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2019

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Ferguson, Treena L.; Rude, Brian J.; and King, D. Tommy, "American White Pelican (*Pelecanus erythrorhynchos*) Growth, Nutrition and Immunology" (2019). USDA National Wildlife Research Center - Staff Publications. 2246. https://digitalcommons.unl.edu/icwdm\_usdanwrc/2246

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# American White Pelican (*Pelecanus erythrorhynchos*) Growth, Nutrition and Immunology

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**Abstract.**—Limited information about nutrition exists on American White Pelicans (*Pelecanus erythrorhynchos*) from hatching to fledging. To detail immunity, metabolism and nutrition of juvenile American White Pelicans, during 22-23 July 2011, 103 samples of regurgitate matter were collected at five Chase Lake, North Dakota, USA, and three Bitter Lake, South Dakota, USA, sub-colonies. Regurgitate sample nutrient content was significantly different for organic matter (P = 0.012), crude protein (P = 0.001), neutral detergent fiber (P = 0.014), acid detergent fiber (P = 0.005) and energy (P = 0.034) between North (n = 5) and South (n = 3) Dakota American White Pelican colonies. Average concentrations of immunoglobulins Y ( $2.74 \pm 1.85 \text{ ng/mL}$ ) and A ( $9.04 \pm 9.41 \text{ ng/mL}$ ) demonstrated passive transfer of immunity in regurgitate. To enhance information on growth and morphology in hand-reared American White Pelicans (n = 8), a 9-week captive trial was also conducted raising chicks from hatching to fledging. Predictive models were created to describe chick growth for intake, body weight, culmen length and tarsus length. Data collected during this study enhances both American White Pelican general ecology and conservation with implications for both captive and wild bird management. *Received 15 August 2018, accepted 22 October 2018.* 

Key words.—American White Pelican, growth, immunology, metabolism, morphology, nutrition, *Pelecanus erythrorhynchos*.

Waterbirds 42(1): 61-69, 2019

As American White Pelicans (Pelecanus erythrorhynchos; hereafter, pelicans) continue to lose habitat and have a high mortality rate prior to fledging (Knopf 1976; Anderson and King 2005), it is important to consider future management and conservation of this species by further detailing information about growth, nutrition, immunology, caregiving, hand rearing and behavior. The composition of regurgitate fed to chicks is predominately partially digested fish with occasional crayfish (Cambarus) and salamanders (Ambystoma) (Sloan 1973). Schreiber (1976) estimated that 50,000 g of fish would be required to raise a Brown Pelican (Pelecanus occidentalis) from hatching to fledging. Although Hall (1925) estimated it would take 68,000 g of food to rear one American White Pelican fledgling, the specific daily intake requirements of pelican chicks from hatching to fledging have not been reported (Knopf and Evans 2004).

Passive transfer of immunoglobulin Y and A (hereafter, IgY and IgA) is a life history strategy for piscivorous birds because it enhances chick survival (McDade 2003). Little is known about pre-fledged pelican intake, nutritional requirements and metabolism of regurgitate and whether there is potential transfer of passive immunity through regurgitate (Knopf and Evans 2004). Knopf (1976) reported a 70% mortality rate for chicks up to 3 months of age due to various causes, including disease. Determining if and how many immunoglobulins are passively transferred to pelican chicks during rearing may be important for reducing prefledging mortality. Examining factors such as passive immunity, disease and energetics also provides insight into population success in terms of survival and recruitment.

Nearly half of the American White Pelican population is believed to nest in several large colonies in the northern plains of the USA, including Chase Lake, North Dakota, and Bitter Lake, South Dakota (King and Anderson 2005), and it is important to ensure sustained productivity from these colonies (Sovada *et al.* 2013). The loss of foraging habitat has been documented as an important limiting factor for pelican populations (Sovada *et al.* 2013). Movement data for pelicans from Chase Lake, North Dakota, and Bitter Lake, South Dakota, show that the foraging sites for these colonies differ (Sovada *et al.* 2013). Since foraging conditions directly impact fledgling production, we developed a study to determine if there were differences in the nutrient content of food (regurgitate) fed to chicks.

