992). We assumed statistical significance at the $\alpha = 0.05$ level. All statistical analyses were completed using JMP software (SAS Institute 2012).

Results

Linear egg dimensions explained more than 95% of the variation in the mass of freshly laid eggs. We collected size measurements for 241 freshly laid eggs (89 in 2011, 64 in 2012, 20 in 2014 and 68 in 2015), and the power function $\mathrm{M}_0 = k_m \cdot \mathrm{L}^c \cdot \mathrm{B}^d$ (with estimates ± standard errors of $k_m = 0.00047 \pm 0.00008$, $c = 1.022 \pm 0.028$ and $d = 2.02 \pm 0.033$) explained more than 95% of the variance in mass ($F_{2,\,238} = 3229.03$, $P < 0.001$, $r^2 = 0.96$). Mass of freshly laid eggs did not differ among years ($F_{3,\,237} = 0.43$, $P = 0.732$, $r^2 < 0.01$), and including a term for year in the power function did not increase variation explained nor was the term significant.

Linear egg dimensions also explained more than 95% of the variation in the egg volume. We measured size and volume (by difference of mass in air and mass in water) for 151 freshly laid eggs (64 in 2012, 20 in 2014 and 67 in 2015), and the power function $\mathrm{V} = k \cdot \mathrm{L}^a \cdot \mathrm{B}^b$ (with $k = 0.00041 \pm 0.00008$, $a = 1.034 \pm 0.029$ and $b = 2.02 \pm 0.039$) explained more than 95% of the variance in volume ($F_{2,\,148} = 2425.32$, $P < 0.001$, $r^2 = 0.97$). Egg volume did not differ among years ($F_{2,\,148} = 1.08$, $P = 0.340$, $r^2 = 0.01$), and including a term for year in the power function did not increase variation explained nor was the term significant. Volume measurements from mass difference were positively correlated with measurements of volume obtained by displacement ($\rho^2 = 0.93$, $P < 0.001$, n = 64).

The difference in log-transformed mass of eggs at a specific age and mass when laid declined linearly with age. We measured the change in mass during incubation for 24 eggs (all of which were the first-laid egg of the clutch) with known laying date from nests in the Marsh Lake colony in 2012. An orthogonal regression of $log(\mathrm{M}_{\mathrm{days}}) - log(\mathrm{M}_0) = A + r \cdot \mathrm{days}$ (with A = 0.00396 and r = -0.00377) indicated change in log-transformed mass of an egg was negatively correlated with days of incubation ($\rho^2 = 0.95$, $P < 0.001$ for 59 observations from 24 eggs) (Fig. 4.2).

We captured 40 incubating adults from late April to late May in 2015 to characterize size, condition, age of nesting adults and fate of nests. Nests of the captured pelicans were located on three islands (27 on Big Island, 12 on Eight-acre Island, one on One-acre Island). Body mass ranged from 3.84 – 8.34 kg (mean ± standard error of 5.99 ± 0.17 kg, n = 39), tarsus length ranged from 106.7 – 130.2 mm (mean ± standard error of 120.9 ± 1.0 mm, n = 37), minimum

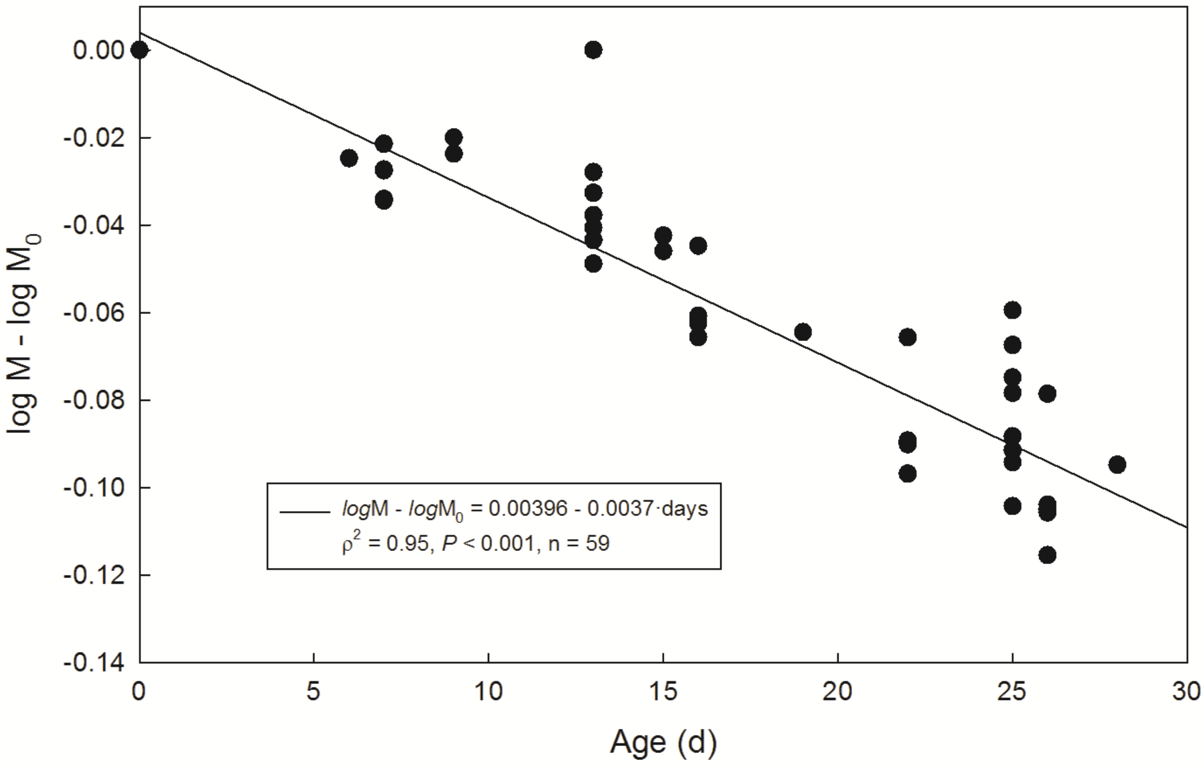

Figure 4.2. Negative correlation between log-transformed egg mass minus log-transformed fresh egg mass and the number of days of incubation for 59 observations from 24 naturally incubated American white pelican eggs at Marsh Lake in 2012. The solid line indicates the orthogonal regression fit to the observed values (filled circles).

thickness of the tarsus ranged from 15.2 – 21.3 mm (mean ± standard error of 18.1 ± 0.5 mm, n = 15), wing chord length ranged from 495.0 – 640.0 mm (mean ± standard error of 580.0 ± 5.7 mm, n = 33), and culmen length ranged from 267.0 – 372.0 mm (mean ± standard error of 325.0 ± 5.5 mm, n = 37). All body size measurements were positively correlated (with $\rho^2 > 0.62$ and $P < 0.014$ for all pairwise comparisons) except tarsus length and minimum thickness of the tarsus ($\rho^2 = 0.39$, $P = 0.148$, n = 15). Condition (quantified as residual along the mass axis from the orthogonal regression tarsus length = 87.4 + 5.61· mass, $\rho^2 = 0.80$, $P < 0.001$, n = 37) ranged from -1.20 – 0.67 kg (mean ± standard error of 0.00 ± 0.06 kg, n = 37). Body mass ($F_{1, 36} = 3.57$, $P = 0.067$, $r^2 = 0.09$), tarsus length ($F_{1, 34} = 0.24$, $P = 0.629$, $r^2 = 0.01$), minimum tarsus thickness ($F_{1, 13} = 0.13$, $P = 0.726$, $r^2 = 0.01$) and wing chord length ($F_{1, 30} = 0.45$, $P = 0.509$, $r^2 = 0.01$) did not differ between pelicans captured on Big Island and Eight-acre Island. However body condition was higher for pelicans captured on Big Island (mean ± standard error of 0.09 ± 0.07 kg) compared to Eight-acre Island (mean ± standard error of -0.15 ± 0.09 kg; $F_{1,\,34} = 4.39$, $P = 0.044$, $r^2 = 0.11$). For known-age pelicans (Fig. 4.3), ages ranged from 6 – 20 years (mode of 10 years, n = 28). Twenty-seven of the known-age pelicans were banded as chicks at the Marsh Lake Colony, and one individual was banded as a chick at Chase Lake, North Dakota. Age did not affect body mass ($F_{1,25} = 0.83$, $P = 0.372$, $r^2 = 0.03$), tarsus length ($F_{1,\,25} = 0.43$, $P = 0.519$, $r^2 = 0.02$), minimum tarsus thickness ($F_{1,\,25} = 3.37$, $P = 0.093$, $r^2 = 0.23$), wing chord length ($F_{1,\,25} = 2.13$, $P = 0.159$, $r^2 = 0.09$), culmen length ($F_{1,\,25} < 0.01$, $P = 0.994$, $r^2 < 0.01$) or condition ($F_{1,\,25} = 0.14$, $P = 0.714$, $r^2 = 0.01$). We were able to determine the fate of 35 of the nests associated with captured adults. Seven nests were abandoned soon after capture, 16 nests failed (five due to flooding and 11 due to unknown causes) to produce chicks but the captured adult associated with the nest was observed incubating after capture, and 12 nests successfully hatched at least one chick. We were unable to determine if any of the pelicans with failed nests later renested.