Our primary objective was to further detail immunity, metabolism, nutrition, morphology, behavior and disease in juvenile American White Pelicans. A secondary objective included determining what differences exist between juvenile American White Pelicans from North and South Dakota. Both objectives aim to enhance conservation and management of both captive and wild American White Pelicans.

### METHODS

#### Study Area

In 2011, we collected American White Pelican regurgitate samples from five Chase Lake, North Dakota ( $46^{\circ}$  59' 49" N, 99° 25' 53" W) and three Bitter Lake, South Dakota ( $45^{\circ}$  15' 43" N, 97° 24' 57" W) sub-colonies less than 1.6 km apart. In 2012, we collected eggs from several sub-colonies in Chase Lake, North Dakota, and Bitter Lake, South Dakota, for captive rearing of pelicans.

#### Wild Pelican Regurgitate

During 22-23 July 2011, we collected 103 samples of regurgitate matter. Samples were collected from stomach contents regurgitated on the ground by adult birds. The samples were placed into labeled sealable plastic bags, placed on ice and transported to a laboratory 2,189 km away. Prior to analysis, we pooled regurgitate samples by location and dried the samples at 60 °C in a forced air oven. After drying, we ground the regurgitate samples by passing them through a 2-mm screen in a mill (Thomas Wiley). All regurgitate samples were analyzed for dry matter, organic matter, neutral detergent fiber, fat and crude protein (Association of Official Analytical Chemists 2003). We also determined gross energy using an isoperibol oxygen bomb calorimeter (Parr Instrument Company).

In addition to regurgitate samples, we collected two serum samples from wild adult pelicans in Belzoni, Mississippi, USA (33° 10′ 52″ N, 90° 29′ 8″ W), which were used to validate testing for IgY and IgA samples collected in wild pelican regurgitate. Regurgitate and two serum samples were analyzed for concentrations of IgA and IgY, prior to dehydrating the samples. We compiled, blended in a mixer and then spun in a centrifuge (1,228 x g for 8 min) several wet ~10-g samples of regurgitate for each sub-colony before collecting supernatant for analysis.

#### Captive Rearing

During 23-27 May 2012, we collected pelican eggs and transported them to a Biosecurity Level 2 laboratory in coolers lined with protective dryfast foam padding and kept warm (37.5 °C) using a heating pad and a digital thermometer. We used a water-filled spray bottle to moisten the eggs every 4 hr. We incubated the eggs at 37.5 °C in a Sportsman Cabinet Egg Incubator 1502 equipped with a 19-L water reserve system and maintained 60% room humidity. Eggs began hatching soon after, with the first pelican emerging on 29 May 2012. Between 29 May and 2 June 2012, 36 additional eggs hatched. We maintained eggs and chicks for ~1 week. All eggs from North and South Dakota hatched, and all chicks appeared healthy. We randomly selected pelicans from North Dakota (n = 8) and South Dakota (n= 8) for captive trials. Of the 16 pelicans selected for the captive energetics trial, only the eight control birds are discussed here (four from North Dakota, four from South Dakota) as we artificially infected the other eight pelicans with a digenetic trematode (Bolbophorus dam*nificus*) to determine its effects on growing pelicans as part of another study (Ferguson 2016).

As egg pipping began, we reduced the room temperature to ~36.0 °C and monitored room temperature using a digital thermometer. Dehumidifiers kept the humidity of the room at ~60%. Once chicks emerged from the eggs, we did not feed them for 12-24 hr to allow the nutrients in the placental lining of the egg to be absorbed. We then placed chicks in plastic-coated wire cages (0.5 m x 0.5 m x 0.8 m) equipped with heating lamps covering ~30% of the cage 12-24 hr post-hatching. We also placed black foam pads 25 cm long and 15 cm wide inside the cages to allow chicks a softer alternative to wire flooring to reduce potential foot problems. Additional chicks that we did not select for use in the trial were euthanized using carbon dioxide following the American Veterinary Medical Association (AVMA) Guidelines on Euthanasia (American Veterinary Medical Association 2007).