Culmen lengths were bimodally distributed. Of the 37 pelicans captured for which we had culmen length measurements, 13 had culmen lengths less than 299.0 mm and 24 had culmen lengths greater than 310.0 mm (Fig. 4.4). Dorr *et al*. (2005) found adult pelican females have culmen length less than 310.0 mm, which indicates there were 13 females and 24 males in the 37 captures for which we had culmen length measurements (Fig. 4.4). Of these 37 individuals, 11 (6:5 ratio of females:males) did not have a metal leg band at capture compared to 26 with metal leg bands (7:19 ratio of females:males), but the differential sex ratio for the groups was not significant ($\chi^2 = 2.53$, $P = 0.112$, n = 37).

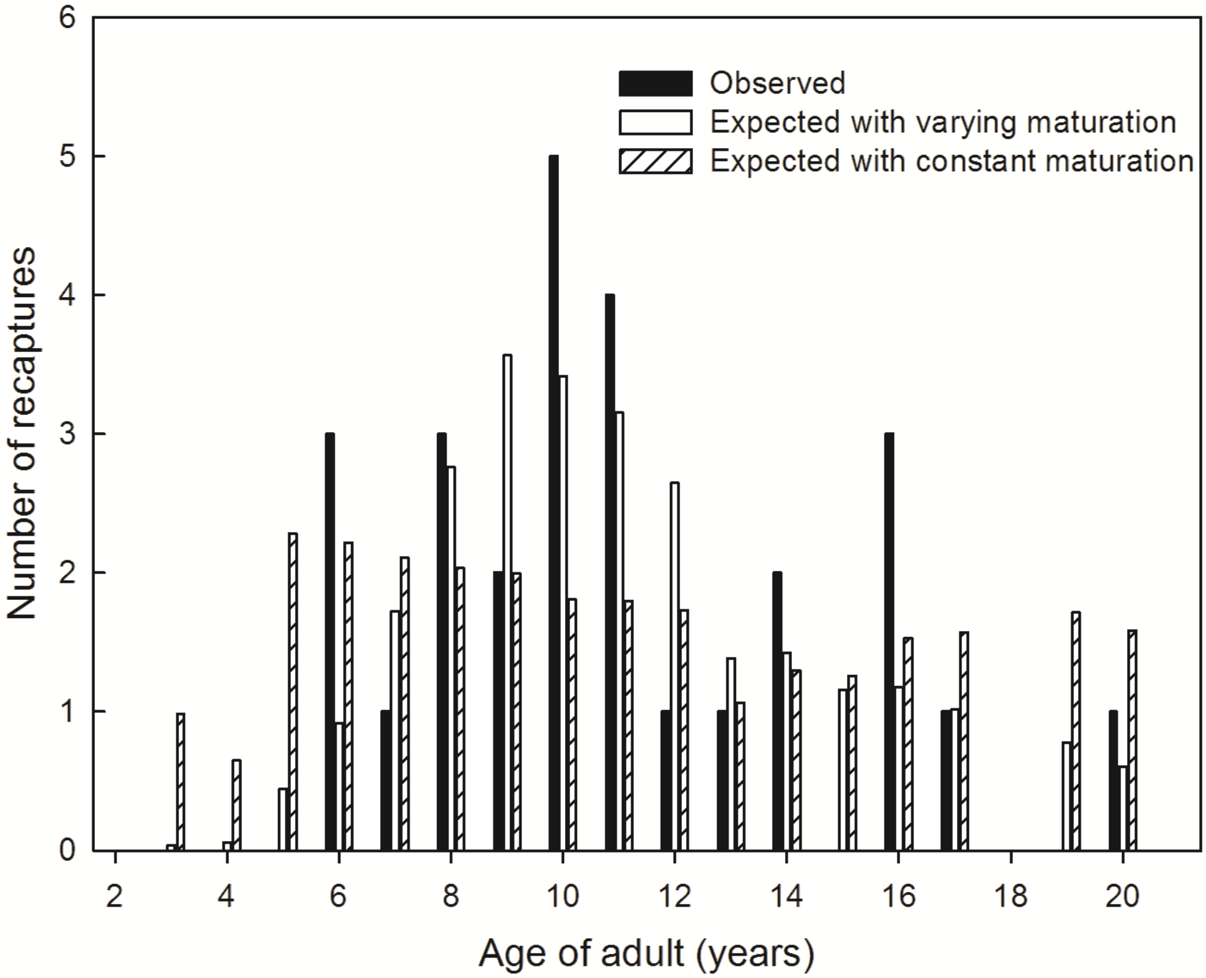

Figure 4.3. Distribution of observed captures (solid bars), expected captures according to the model with age-varying maturation (open bars) and expected captures according to the model without age-varying maturation (diagonal-lined bars) by age.

Males were larger in size than females, but did not differ in condition or by capture location. Based on sex determination from the culmen length, males had significantly greater mass (6.60 ± 0.14 kg versus 4.85 ± 0.19 kg; $F_{1,\,35} = 53.10$, $P < 0.001$, $r^2 = 0.60$), tarsus length (124.6 ± 0.7 mm versus 113.9 ± 0.9 mm; $F_{1,\,35} = 89.77$, $P < 0.001$, $r^2 = 0.72$), tarsus thickness (19.3 ± 0.4 mm versus 16.7 ± 0.4 mm; $F_{1,\,13} = 18.68$, $P < 0.001$, $r^2 = 0.59$), and wing chord length (600.0 ± 4.6 mm versus 549.0 ± 5.8 mm; $F_{1,\,31} = 47.65$, $P < 0.001$, $r^2 = 0.61$) than females. However body condition did not differ between males and females ($F_{1,\,35} = 0.46$, $P =$

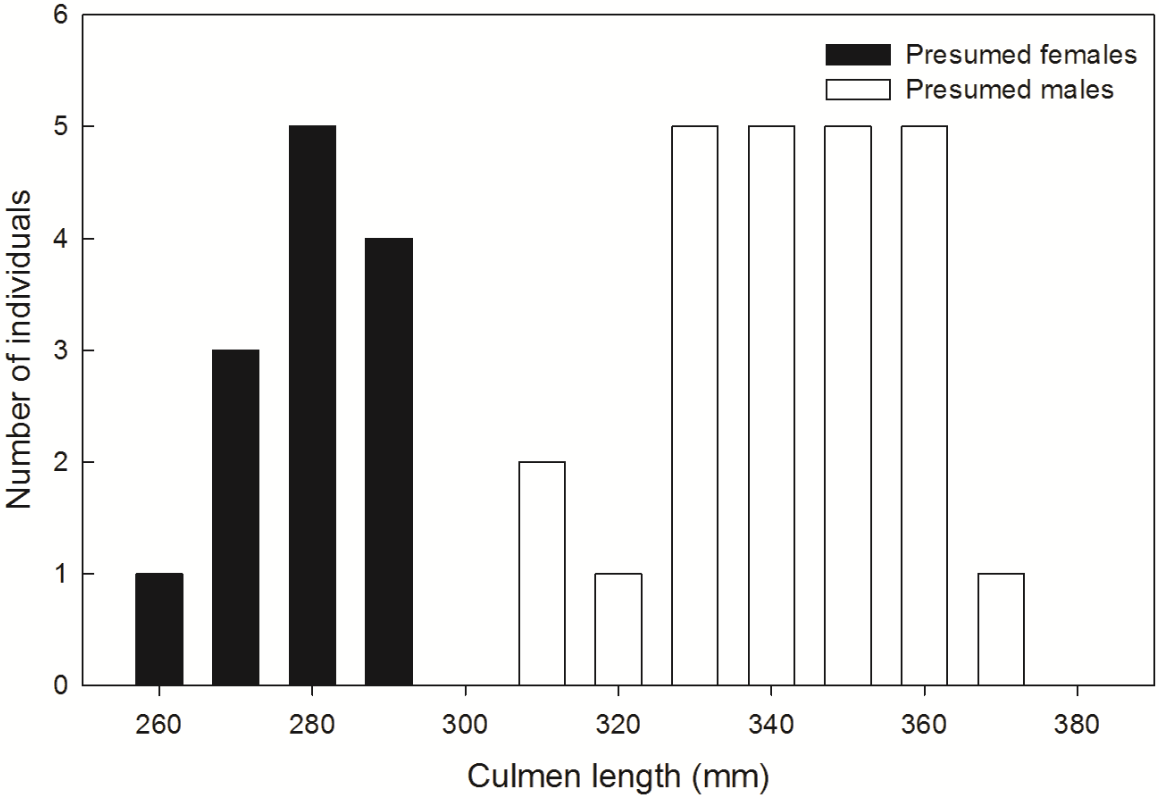

Figure 4.4. Distribution of culmen lengths from nesting American white pelicans captured at Marsh Lake in 2012. Filled bars indicate females and unfilled bars indicate males, based on criteria for culmen length from Dorr et al. (2005).

0.502, $r^2 = 0.01$). The ratio of males and females captured did not differ between Big Island and Eight-acre Island ($\chi^2 = 0.55$, $P = 0.457$, n = 36).

Estimated days of incubation at capture were correlated, but significantly different among methods. The estimated number of days of incubation at capture based on O’Malley and Evans (1980) ranged from 0 – 35 days (mean ± standard error of 11.3 ± 1.6 days, n = 40). When we calculated specific gravity from our measurements of mass, length and breadth of the eggs and applied the O’Malley and Evans (1980) formula to estimate number of days of incubation, values ranged from 0 – 39 days (mean ± standard error of 15.4 ± 1.8 days, n = 40), were correlated with ($\rho^2 = 0.99$, $P < 0.001$, n = 40), but significantly greater than (with mean difference ± standard error of 4.2 ± 0.3 days, $t_{39} = 14.59$, $P < 0.001$), the standard O’Malley and Evans (1980) estimates. Estimated number of days of incubation based on the orthogonal regression ranged from 0 – 32 days (mean ± standard error of 10.1 ± 1.5 days, n = 40) were correlated with (ρ^2 = 0.99, $P < 0.001$, n = 40), but significantly less than (with mean difference ± standard error of -1.1 ± 0.2 days, $t_{39} = -6.67$, $P < 0.001$), the standard O'Malley and Evans (1980) estimates.

Nest initiation date did not differ by age, sex, or body condition of the adult captured at the nest, but nests located on Big Island were initiated earlier than nests on Eight-acre Island. For the 28 known-age individuals, nest initiation date (i.e., difference between capture day and number of days of incubation estimated by the orthogonal regression) did not vary with age in years of the adult captured at the nest ($F_{1,\,26} = 2.13$, $P = 0.157$, $r^2 = 0.08$) (Fig. 4.5). Nest initiation date was not related to sex ($F_{1,\,35} = 0.44$, $P = 0.510$, $r^2 = 0.01$) nor body condition ($F_{1,\,35} = 2.18$, $P = 0.149$, $r^2 = 0.06$) (Fig. 4.5). However nest initiation date was earlier for nests on Big Island (mean ± standard error of Julian day 121.0 ± 2.0) compared to Eight-acre Island (mean ± standard error of Julian day 129.0 ± 2.9; $F_{1,\,35} = 5.20$, $P = 0.028$, $r^2 = 0.12$) (Fig. 4.5). When analyzed separately, nest initiation date was still not related to age in years for females ($F_{1,\,6} = 0.42$, $P = 0.540$, $r^2 = 0.07$) nor males ($F_{1,\,17} = 1.10$, $P = 0.310$, $r^2 = 0.06$). When analyzed separately, nest initiation date was not related to age in years on Big Island ($F_{1,\,14} = 3.74$, $P = 0.074$, $r^2 = 0.21$; but power test indicates this would be significant with a sample size of 19 nests) nor Eight-acre Island ($F_{1,\,9} = 0.08$, $P = 0.784$, $r^2 = 0.01$). Results for analysis of nest initiation date were qualitatively similar (i.e., non-significant for effects of age, sex and body condition, but significant for location) for each method for estimating number of days of incubation experienced by the nest. We only present results based on estimation by the orthogonal regression for conciseness.

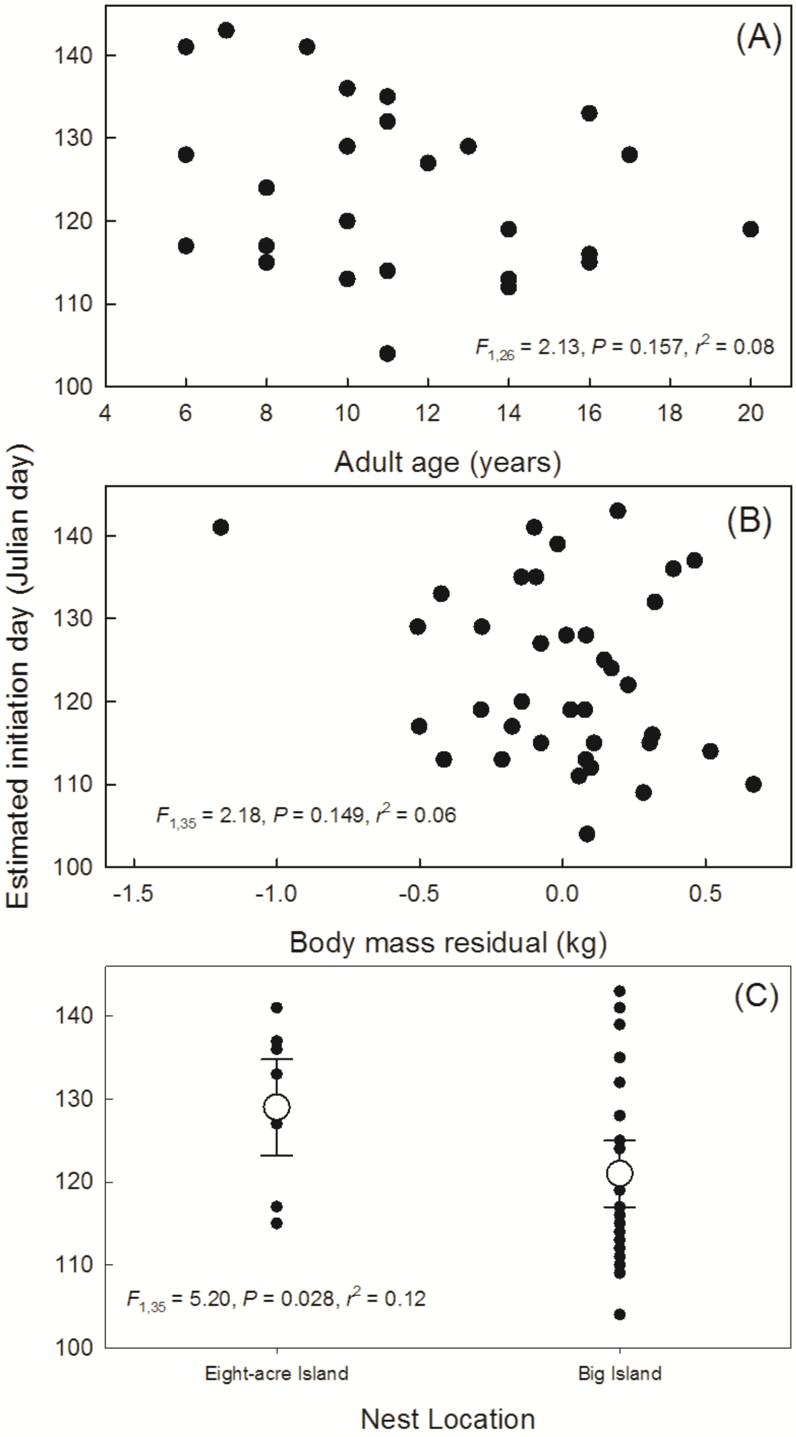

Figure 4.5. Variation in the nest initiation day was not related to adult age (A) or body condition as measured by the residual (along the mass axis) from an orthogonal regression of tarsus length and body mass (B), but did differ significantly between Eight-acre and Big Islands (C). Filled circles indicate observed values and open circles indicate means (with bars for 95% confidence intervals for the mean).

Both models for expected captures of adults adequately fit the observations, but the model in which probability of maturation varied with age had significantly better fit. The goodness of fit test indicated that observed captures did not differ from expected captures based on the capture model with varying age at maturation ($\chi^2 = 14.27$, $P = 0.430$, n = 27 recaptures) or the model in which maturation was constant for all ages ($\chi^2 = 11.94$, $P = 0.684$, n = 27) (Fig. 4.3). However the model in which maturation varied explained significantly more variation than the model with constant maturation ($\chi^2 = 9.47$, $P = 0.002$, n = 27) and had higher rank based on an information-theoretic approach (ΔAICc = 0.0 for the model with varying probability of maturation versus ΔAICc = 6.11 for the model in which maturation did not differ among ages). In the model with varying probability of maturation, estimates for adult annual survival (S_a) were 0.813 ± 0.079 (estimate ± standard error), and age at which 50% of individuals are mature (mat) of 8.3 ± 1.1 (estimate ± standard error) years. In the model in which all individuals are assumed mature, the estimate for adult annual survival was 0.971 ± 0.042 (estimate ± standard error).

Discussion

The timing of breeding can have significant consequences for reproductive success in migratory birds. Generally, early-nesting individuals contribute more recruits (Lack 1968). For many species, nest initiation is related to age (Claassen *et al*. 2014; Devries *et al*. 2008; Haymes and Blokpoel 1980; Nisbet *et al*. 1984). Contrary to the hypothesis that older, more experienced pelicans are first to initiate nesting each year (O'Malley and Evans 1980; Orr 1980), our findings, albeit from a limited sample for a single year, suggests there is no relationship between age and nest initiation for pelicans at Marsh Lake (Fig. 4.5). Ward (1924) and Behle (1958) proposed that nest initiation for pelicans was dependant on arrival date, with the first individuals arriving at the breeding site also initiating the first nests in the colony. However the concept that the first to arrive are the first to nest has not been evaluated, and the mechanisms regulating arrival date are not known. Schaller (1964) noted that it is possible that pelicans arrive at about the same time but that nesting behavior of those that are physiologically ready to breed is synchronized by the stimulating effect of group courtship and egg laying. Physiological condition upon arrival could be due to conditions at wintering sites (Schamber *et al*. 2012), staging sites during spring migration (Bêty *et al*. 2003; Finch *et al*. 2014) or weather experienced during migration (Both *et al*. 2005).

Body condition can affect the timing of nesting. In some birds, female body condition is negatively related to nest initiation date and positively related to subsequent reproductive output (Bêty *et al*. 2003; Christians *et al*. 2001; Gladbach *et al*. 2010). However, nest initiation date did not vary with adult (or female) body condition in pelicans at Marsh Lake. Males were larger than females, but there was no difference in their body condition. Size and body condition did not vary by age.

The timing of nesting can be related to nest-site selection, and we observed this in pelicans at Marsh Lake. Nest initiation date was earlier and body condition at capture was higher on Big Island than on Eight-acre Island. Big Island is the preferred nesting site for pelicans at Marsh Lake. Predation rates are lower at this site but the likelihood of flooding is greater (DiMatteo *et al*. 2015). Nest initiation dates are earlier at preferred nesting sites in other colony-nesting waterbirds (MacCarone *et al*. 1993; Robinson and Dindo 2011; Severinghaus 1982). Common eiders (*Somateria mollissima*) will nest later in preferred habitats rather than nesting earlier in suboptimal habitats (Öst and Steele 2010).