We formulated a diet using data collected on the nutrient content of regurgitate matter collected in the colonies. Fish were cut up and/or thawed prior to each feeding. We fed pelican chicks an *ad libitum* diet composed of the following four types of fish: channel catfish (*Ictalurus punctatus*), specific pathogen free channel catfish (*Ictalurus punctatus*), gizzard shad (*Dorosoma cepedianum*) and menhaden (*Brevoortia patronus*). These four fish types were used because they are often consumed by pelicans wintering in the southeastern USA (King *et al.* 2010) and were readily available. Percentage of fish consumed was reported on a dry matter basis. Menhaden and gizzard shad were previously frozen, whereas both types of catfish were fed fresh. Nutrient metabolism, discussed on a dry matter basis, was determined by calculating the amount of nutrients fed using intake of all fish species and subtracting those excreted in feces.

Chicks began consuming pieces of fish (~2 g) ~24 hr after hatching. We bottle fed chicks water prior to and following each feeding. Once chicks were accepting whole fish (at approximately 3 weeks of age), we transported them to an outdoor research aviary approximately 1 km away. Each chick was banded and then placed in an individual metabolism pen (115.6 cm x 58.4 cm x 147.3 cm) customized for energetics work. Each pen was additionally equipped with a heat lamp covering ~30% of the pen, which the chicks could move in and out of to keep warm. Chicks remained inside their pens from ~3-9 weeks of age (fledging).

For the first week, we fed pelicans four times a day; for the next 2 weeks, we fed them three times a day; and from 3-9 weeks of age, the chicks were fed twice daily (once in the morning and once in the afternoon). We weighed the chicks once daily in the morning, prior to feeding. To measure body weight (g), we removed individuals from their cages and placed them in a large pre-weighed bin secured on a scale (Ohaus Champ SQ CQ10RW). We recorded food intake daily and measured culmen and tarsus lengths every 3 days. During measurements, one person held the bird while another measured using a dial caliper (to the nearest 0.02 mm) or a steel rule (to the nearest mm). We assigned each individual a fecal collection pan for both indoor and outdoor metabolism pens. Pre-weighed pans were placed underneath the wire flooring of each pen, and we collected feces at 1- to 2-week intervals. We collected feces by scraping fecal matter from each collection pan into pre-weighed plastic bags. Pans were then cleaned and reweighed prior to the next collection period.

We calculated both means and standard deviation (SD) for all individuals (n = 8) on a weekly basis except for fecal data, which we averaged over the entire trial. We also reported means and SD for hatching and final weights, culmen lengths and tarsus lengths. Predictive models were also created for daily body weight, daily intake, culmen length and tarsus length to allow for further growth analysis.

#### Statistical Analysis

We subjected regurgitate data to an analysis of variance (ANOVA) using the general linear model (GLM) procedures in statistical program SAS (SAS Institute, Inc. 2008). We considered individual pelican regurgitate the experimental unit and the response variable was nutrient content of regurgitate samples compiled by sub-colony, with each State (North Dakota or South Dakota) being the explanatory variable. When means differed (P <0.05), they were separated using Fisher's protected least significant difference. We made comparisons between North and South Dakota fecal data using an ANOVA in statistical program R (R Development Core Team 2016). Values were reported as mean  $\pm$  SE and a P < 0.05 was considered as statistically significant. Coefficients of variation were calculated in Microsoft Excel for each individual colony (North Dakota and South Dakota) and as a group so we could compare variation of food consumed. To accurately determine the concentrations of antibodies within the samples, we devised a modified direct (serum) and indirect (regurgitate) ELISA test (Crowther 2001; Martinez *et al.* 2003; Cray and Villar 2008). It was necessary to devise a novel ELISA test due to the uncertainty of tested IgA and IgY ELISA commercial kits regarding non-chicken avian species (Crowther 2001; Martinez *et al.* 2003; Cray and Villar 2008). The intra-assay coefficients of variation of IgY and IgA were 7.0% and 2.0%, respectively, with no reportable inter-assay variation as we only performed one test.