Our estimates of survival based on recaptures are similar to previous estimates reported for pelicans. Ryder (1981) estimated adult annual survival of 0.737 ± 0.011 from a population described as stable. This estimate is not appreciably different from our estimate of 0.813 ± 0.079 for the Marsh Lake colony, which exhibits density-dependent patterns in nesting colony size (DiMatteo *et al*. 2015). Both estimates may be biased low because of band loss (Evans and Knopf 2004; Ryder 1981) or inter-colony movements (Oomen *et al*. 2011; Reudink *et al*. 2011). In our study, females had significantly thinner tarsi than males and the female:male ratio was trending lower for banded birds, suggesting survival estimates also may be sex-biased.

Age at first reproduction is an important life-history trait that is not well-documented in birds. Delayed probability of maturation indicates a slower position on the slow-fast life-history continuum (Charlesworth 1994; Péron *et al*. 2010; Pianka 1970; Stearns 1992). The age at which individuals mature represents the balance between current versus future reproductive output (Becker *et al*. 2008; Brommer *et al*. 1998). When the costs of reproduction early in life exceed the benefits of reproduction later in life for long-lived birds, delayed maturation is expected (Reed *et al*. 2008). Birds that delay early-life reproduction often exhibit delayed development of adult plumage by developing a subadult plumage (Conover *et al*. 2000; Procter-Gray and Holmes 1981; Reed *et al*. 2008). Two-year-old pelicans have different plumage and different bill knob morphology than breeding adults (Evans and Knopf 2004). Pelicans are not known to breed as two-year-olds (Evans and Knopf 2004). Williams and Joanen (1974) noted that brown pelicans (*Pelecanus occidentalis*) nested at three years of age, Sloan (1982) reported three-year-old pelicans that dispersed from North Dakota nesting in Minnesota, and Chapman and Chapman (1990) report a three-year-old nesting in a non-migratory population. However, we quantified the probability of nesting with age from the recapture data, and the most parsimonious statistical model characterizing that probability indicates that pelicans at Marsh Lake are unlikely to breed until they are at least five years of age.

Because pelicans mature slowly and have low annual reproductive potential, high adult survival is critical for sustaining populations (Sæther *et al*. 2013). However age of adults does not predict the timing of reproduction. We conjecture that adults balance the benefits of nesting on low predation risk sites against the costs of increased risk of loss from flooding at Marsh Lake that might be temporally-driven by spring run-off. How predation risk varies through time at Marsh Lake and other pelican colonies is not known. In addition, information on the movements and ecology of subadult pelicans are needed to fully understand factors affecting recruitment, dispersal, and time of first breeding.

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GENERAL SUMMARY

The American white pelican (*Pelecanus erythrorhynchos*) is a species of management interest in Minnesota and the surrounding region (Hagen *et al*. 2005; SDGFP 2005; MN DNR 2006), but there are gaps in information on their basic biology and reproductive ecology (Evans and Knopf 2004) which limit the ability to formulate effective management strategies. The breeding colony of American white pelicans on Marsh Lake in Big Stone County, Minnesota is among the largest in North America (DiMatteo *et al*. 2015), and management of this colony could have significant implications for the continental population. In addition, knowledge of the ecology of the Marsh Lake colony could provide insight into the ecology of other American white pelican and mixed-species waterbird colonies in the Upper Midwest. For migratory birds reproducing in temperate regions, timing of nesting can affect recruitment. The timing of nest initiation has been linked to clutch and egg size (Krapu *et al*. 2002; Gladbach *et al*. 2010; Tsuboi and Ashizawa 2011; Cotter *et al*. 2013; Blomberg *et al*. 2014) and to chick size, growth, and survival (Catry *et al*. 1998; Arnold *et al*. 2004; Ritz *et al*. 2005; Hipfner *et al*. 2010). In general, individuals that nest earlier produce offspring that are more likely to survive than those that nest later (Arnold *et al*. 2006; Harris *et al*. 2007; Minias *et al*. 2013; Saunders *et al*. 2014), but there are exceptions (e.g., Braasch *et al*. 2009).

It has been assumed that American white pelicans prefer to nest on islands to avoid disturbance during the breeding season (Evans and Knopf 2004). Vermeer (1970) suggested the availability of remote, isolated islands determined the distribution of American white pelican colonies in Canada, and that the refuge from mammalian predators provided by nesting on those islands outweighed the costs of flight to foraging areas distant from those islands (i.e., the island hypothesis). Analysis of nest distribution of American white pelicans at Marsh Lake indicated that pelicans disproportionately nest on insular habitat (supporting the island hypothesis), but insular habitat availability is influenced by seasonal variability in spring river flow. Moreover, nest densities in preferred habitats at Marsh Lake become saturated each year, which is consistent with density-dependent regulation of nesting population size. In addition, annual census data of the Marsh Lake breeding colony indicates the population size has reached a plateau since 2000, which also supports a density dependence hypothesis. Planned changes in control structures and water management on the Upper Minnesota River (which includes Marsh Lake) will allow manipulation of lake levels for the first time, and therefore present the opportunity to develop management plans providing availability of specific amounts of preferential nesting habitat on the lake. Results from this study could be used to provide quantitative estimates for nest numbers on preferred sites under a variety of water management scenarios, which would be a significant resource for managers developing those scenarios.

The typical trend for water flow in the Upper Minnesota River basin is for higher flows and water levels earlier in the spring compared to reduced flows and lower water levels as spring transitions into summer. Therefore, preferred nesting islands at Marsh Lake are more likely to be above the waterline, and have more habitat above water, as spring progresses. As such, American white pelicans arriving or nesting later would be more likely to encounter preferred nesting habitat that is not inundated. Therefore later nesting may have benefits in terms of habitat availability. However, seasonal declines in reproductive success or offspring performance in other avian species (Catry *et al*. 1998; Arnold *et al*. 2004; Harris *et al*. 2007; Gladbach *et al*. 2010) suggest there may be costs associated with later nesting. Indeed, within-breeding season variation in patterns of American white pelican chick size at hatching and growth at Marsh Lake exceeded variation among breeding seasons. How within-breeding season variation in chick size and development relates to survival, recruitment and maturation in American white pelicans (or other long-lived birds that produce one clutch per breeding season) is not known. Results from my research at Marsh Lake suggest there are tradeoffs between timing of arrival or nest initiation and chick performance. For example, while later nesting could increase the availability of preferred nesting habitat, earlier nesting may result in less competition for nest sites, alter chick size at hatching and post-hatching growth and provides more time for offspring to develop in preparation for fall migration. Changes in the timing of migration for some American white pelicans (Sovada *et al*. 2014) and other avian species (Jenni and Kéry 2003; Jonzen *et al*. 2006; Gunnarsson and Tómasson 2011; Knudsen *et al*. 2011; Chambers *et al*. 2014) likely affect the timing of arrival or nest initiation, so my findings on within-season variation in offspring size and growth of American white pelicans at Marsh Lake have broad implications.

Age has also frequently been linked to timing of nesting in migratory birds, with older individuals nesting earlier than younger individuals (Haymes and Blokpoel 1980; Nisbet *et al*. 1984; Massey and Fancher 1989; Wendeln *et al*. 2000; Devries *et al*. 2008; Hipfner *et al*. 2010; Bulluck *et al*. 2013; Claassen *et al*. 2014). Within American white pelican colonies, nests are segregated into spatially and temporally distinct groups or subcolonies (Knopf 1979), and age has been proposed as the mechanism responsible for this distribution, with older individuals thought to initiate nests before younger individuals (O'Malley and Evans 1980; Orr 1980). However, this hypothesis had not been tested prior to my study. I found no evidence of a relationship between age and timing of nesting for American white pelicans at Marsh Lake. Moreover, band returns suggested that individuals are unlikely to nest at Marsh Lake until at least five years old. This could be a function of density-dependent natal dispersal, in which younger birds are more likely to disperse to nest in other areas upon reaching breeding age.

Density-dependent dispersal has been observed in a number of birds and mammals (Greenwood 1980; Matthysen 2005), and at least one other colonial-nesting waterbird (Kim *et al*. 2009). If density-dependent dispersal dynamics are occurring, management implications for the Marsh Lake colony are substantial, as the colony may be serving as a source of new individuals for other colonies in the region, including new colonies. My findings highlight a need for more information on the movements and distribution of young American white pelicans.

Outcomes from this study may also provide the parameters for developing population models for American white pelicans. My study provides current data on reproductive success, chick growth, adult survival, and maturation rates, which are key components in any population model. Together with models for river flow, a comprehensive model for the population dynamics of the Marsh Lake colony could be developed, providing resource managers with an important new approach to evaluating plans for habitat and water management.

LITERATURE CITED

Adkins, J. Y., D. E. Lyons, P. J. Loschl, D. D. Roby, K. Collis, A. F. Evans, and N. J. Hostetter. 2014. Demographics of piscivorous colonial waterbirds and management implications for ESA-listed salmonids on the Columbia Plateau. Northwest Science 88:344–359.

Adolphson, D. G. and M. Adolphson. 1968. Size, distribution, and population of three colony nesting species in South Dakota. South Dakota Bird Notes 20:4-10.

Allen, J. A. 1910. Check-list of North American birds. Third Edition. American Ornithologists' Union, New York.

Anderson, D. W. and D. T. King. 2005. Introduction: biology and conservation of the American white pelican. Waterbirds (Special Publication 1) 28:1-8.

Anteau, M. J., T. L. Shaffer, M. H. Sherfy, M. A. Sovada, J. H. Stucker, and M. T. Wiltermuth. 2012. Nest survival of piping plovers at a dynamic reservoir indicates an ecological trap for a threatened population. Oecologia 170:1167–1179.

Anteau, M. J., T. L. Shaffer, M. T. Wiltermuth, and M. H. Sherfy. 2014. Landscape selection by piping plovers has implications for measuring habitat and population size. Landscape Ecology 29:1033–1044.

Arnold, J. M., J. J. Hatch, and I. C. T. Nisbet. 2004. Seasonal declines in reproductive success of the common tern *Sterna hirundo*: timing or parental quality? Journal of Avian Biology 35:33-45.

Arnold, J. M., J. J. Hatch, and I. C. T. Nisbet. 2006. Effects of egg size, parental quality and hatch-date on growth and survival of common tern *Sterna hirundo* chicks. Ibis 148:98-105.

Arnold, T. W., D. Shizuka, B. E. Lyon, J. T. Pelayo, K. R. Mehl, J. J. Traylor, W. L. Reed, and C. L. Amundson. 2011. Use of nape tags for marking offspring of precocial waterbirds. Waterbirds 34:312-318.

Baumhofer, J. A. 1972. White pelicans nesting at Heron Lake. Loon 44:124.

Becker, P. H., T. Dittmann, J.-D. Ludwigs, B. Limmer, S. C. Ludwig, C. Bauch, A. Braasch, and H. Wendeln. 2008. Timing of initial arrival at the breeding site predicts age at first reproduction in a long-lived migratory bird. Proceedings of the National Academy of Sciences 105:12349-12352.

Behle, W. H. 1958. The bird life of Great Salt Lake. University of Utah Press, Salt Lake City, Utah.

Benowitz-Fredericks, Z. M. and A. S. Kitaysky. 2005. Benefits and costs of rapid growth in common murre chicks *Uria aalge*. Journal of Avian Biology 36:287-294.

Bent, A. C. 1922. Life histories of North American petrels and pelicans and their allies. U. S. National Museum Bulletin 121. Government Printing Office, Washington.

Bêty, J., G. Gauthier, and J. F. Giroux. 2003. Body condition, migration, and timing of reproduction in snow geese: a test of the condition-dependent model of optimal clutch size. American Naturalist 162:110-121.

Blomberg, E. J., D. Gibson, M. T. Atamian, and J. S. Sedinger. 2014. Individual and environmental effects on egg allocations of female greater sage-grouse. Auk 131:507-523.

Boellstorff, D. E., D. W. Anderson, H. M. Ohlendorf, and E. J. O'Neill. 1988. Reproductive effects of nest-marking studies in an American white pelican colony. Colonial Waterbirds 11:215–219.

Boellstorff, D. E., H. M. Ohlendorf, D. W. Anderson, E. J. O'Neill, J. O. Keith, and R. M. Prouty. 1985. Organochlorine chemical residues in white pelicans and western grebes from the Klamath basin, California. Archives of Environmental Contamination and Toxicology 14:485–493.

Both, C., R. G. Bijlsma, and M. E. Visser. 2005. Climatic effects on timing of spring migration and breeding in a long-distance migrant, the pied flycatcher *Ficedula hypoleuca*. Journal of Avian Biology. 36:368-373.

Braasch, A., C. Schauroth, and P. H. Becker. 2009. Post-fledging body mass as a determinant of subadult survival in common terns *Sterna hirundo*. Journal of Ornithology 150:401-407.

Braud, D. 1997. Pelicans of Marsh Lake. Minnesota Volunteer 60:8–17.

Breckenridge, W. J. 1968. Minnesota nesting of white pelicans. Loon 40:100.

Brommer, J. E., H. Pietiainen, and H. Kolunen. 1998. The effect of age at first breeding on Ural owl lifetime reproductive success and fitness under cyclic food conditions. Journal of Animal Ecology 67:359-369.

Buenau, K. E., T. L. Hiller, and A. J. Tyre. 2014. Modelling the effects of river flow on population dynamics of piping plovers (*Charadrius melodus*) and least terns (*Sternula antillarum*) nesting on the Missouri River. River Research and Applications 30:964–975.

Bullis, O. 1892. Ornithology. Annual report of the Minnesota State Horticultural Society 20:360-364.

Bulluck, L., S. Huber, C. Viverette, and C. Blem. 2013. Age-specific responses to spring temperature in a migratory songbird: older females attempt more broods in warmer springs. Ecology and Evolution 3:3298-3306.

Bunnell, F. L., D. Dunbar, L. Koza, and G. Ryder. 1981. Effects of disturbance on the productivity and numbers of white pelicans in British Columbia: observations and models. Colonial Waterbirds 4:2–11.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York.

Cantwell, G. G. 1890. A list of the birds of Minnesota. Ornithologist and Oologist 15:129-137.

Carney, K. M. and W. J. Sydeman. 1999. A review of human disturbance effects on nesting colonial waterbirds. Waterbirds 22:68–79.

Carver, J. 1778. Travels through the interior parts of North America. J. Carver, London.

Catry, P., N. Ratcliffe, and R. W. Furness. 1998. The influence of hatching date on different life-history stages of great skuas *Catharacta skua*. Journal of Avian Biology 29:299-304.

Chambers, L. E., L. J. Beaumont, and I. L. Hudson. 2013. Continental scale analysis of bird migration timing: influences of climate and life history traits—a generalized mixture model clustering and discriminant approach. International Journal of Biometeorology 58:1147-1162.

Chapman, B. R. and S. S. Chapman. 1990. Patagial tag causes white pelican death. North American Bird Bander 15:17.

Chapman, F. M. 1896. Handbook of birds of eastern North America. Third Edition. D. Appleton and Company, New York.

Chapman, F. M. 1908. Camps and cruises of an ornithologist. D. Appleton and Company, New York.

Chapman, F. M. and C. A. Reed. 1903. Color key to North American birds. Doubleday, Page and Company, New York.

Charlesworth, B. 1994. Evolution in age-structured populations. Second edition. Cambridge University Press, Cambridge, England; New York.

Christians, J. K., M. Evanson, and J. J. Aiken. 2001. Seasonal decline in clutch size in European starlings: a novel randomization test to distinguish between the timing and quality hypotheses. Journal of Animal Ecology. 70:1080-1087.

Claassen, A. H., T. W. Arnold, E. A. Roche, S. P. Saunders, and F. J. Cuthbert. 2014. Factors influencing nest survival and renesting by piping plovers in the Great Lakes region. Condor 116:394-407.

Cohn, J. P. 2006. Chase Lake pelicans make a comeback. BioScience 56:704.

Conover, M. R., J. G. Reese, and A. D. Brown. 2000. Costs and benefits of subadult plumage in mute swans: testing hypotheses for the evolution of delayed plumage maturation. American Naturalist 156:193-200.

Cooch, E. G., D. B. Lank, A. Dzubin, R. F. Rockwell, and F. Cooke. 1991. Body size variation in lesser snow geese: environmental plasticity in gosling growth rates. Ecology 72:503-512.

Cooke, W. W. 1888. Report on bird migration in the Mississippi Valley in the years 1884 and 1885. U. S. Department of Agriculture Division of Economic Ornithology Bulletin 2.

Cory, C. B. 1909. The birds of Illinois and Wisconsin. Chicago Field Museum of Natural History. Zoological Series 9.

Cotter, R. C., R. J. Hughes, P. May, P. Novalinga, J. Johannes, J. J. Hindman, and P. I. Padding. 2013. Breeding biology of Atlantic population Canada geese in Nunavik, Northern Quebec. Arctic 66:301-311.

Coues, E. 1877. Birds of the North-west. Estes and Lauriat, Boston.

Coues, E. (ed.). 1897. New light on the early history of the Greater Northwest: the manuscript journals of Alexander Henry and of David Thompson, 1799-1814: exploration and adventure among Indians on the Red, Saskatchewan, Missouri and Columbia rivers. (Volume 1). Francis P. Harper, New York.

Covert, C. C., A. H. Horton, and R. H. Bolster. 1912. Surface water supply of the United States 1910: IV. St. Lawrence River basin. U. S. Geological Survey Water-supply Paper 284, Washington.

Cronin, D. W. 1895. Historico-geographical chart of the Upper Mississippi River. Francis P. Harper, New York.

Currier, E. S. 1904. Summer birds of the Leech Lake region, Minnesota. Auk 21:29-44.

Danchin, E. and R. H. Wagner. 1997. The evolution of coloniality: the emergence of new perspectives. Trends in Ecology and Evolution 12:342-347.

David, J. H. M., P. Cury, R. J. M. Crawford, R. M. Randall, L. G. Underhill, and M. A. Meyer. 2003. Assessing conservation priorities in the Benguela ecosystem, South Africa: analysing predation by seals on threatened seabirds. Biological Conservation 114:289-292.

Dawson, R. D. and R. G. Clark. 2000. Effects of hatching date and egg size on growth, recruitment, and adult size of lesser scaup. Condor 102:930-935.

Deane, R. 1923. Extracts from the field notes of George B. Sennett. Auk 40:626-633.

Devries, J. H., R. W. Brook, D. W. Howerter, and M. G. Anderson. 2008. Effects of spring body condition and age on reproduction in mallards (*Anas platyrhynchos*). Auk 125:618-628.

Diem, K. L. and B. H. Pugesek. 1994. American white pelicans at the Molly Islands, in Yellowstone National Park: twenty-two years of boom-and-bust breeding, 1966-87. Colonial Waterbirds 17:130-145.