Although several candidate models for each parameter (intake, culmen length, tarsus length and body weight) were examined, the model best representing the data was chosen. Intake and culmen data models were compared using the REG procedure in SAS (SAS Institute, Inc. 2008) using  $R^2$  to index fit. A polynomial predictive model ( $R^2$ = 0.94) best fit intake data, whereas a linear predictive model ( $R^2$  = 0.98) best fit data for culmen growth. For body weight and tarsus data, models were compared using the NLIN procedure in SAS (SAS Institute, Inc. 2008). Data collected on both body weight and tarsus length were best represented using a Gompertz predictive model.

# RESULTS

# **Regurgitate Nutrient Analysis**

We determined that regurgitate samples from American White Pelicans in South Dakota contained more organic matter  $(F_{16} = 12.9, P = 0.012)$ , crude protein  $(F_{16} =$ 34.5, P = 0.001), and energy ( $F_{1.6} = 7.53$   $\hat{P} =$ 0.034) than those in North Dakota. Regurgitate samples from North Dakota contained more neutral detergent fiber ( $F_{1,6} = 11.9, P =$ 0.014) and acid detergent fiber ( $F_{16} = 19.3$ , P = 0.005; Table 1) than those from South Dakota. There were no statistical differences for dry matter content ( $F_{1.6} = 0.00, P = 0.99$ ) and fat content ( $F_{1,6} = 0.20$ , P = 0.67) between samples collected from the two States. Differences within each State's sub-colonies could not be determined as we pooled sample material prior to analysis; however, some general trends were observed. Pelicans in North Dakota had a large variation in neutral detergent fiber (CV = 52.60) and acid detergent fiber (CV = 58.56) among sub-colonies. South Dakota colonies had a moderate variation in acid detergent fiber (CV = 35.01) and crude protein (CV = 32.83). Overall, acid detergent fiber (CV = 83.41) was the most variable nutrient for both colonies.

				Dry Mat	ter Basis		
State	Dry Matter (%)	Organic Matter (%)	Crude Protein (%)	Neutral Detergent Fiber (%)	Acid Detergent Fiber (%)	Fat (%)	Energy (kcal/g)
South Dakota	32.36	81.58	55.83	17.52	2.62	18.35	5.02
North Dakota	32.30	62.10	25.52	43.48	33.30	19.41	3.95
Standard error of mean	3.70	4.29	4.08	5.94	5.52	1.86	3.09
<i>P</i> -value	0.991	0.012	0.001	0.014	0.005	0.667	0.034

Table 1. Nutrient analysis, on a dry matter basis, of regurgitate samples collected from American White Pelican (*Pelecanus erythrorhynchos*) sub-colonies at Chase Lake, North Dakota (n = 5) and Bitter Lake, South Dakota (n = 3) in July 2011. Significant differences in nutrient content of regurgitate indicated by P < 0.05.

# Regurgitate Immunoglobulins Y and A

The average concentration of IgY in both South Dakota (n = 3) and North Dakota (n = 5) pelican regurgitate samples averaged  $2.74 \pm 1.85$  ng/mL. The average concentration of IgA in both South Dakota (n = 3) and North Dakota (n = 4) sub-colonies was  $9.04 \pm 9.41$  ng/mL. Due to a failure in testing, the average concentration of IgA in one of the North Dakota sub-colonies could not be determined; therefore, the average is represented by the remaining four subcolonies. Concentration of IgY and IgA in serum we collected from pelicans (n = 2)captured in Mississippi were reported at  $20.61 \pm 0.24$  ng/mL and  $1.16 \pm 0.03$  ng/mL, respectively.