DiMatteo, J. J., J. E. Wollenberg, and M. E. Clark. 2015. Implications of spring water levels on the production of American white pelicans nesting at Marsh Lake, Minnesota. Journal of Wildlife Management 79:1129-1140.

Dorr, B., D. T. King, J. B. Harrel, P. Gerard, and M. G. Spalding. 2005. The use of culmen length to determine sex of the American white pelican. Waterbirds (Special Publication 1) 28:102-106.

Eason, P., B. Rabea, and O. Attum. 2012. Island shape, size, and isolation affect nest-site selection by little terns. Journal of Field Ornithology 83:372–380.

Eckert, K. R. 1971. The summer season. Loon 43:114.

Erickson, A. B. and R. Upson. 1938. 1938 Minnesota nesting records. Flicker 10:4.

Evans, R. M. 1969. Specific gravity of white pelican eggs. Auk 86:560-561.

Evans, R. M. 1996. Hatching asynchrony and survival of insurance offspring in an obligate brood reducing species, the American white pelican. Behavioral Ecology and Sociobiology 39:203-209.

Evans, R. M. and F. L. Knopf. 2004. American white pelican (*Pelecanus erythrorhynchos*). Account 057 *in* A. Poole, editor. The birds of North America online. Cornell Laboratory of Ornithology, Ithaca, New York.

Evans, R. M. and B. F. McMahon. 1987. Within-brood variation in growth and condition in relation to brood reduction in the American white pelican. Wilson Bulletin 99:190-201.

Fall, B. 1994. Newly discovered American white pelican colonies in southern Minnesota: Minnesota Lake. Loon 66:111-113.

Farrar, M. 1880. Five years in Minnesota. Sampson Low, Marston, Searle, and Rivington, London.

Finch, T., J. W. Pearce-Higgins, D. I. Leech, and K. L. Evans. 2014. Carry-over effects from passage regions are more important than breeding climate in determining the breeding phenology and performance of three avian migrants of conservation concern. Biodiversity and Conservation 23:2427-2444.

Findholt, S. L. and S. H. Anderson. 1995. Foraging areas and feeding habitat selection of American white pelicans (*Pelecanus erythrorhynchos*) nesting at Pathfinder Reservoir, Wyoming. Colonial Waterbirds 18:47–57.

Gaudet, C. A. and C. M. Somers. 2014. American white pelicans and recreational boaters on lakes of the North American Great Plains: habitat use overlap. Open Ornithology Journal 7:1–10.

Gille, U., F. V. Salomon, and J. Ronnert. 1999. Growth of the digestive organs in ducks with considerations on their growth in birds in general. British Poultry Science 40:194-202.

Gladbach, A., D. J. Gladbach, and P. Quillfeldt. 2010. Seasonal clutch size decline and individual variation in the timing of breeding are related to female body condition in a non-migratory species, the upland goose *Chloephaga picta leucoptera*. Journal of Ornithology 151:817-825.

Goss, N. S. 1891. History of the birds of Kansas. George W. Crane and Company, Topeka, Kansas.

Green, A. J. 2001. Mass/length residuals: Measures of body condition or generators of spurious results? Ecology 82:1473-1483.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28:1140-1162.

Greño, J. L., E. J. Belda, and E. Barba. 2008. Influence of temperatures during the nestling period on post-fledging survival of great tit *Parus major* in a Mediterranean habitat. Journal of Avian Biology 39:41-49.

Guertin, D. S. 1984. Colonial waterbirds in Minnesota. Minnesota Department of Natural Resources Nongame Wildlife Program Report, St. Paul, Minnesota.

Gunnarsson, T. G. and G. Tómasson. 2011. Flexibility in spring arrival of migratory birds at northern latitudes under rapid temperature changes. Bird Study 58:1-12.

Hagen, S. K., P. T. Isakson, and S. R. Dyke. 2005. North Dakota comprehensive wildlife conservation strategy. North Dakota Game and Fish Department, Bismarck, North Dakota.

Harris, M. P., M. Frederiksen, and S. Wanless. 2007. Within- and between-year variation in the juvenile survival of common guillemots *Uria aalge*. Ibis 149:472-481.

Hatch, P. L. 1874. Report on the birds of Minnesota. Bulletin of the Minnesota Academy of Natural Sciences 1:43-68.

Hatch, P. L. 1881. Ornithology. Biennial report of the Board of Regents of the University of Minnesota for the fiscal years 1879 and 1880 12:449-462.

Hatch, P. L. 1892. First report of the State Zoologist, accompanied with notes on the birds of Minnesota for the fiscal years 1879 and 1880. Harrison and Smith, Printers, Minneapolis.

Haymes, G. T. and H. Blokpoel. 1980. The influence of age on the breeding biology of ring-billed gulls. Wilson Bulletin 92:221-228.

Henry, A. 1809. Travels and adventures in Canada and the Indian territories, between the years 1760-1776. I. Riley, New York.

Hiemenz, N. 1994. Newly discovered American white pelican colonies in southern Minnesota: Lake Johanna. Loon 66:112-113.

Hipfner, J. M., L. A. McFarlane-Tranquilla, and B. Addison. 2010. Experimental evidence that both timing and parental quality affect breeding success in a zooplanktivorous seabird. Auk 127:195-203.

Hirose, F., K. Kazama, M. Ito, and Y. Watanuki. 2012. Accelerated growth rates in late-hatched rhinoceros auklet *Cerorhinca monocerata* chicks depend on food conditions and growth stage: an experimental approach. Ibis 154:296-306.

Hornaday, W. T. 1913. Our vanishing wild life. New York Zoological Society, New York.

Hunt, K. L., N. Taygan, D. H. Catlin, J. H. Felio, and J. D. Fraser. 2013. Demography of snowy plovers (*Charadrius nivosus*) on the Missouri River. Waterbirds 36:220–224.

Jakubas, D. and K. Wojczulanis-Jakubas. 2014. Consequences of experimental clutch enlargement in a High Arctic single-egg layer, the little auk (*Alle alle*). Canadian Journal of Zoology 92:681-687.

Janssen, R. B. 1974. New nesting location for the white pelican in Minnesota. Loon 46:36-37.

Janoschek, A. 1957. Das reaktionskinetische Grundgesetz und seine Beziehungen zum Wachstums- und Ertragsgesetz. Statistiche Vierteljahresschrift 10:25-37.

Johnson, G., N. Panella, K. Hale, and N. Komar. 2010. Detection of West Nile virus in stable flies (Diptera: Muscidae) parasitizing juvenile American white pelicans. Journal of Medical Entomology 47:1205–1211.

Johnson, J., R. F. and N. F. Sloan. 1976. The effects of human disturbance on the white pelican colony at Chase Lake National Wildlife Refuge, North Dakota. Inland Bird Banding News 48:163–170.

Johnson, R. F. and N. F. Sloan. 1978. White pelican production and survival of young at Chase Lake National Wildlife Refuge, North Dakota. Wilson Bulletin 90:346-352.

Jonzén, N., A. Lindén, T. Ergon, E. Knudsen, J. O. Vik, D. Rubolini, D. Piacentini, C. Brinch, F. Spina, L. Karlsson, M. Stervander, A. Andersson, J. Waldenström, A. Lehikoinen, E. Edvardsen, R. Solvang, and N. C. Stenseth. 2006. Rapid advance of spring arrival dates in long-distance migratory birds. Science 312:1959-1961.

Jovani, R. and V. Grimm. 2008. Breeding synchrony in colonial birds: from local stress to global harmony. Proceedings of the Royal Society: Biological Sciences 275:1557-1563.

Kasprzykowski, Z., M. Polak, and P. Chylarecki. 2014. Effects of weather conditions, time of breeding, brood size and hatching order on Eurasian bittern nestling growth in a food-rich fishpond habitat. Annales Zoologici Fennici 51:477-487.

Keith, J. O. 2005. An overview of the American white pelican. Waterbirds (Special Publication 1) 28:9-17.

Kenni, L. and M. Kéry. 2003. Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. Proceedings of the Royal Society: Biological Sciences 270:1467-1471.

Kim, S., R. Torres, and H. Drummond. 2009. Simultaneous positive and negative density-dependent dispersal in a colonial bird species. Ecology 90:230-239.

King, D. T. and D. W. Anderson. 2005. Recent population status of the American white pelican: a continental perspective. Waterbirds (Special Publication 1) 28:48–54.

King, D. T. and S. J. Werner. 2001. Daily activity budgets and population size of American white pelicans wintering in south Louisiana and the delta region of Mississippi. Waterbirds 24:250-254.

Knopf, F. L. 1979. Spatial and temporal aspects of colonial nesting of white pelicans. Condor 81:353-363.

Knudsen, E., A. Lindén, C. Both, N. Jonzén, F. Pulido, N. Saino, W. J. Sutherland, L. A. Bach, T. Coppack, T. Ergon, P. Gienapp, J. A. Gill, O. Gordo, A. Nilsson, G. Péron, E. Ranta, D. Rubolini, T. H. Sparks, F. Spina, C. E. Studds, S. A. Sæther, P. Tryjanowski, and N. C. Stenseth. 2011. Challenging claims in the study of migratory birds and climate change. Biological Reviews 86:928-946.

Koczur, L. M., A. E. Munters, S. A. Heath, B. M. Ballard, M. C. Green, S. Dinsmore, and F. Hernandez. 2014. Reproductive success of the American oystercatcher (*Haematopus palliatus*) in Texas. Waterbirds 37:371–380.

Krapu, G. L., G. A. Sargeant, and A. E. H. Perkins. 2002. Does increasing daylength control seasonal changes in clutch sizes of northern pintails (*Anas acuta*)? Auk 119:498-506.