# **Captive Rearing**

Hatchability of eggs used in the trial from both North Dakota and South Dakota was 100% (*n* = 8). During the captive trial, we allowed chicks access to a diet consisting of 83.5% menhaden, 8.5% gizzard shad, 5.1% specific pathogen free catfish and 2.9% channel catfish (Table 2). We detected no differences for pelican nutrient metabolism of fish species fed in dry matter ( $F_{1.14} = 0.12, P$ = 0.67), organic matter ( $F_{1,14}$  = 0.47, P = 0.51), crude protein ( $F_{1.14} = 0.51, P = 0.49$ ), neutral detergent fiber ( $F_{1.14} = 0.28, P = 0.64$ ), acid detergent fiber ( $F_{1,14} = 0.21$ , P = 0.65), fat  $(F_{1.14} = 1.17, P = 0.30)$  and gross energy  $(F_{1.14} = 0.30)$ = 0.34, P= 0.57) between growing birds from North and South Dakota.

The total amount of fish consumed per bird over 62 days averaged 50,314.0 g  $\pm$ 5,719.6 g. Intakes peaked during week six at 1,256.0 g  $\pm$  170.0 g and week seven at 1,238.1 g  $\pm$  254.8 g. Intake as a percentage of body weight ranged from 8.5% to 42.7%, averaging 26.3% over the entire trial. The average daily intake of growing pelicans (n = 8) is shown in Fig. 1. Each pelican (n = 8) averaged a fecal output of 8,342.9 g  $\pm$  1,139.2 g over the 62-day period (~134 g per day). During week nine, there was an average decrease in intake of 615.3 g  $\pm$  253.0 g for each bird.

During the trial, pelicans (n = 8) averaged an initial body weight of 107.4 g ± 10.7 g, ranging from 94-123 g at hatching (Fig. 2). Final body weights of pelicans by the end of the trial averaged 5,890.8 g ± 845.2 g, ranging from 4,828-7,189 g. Peak body weight for pelicans averaged 6,727.6 g ± 1,033.8 g and occurred during week eight on different days for most birds. Following body weight peaks, we noticed a reduction in weight for all birds after day 50. The average reduction of weight for birds from peak body weight to final body weight was 837.4 g ± 306.8 g.

Pelican culmen lengths (n = 8) averaged 21.2 mm ± 1.1 mm (Range = 19.5-23.2 mm) at hatching (Fig. 3). Culmen lengths for fledged pelicans averaged 234.9 mm ± 16.0 mm (Range = 216-259 mm). Pelican tarsus length at hatching averaged 21.0 mm ± 1.1 mm (Range = 19.5-22.2 mm; Fig. 4). Rapid tarsus growth occurred from day 2 to day 30 (2 June to 30 June, respectively), peaking around day 30 (Fig. 4). Final tarsus lengths

hatching to fledging during 31 May through 20 July 2012.	12.							
				Dry Matter Basis	ter Basis			
	Dry Matter	Organic Matter	Crude Protein	Neutral Detergent Fiber	Acid Detergent Fiber	Fat	Energy	Ę
Species	(%)	(%)	(%)		(%)	(%)	(kcal/g)	% Diet
Menhaden (Brevoortia patronus)	28.80	83.19	59.78	9.70	0.97	24.65	5.18	83.5
Gizzard Shad (Dorosoma cepedianum)	23.80	83.87	60.84	8.58	1.16	26.14	5.50	8.5
Specified Pathogen Free Catfish (Ictalurus punctatus)	29.48	82.75	54.35	34.83	2.91	30.09	5.25	5.1
Channel Catfish (Ictalurus punctatus)	28.74	80.77	51.76	29.96	2.70	29.97	5.26	2.9

Table 2. Nutrient analysis and proportion of fish types (n = 4) reported on a dry matter basis fed to American White Pelicans (*Pelecanus erythrorhynchos*, n = 8) captive raised from

averaged 125.0 mm ± 7.7 mm (Range = 111.3-133.7 mm).

The polynomial model, Gompertz model, and linear model best predicted daily intake (Fig. 1), daily body weight (Fig. 2), and culmen length (Fig. 3), respectively. The Gompertz model also best predicted tarsus length (Fig. 4).

Pelican chicks developed natal down by day six. Newly hatched chicks remained extremely vocal until after feedings when they would usually become quiet and fall asleep. After 1-2 hr, chicks would again become extremely vocal. Chicks were transferred to the outdoor facility at around 3 weeks of age with thick down.

All individuals (n = 8) exhibited peeling and redness of the legs, back and head during the first few weeks, which may be a result of rapid growth. We took additional measures to sooth the dry cracking skin by wrapping the young chicks in a wet cloth containing a mild amount of aloe vera (Aloe sp.) gel while being fed; however, this did not seem to have any observable effects on the chicks.

## DISCUSSION

Regurgitate samples collected from parent pelicans in South Dakota sub-colonies had a narrow range of variation, perhaps indicating that birds in this region are sharing a common food resource or have dietary preferences (Ferguson et al. 2011). It is notable that regurgitate from South Dakota pelicans contained a large proportion of tiger salamanders (Ambystoma tigrinum; 50-90%), whereas regurgitate from North Dakota pelicans contained a much wider variety of fish species. Nutrient values for pelicans in North Dakota indicate regurgitate was less digestible and lower in energy, which could be affected by composition (Hoar et al. 1979) or retention time (Hilton et al. 1998). If pelicans are traveling long distances of 96 to 240 km (Johnson and Sloan 1976) to forage in a variety of estuaries, rivers and potholes (King and Michot 2002), retention time increases and composition becomes more variable. South Dakota pelicans consumed a more

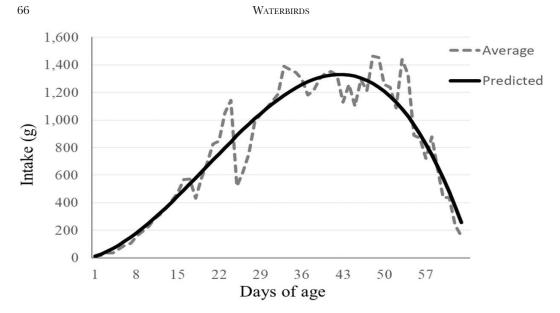


Figure 1. Average dietary intake of American White Pelicans (*Pelecanus erythrorhynchos*; n = 8) from hatching to fledging, 31 May to 1 August 2012 and the polynomial predictive model.

digestible higher energy diet, which also indicates they traveled less distance (Hilton *et al.* 1998) to possibly share a more common resource. These data support differences in foraging strategy, possibly due to reduced foraging habitat (Sovada *et al.* 2013).

Baseline concentrations of IgA and IgY reported in our study demonstrate that passive transfer of immunity does occur through regurgitate. The large variation in IgY and IgA concentrations reported in this study may be due to differences in regurgitate volume, retention time and composition, in addition to age of chick (Hoar *et al.* 1979; Hilton *et al.* 1998). Pelicans used in the captive trial beginning in May 2012 were not supplemented with IgA and IgY, and although growth seemed unaffected,

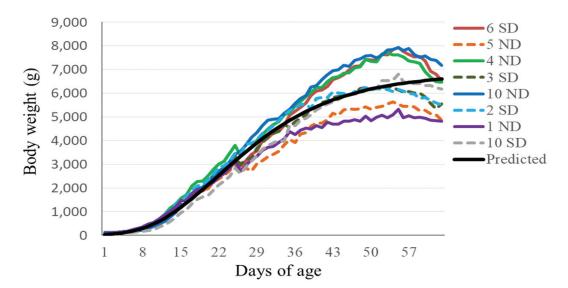


Figure 2. Body weight of North Dakota (ND) and South Dakota (SD), USA, captive-raised American White Pelicans (*Pelecanus erythrorhynchos*; n = 8) from hatching to fledging, 31 May to 1 August 2012 and the Gompertz predicted model.