Krause, E. T. and M. Naguib. 2011. Compensatory growth affects exploratory behaviour in zebra finches, *Taeniopygia guttata*. Animal Behaviour 81:1295-1300.

Krider, J. 1879. Forty years notes of a field ornithologist. Joseph H. Weston, Philadelphia.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

Laliberte A. S. and W. J. Ripple. 2003. Automated wildlife counts from remotely sensed imagery. Wildlife Society Bulletin 31:362–371.

Lanman, C. 1847. A summer in the wilderness; embracing a canoe voyage up the Mississippi and around Lake Superior. D. Appleton and Company, New York.

Lano, A. 1922. White pelican (*Pelecanus erythrorhynchos*) nesting in Minnesota. Auk 39:105.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals - a unified approach with case-studies. Ecological Monographs 62:67-118.

Lee, F. B. 1951. Notes of the white pelican. Flicker 23:55-56.

Lies, M. F. and Behle, W. H. 1966. Status of the white pelican in the United States and Canada through 1964. Condor 68:279-292.

Lindholm, A., G. Gauthier, and A. Desrochers. 1994. Effects of hatch date and food supply on gosling growth in Arctic-nesting greater snow geese. Condor 96:898-908.

Lingle, G. R. and N. F. Sloan. 1979. Sexing and aging criteria for the white pelican. Prairie Naturalist 116:83-88.

Lingle, G. R. and N. F. Sloan. 1980. Food habits of white pelicans during 1976 and 1977 at Chase Lake National Wildlife Refuge, North Dakota. Wilson Bulletin 92:123-125.

MacCarone, A. D., J. N. Brzorad, and K. C. Parsons. 1993. Nest-site selection by herring gulls in an urban estuary. Colonial Waterbirds 16:216-220.

Madden, E. M. and M. Restani. 2005. History and breeding ecology of the American white pelican at Medicine Lake National Wildlife Refuge, Montana. Waterbirds (Special Publication 1) 28:23-26.

Magnus, L. T. 1960. Recent nesting of the white pelican in the Lake of the Woods area. Flicker 32:62.

Makhado, A. B., R. J. M. Crawford, and L. G. Underhill. 2006. Impact of predation by Cape fur seals *Arctocephalus pusillus pusillus* on Cape gannets *Morus capensis* at Malgas Island, Western Cape, South Africa. African Journal of Marine Science 28:681-687.

Makhado, A. B., R. J. M. Crawford, L. J. Waller, and L. G. Underhill. 2013. An assessment of the impact of predation by Cape fur seals *Arctocephalus pusillus pusillus* on seabirds at Dyer Island, South Africa. Ostrich 84:191-198.

Massey, B. W. and J. M. Fancher. 1989. Renesting by California least terns. Journal of Field Ornithology 60:350-357.

Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. Ecography 28:403-416.

Mayfield, H. 1975. Suggestions for calculating nest success. Wilson Bulletin 73:255–261.

McChesney, C. E. 1879. Notes on the birds of Fort Sisseton, Dakota Territory. Bulletin of the U. S. Geological and Geographical Survey of the Territories 5:71-103.

Meeker, D. W. 1907. Disappearing birds and game birds. Pages 186-190 *in* Wilcox, A. H. A pioneer history of Becker County Minnesota. Pioneer Press Company, St. Paul, Minnesota.

Mindwell, S. 1901. The American white pelican. Birds and Nature 9:110-114.

Minias, P., T. Janiszewski and B. Lesner. 2013. Center-periphery gradients of chick survival in the colonies of whiskered terns *Chlidonias hybrida* may be explained by the variation in the maternal effects of egg size. Acta Ornithologica 48:179-186.

Minnesota Department of Natural Resources (MN DNR). 1997. Lac qui Parle Area management plan. Minnesota Department of Natural Resources, St. Paul, Minnesota.

Minnesota Department of Natural Resources (MN DNR). 2006. Tomorrow’s habitat for the wild and rare: an action plan for Minnesota wildlife comprehensive wildlife conservation strategy. Minnesota Department of Natural Resources, St. Paul, Minnesota.

Moreno-Matiella, L. A. and D. W. Anderson. 2005. Water level variation and its effects on nesting habitat configuration and availability for the American white pelican at Clear Lake Reservoir, California. Waterbirds (Special Publication 1) 28:73-82.

Mortensen, S. and J. Ringle. 2007. Changes in colonial waterbird populations on Leech Lake. Loon 79:130-142.

Mortensen, S. and J. Ringle. 2008. Double-crested cormorant conflict management and research on Leech Lake: 2008 annual report. Fish, Wildlife, and Plant Resources Program, Division of Resources Management, Leech Lake Band of Ojibwe. Cass Lake, Minnesota.

Murphy, E. C. and J. C. Tracy. 2005. Century-long impacts of increasing human water use on numbers and production of the American white pelican at Pyramid Lake, Nevada. Waterbirds (Special Publication 1) 28:61–72.

Natural Resources Conservation Service (NRCS). 2000. Official soil series descriptions: Big Stone series., U. S, Department of Agriculture, Lincoln, Nebraska.

Nisbet, I. C. T., J. M. Winchell, and A. E. Heise. 1984. Influence of age on the breeding biology of common terns. Colonial Waterbirds 7:117-126.

O'Malley, J. B. E. and R. M. Evans. 1980. Variations in measurements among white pelican eggs and their use as a hatch date predictor. Canadian Journal of Zoology 58:603-608.

O'Malley, J. B. E. and R. M. Evans. 1982. Flock formation in white pelicans. Canadian Journal of Zoology 60:1024-1031.

Oomen, R. A., M. W. Reudink, J. J. Nocera, C. M. Somers, M. C. Green, and C. J. Kyle. 2011. Mitochondrial evidence for panmixia despite perceived barriers to gene flow in a widely distributed waterbird. Journal of Heredity 102:584-592.

Orr, D. J. 1980. Ecology of a white pelican colony in Big Stone County, Minnesota. Thesis, St. Cloud State University, St. Cloud, Minnesota.

Öst, M. and B. B. Steele. 2010. Age-specific nest-site preference and success in eiders. Oecologia 162:59-69.

Owen, D. D. 1852. Report of a geological survey of Wisconsin, Iowa, and Minnesota. Lippincott, Grambo, and Company, Philadelphia.

Penney, R. L. and G. Lowry. 1967. Leopard seal predation on Adélie penguins. Ecology 48:878-882.

Péron, G., O. Gimenez, A. Charmantier, J.-M. Gaillard, and P.-A. Crochet. 2010. Age at the onset of senescence in birds and mammals is predicted by early-life performance. Proceedings of the Royal Society B-Biological Sciences 277:2849-2856.

Pianka, E. R. 1970. On r- and K-selection. American Naturalist 104:592-597.

Pietz, P. J., M. A. Sovada, C. M. Custer, T. W. Custer, and K. M. Johnson. 2008. Contaminant levels in eggs of American white pelicans, *Pelecanus erythrorhynchos*, from Chase Lake, North Dakota. Canadian Field-Naturalist 122:312–315.

Pike, Z. M. 1895. The expeditions of Zebulon Montgomery Pike (Volume 1). Coues Edition. Francis P. Harper, New York.

Procter-Gray, E. and R. T. Holmes. 1981. Adaptive significance of delayed attainment of plumage in male American redstarts: tests of two hypotheses. Evolution 35:742-751.

Reagan, A. B. 1917. Birds of the Bois Fort Indian Reservation and adjacent territory in Minnesota. Transactions of the Kansas Academy of Science 28:232-240.

Reed, J. M., E. M. Gray, D. Lewis, L. W. Oring, R. Coleman, T. Burr, and P. Luscomb. 1999. Growth patterns of Hawaiian stilt chicks. Wilson Bulletin 111:478-487.

Reed, T. E., L. E. B. Kruuk, S. Wanless, M. Frederiksen, E. J. A. Cunningham, and M. P. Harris. 2008. Reproductive senescence in a long-lived seabird: rates of decline in late-life performance are associated with varying costs of early reproduction. American Naturalist 171: E89-E101.

Reudink, M. W., C. J. Kyle, J. J. Nocera, R. A. Oomen. M. C. Green, and C. M. Somers. 2011. Panmixia on a continental scale in a widely distributed colonial waterbird. Biological Journal of the Linnean Society 102:583-592.

Ricklefs, R. E. 1967. A graphical method of fitting equations to growth curves. Ecology 48:978-983.

Ricklefs, R. E. 1969. Preliminary models for growth rates in altricial birds. Ecology 50:1031-1039.

Ricklefs, R. E. 1984. Components of variance in measurements of nestling European starlings (*Sturnus vulgaris*) in southeastern Pennsylvania. Auk 101:319-333.

Ritz, M. S., S. Hahn, and H. U. Peter. 2005. Factors affecting chick growth in the South Polar skua (*Catharacta maccormicki*): food supply, weather and hatching date. Polar Biology 29:53-60.

Roberts, T. S. and F. Benner. 1880. A contribution to the ornithology of Minnesota. Bulletin of the Nuttall Ornithological Club 5:11-20.

Roberts, T. S. 1907. List of birds of Becker County, Minnesota. Pages 159-186 *in* Wilcox, A. H. A pioneer history of Becker County Minnesota. Pioneer Press Company, St. Paul, Minnesota.

Roberts, T. S. 1919a. Water birds of Minnesota; past and present. Reprinted from Biennial Report of the State Game and Fish Commission of Minnesota, for the Biennial Period ending July 31, 1918. University of Minnesota, Minneapolis, Minnesota.

Roberts, T. S. 1919b. A review of the ornithology of Minnesota. Research Publications of the University of Minnesota 8. University of Minnesota, Minneapolis, Minnesota.

Roberts, T. S. 1932. The birds of Minnesota (Volume 1). University of Minnesota Press, Minneapolis, Minnesota.

Robinson, O. J. and J. J. Dindo. 2011. Egg success, hatching success, and nest-site selection of brown pelicans, Gaillard Island, Alabama, USA. Wilson Journal of Ornithology 123(2):386-390.

Rohwer, V. G. and S. Rohwer. 2013. How do birds adjust the time required to replace their flight feathers? Auk 130:699-707.

Rolfe, E. S. 1896. The passing of species. Oologist 13:42-44.

Ryder, R. A. 1981. Movements and mortality of white pelicans fledged in Colorado. Colonial Waterbirds 4:72-76.

Sæther, B.-E., T. Coulson, V. Grotan, S. Engen, R. Altwegg, K. B. Armitage, C. Barbraud, P. H. Becker, D. T. Blumstein, F. S. Dobson, M. Festa-Bianchet, J.-M. Gaillard, A. Jenkins, C. Jones, M. A. C. Nicoll, K. Norris, M. K. Oli, A. Ozgul, and H. Weimerskirch. 2013. How life history influences population dynamics in fluctuating environments. American Naturalist 182:743-759.

SAS Institute. 2001. SAS, Version 8.02. SAS Institute, Inc., Cary, North Carolina.

SAS Institute. 2012. JMP, Version 10.0. SAS Institute, Inc., Cary, North Carolina.

Saunders, S. P., T. W. Arnold, E. A. Roche, and F. J. Cuthbert. 2014. Age-specific survival and recruitment of piping plovers *Charadrius melodus* in the Great Lakes region. Journal of Avian Biology 45:437-449.

Schaller, G. B. 1964. Breeding behavior of the white pelican at Yellowstone Lake, Wyoming. Condor 66:3-23.

Schamber, J. L., J. S. Sedinger, and D. H. Ward. 2012. Carry-over effects of winter location contribute to variation in timing of nest initiation and clutch size in black brant (*Branta bernicla nigricans*). Auk 129:205-210.

Schladweiler, J. 1984. Expansion of the Marsh Lake pelican colony. Loon 56:136–137.

Schoolcraft, H. R. 1821. Narrative journal of travels through the northwestern regions of the United States extending from Detroit through the great chain of American lakes to the sources of the Mississippi River. E. and E. Hosford, Albany, New York.

Schoolcraft, H. R. 1834. Narrative of an expedition through the upper Mississippi to Itasca Lake. Harper and Brothers, New York.

Schreiber, R. W. 1976. Growth and development of nestling brown pelicans. Bird-Banding 47:19-39.

Sedinger, J. S. and P. L. Flint. 1991. Growth rate is negatively correlated with hatch date in black brant. Ecology 72:496-502.

Severinghaus, L. L. 1982. Nest site selection by the common tern *Sterna hirundo* on Oneida Lake, New York. Colonial Waterbirds 5:11-18.

Sherley, R. B., P. J. Barham, B. J. Barham, R. J. M. Crawford, B. M. Dyer, T. M. Leshoro, A. B. Makhado, L. Upfold, and L. G. Underhill. 2014. Growth and decline of a penguin colony and the influence on nesting density and reproductive success. Population Ecology 56:119–128.

Sidle, J. G., W. H. Koonz, and K. Roney. 1985. Status of the American white pelican: an update. American Birds 39:859–864.

Skinner, M. P. 1917. The birds of Molly Island, Yellowstone National Park. Condor 19:177-182.

Skorka, P., R. Martyka, J. D. Wojcik, and M. Lenda. 2014. An invasive gull displaces native waterbirds to breeding habitats more exposed to native predators. Population Ecology 56:359–374.

Sloan, N. F. 1973. Additional information on white pelican nesting colonies in the United States. Inland Bird Banding News 45:179-181.

Sloan, N. F. 1982. Status of breeding colonies of white pelicans in the United States through 1979. American Birds 36:250–254.

South Dakota Department of Game, Fish and Parks (SDGFP). 2005. South Dakota comprehensive wildlife conservation plan. South Dakota Department of Game, Fish and Parks, Pierre, South Dakota.

Sovada, M. A., L. D. Igl, P. J. Pietz, and A. J. Bartos. 2014. Influence of climate change on productivity of American white pelicans, *Pelecanus erythrorhynchos*. PLoS ONE 9:e83430.

Sovada, M. A., D. T. King, M. Erickson, and C. Gray. 2005. Historic and current status of the American white pelican breeding at Chase Lake National Wildlife Refuge, North Dakota. Waterbirds (Special Publication 1) 28:27-34.

Sovada, M. A., P. J. Pietz, K. A. Converse, D. T. King, E. K. Hofmeister, P. Scherr, and H. S. Ip. 2008. Impact of West Nile virus and other mortality factors on American white pelicans at breeding colonies in the northern plains of North America. Biological Conservation 141:1021–1031.

Sovada, M. A., P. J. Pietz, R. O. Woodward, A. J. Bartos, D. A. Buhl, and M. J. Assemacher. 2013. American white pelicans breeding in the northern plains-productivity, behavior, movements, and migration. U. S. Geological Survey Scientific Investigations Report 2013-5105.

Stahlecker, D. W. 2009. Fluctuations in nesting waterbird population in New Mexico's Rio Grande Valley: 1975-2007. NMOS Bulletin 37:40–53.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, New York.

Stier, A., V. A. Viblanc, S. Massemin-Challet, Y. Handrich, S. Zahn, E. R. Rojas, C. Saraux, M. Le Vaillant, O. Prud'homme, E. Grosbellet, J.-P. Robin, P. Bize, and F. Criscuolo. 2014. Starting with a handicap: phenotypic differences between early- and late-born king penguin chicks and their survival correlates. Functional Ecology 28:601-611.

Streets, T. H. 1877. Description of *Cambarus couesi*, a new species of crawfish from Dakota. Bulletin of the U. S. Geological and Geographical Survey of the Territories 3:803-804.

Takahashi, A., Y. Watanuki, K. Sato, A. Kato, N. Arai, J. Nishikawa, and Y. Naito. 2003. Parental foraging effort and offspring growth in Adelie penguins: does working hard improve reproductive success? Functional Ecology 17:590-597.

Trippe, T. M. 1870. Notes on the birds of Minnesota. Proceedings of the Essex Institute 6:113-119.

Tsuboi, J.-I. and A. Ashizawa. 2011. Seasonal decline of investment in egg production with increasing food abundance on the cormorant in a riverfront colony. Ornithological Science 10:113-118.

Upham, W. 1920. Minnesota geographic names: their origin and historic significance. Minnesota Historical Society, St. Paul, Minnesota.

U. S. Army Corps of Engineers (USACE). 2011. Feasibility report and environmental assessment: Marsh Lake ecosystem restoration project, Minnesota River. St. Paul District, U. S. Army Corps of Engineers, St. Paul, Minnesota.

U. S. G. S. Bird Banding Laboratory. 2013. Unpublished North American bird banding and band encounter data retrieved 19 April. Patuxent Wildlife Research Center, Laurel, Maryland.

U. S. House. 1845. Report intended to illustrate a map of the hydrographical basin of the Upper Mississippi River. By I. N. Nicollet. 28th Cong., 2nd sess. H. Rept. 52. Blair and Rives, Printers, Washington.

Upham, W. 1920. Minnesota geographic names: their origin and historic significance. Minnesota Historical Society, St. Paul, Minnesota.

Vermeer, K. 1970. Distribution and size of colonies of white pelicans, *Pelecanus erythrorhynchos*, in Canada. Canadian Journal of Zoology 48:1029–1032.

Ward, H. B. 1924. Banding white pelicans (with map). Condor 26:136-140.

Warren, W. W. 1885. History of the Ojibway Nation. Minnesota Historical Society, St. Paul, Minnesota.

Weidinger, K. 1997. Variations in growth of Cape petrel *Daption capense* chicks. Journal of Zoology 242:193-207.

Wendeln, H., P. H. Becker, and J. Gonzalez-Solis. 2000. Parental care of replacement clutches in common terns (*Sterna hirundo*). Behavioral Ecology and Sociobiology 47:382-392.

Westerskov, K. 1950. Methods for determining the age of game bird eggs. Journal of Wildlife Management 14:56-67.

White, G. C. and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–139.

Widmann, O. 1907. A preliminary catalog of the birds of Missouri. St. Louis Academy of Science, St. Louis, Missouri.

Williams, Jr., L. E. and T. Joanen. 1974. Age of first nesting in the brown pelican. Wilson Bulletin 86:279-280.

Winchell, N. H. 1899. The geology of Minnesota (Volume 4). University of Minnesota, St. Paul, Minnesota.

Wires, L. R., K. V. Haws, F. J. Cuthbert, N. Drilling and A. C. Smith. 2006. The double-crested cormorant and American white pelican in Minnesota: first statewide breeding census. Loon 78:63-73.

Wires, L. R., F. J. Cuthbert and D. Hamilton. 2011. The American white pelican and double-crested cormorant in Minnesota in 2010: distribution, abundance and population change. Final report: State Wildlife Grants Program, Minnesota Department of Natural Resources, St. Paul, Minnesota.

Youngworth, W. 1935. The birds of Fort Sisseton, South Dakota, a sixty year comparison. Wilson Bulletin 47:209-235.

Zoellick, B. W., H. M. Ulmschneider, B. S. Cade, and A. W. Stanley. 2004. Isolation of Snake River islands and mammalian predation of waterfowl nests. Journal of Wildlife Management 68:650–662.