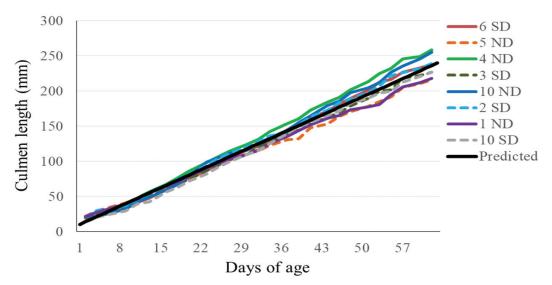


Figure 3. Culmen length of North Dakota (ND) and South Dakota (SD) captive-raised American White Pelicans (*Pelecanus erythrorhynchos*; *n* = 8) from hatching to fledging, 31 May to 1 August 2012 and the linear predictive model.

this may have impacted their susceptibility to disease (Hamal *et al.* 2006). Due to funding limitations and issues with disease (Ferguson 2016), determining or comparing concentrations of IgY and IgA in serum of captive reared chicks was not conducted.

Estimates on intake during the captive trial may be conservative due to pelicans being confined to cages during the trial. The average total amount of fish consumed per bird over 62 days was comparable to estimates made for Brown Pelicans (Schreiber 1976), but less than those for American White Pelicans made by Hall (1925). The nutrient metabolism of fish species consumed by pelicans from hatching to fledging was more efficient than that reported for adults and may be related to diet composition (Ferguson *et al.* 2011). Our fecal output values were likely conservative since pelicans were maintained outdoors and some of the water content of the feces evaporated between collections.

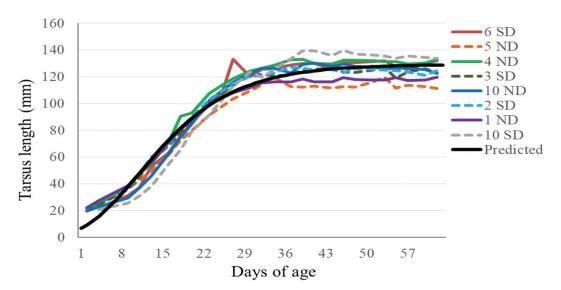


Figure 4. Tarsus length of North Dakota (ND) and South Dakota (SD) captive-raised American White Pelicans (*Pelecanus erythrorhynchos*; n = 8) from hatching to fledging, 31 May to 1 August 2012 and the Gompertz predictive model.

#### ACKNOWLEDGMENTS

Growth patterns for chick body weight, culmen length and tarsus length in captive trial pelicans were similar in proportion to those observed by Schreiber (1976) in nestling Brown Pelicans. For the captive chicks in this study, percentage of body weight being consumed was above the average adult maintenance requirement of ~10% until near the end of the captive trial when pelicans had fledged (Johnsgard 1993; Ferguson et al. 2011). Increased energetic demands during growth are similar to increased energetic demands during flight (Hall 1925). Culmen length for fledged pelicans was 60-80 mm less than values reported for < 7-month-old pelicans (Dorr et al. 2005), indicating culmen growth will continue past fledging. It is notable that pelicans with longer culmen lengths were often heavier. The average tarsi length reported for captive pelicans was also slightly more than the average reported by Dorr et al. (2005) for adult male pelicans, indicating pelican tarsi were either fully grown or perhaps may slightly decrease in length reaching adult maturity.

Since pelicans continue to lose habitat and have a high mortality rate prior to fledging (Knopf 1976; Anderson and King 2005; Sovada et al. 2013), it is important to consider future conservation and management of this species. North Dakota pelican regurgitate was less digestible and lower in energy than South Dakota, and this could be linked to reduced foraging habitat (Sovada et al. 2013). Passive transfer of immunity to chicks does occur through regurgitate and may be vital to survival of pre-fledged chicks by providing immunity against diseases (Hamal et al. 2006). Data collected on intake, body weight, growth, immunology, and behavior during this study could serve as a guideline for hand rearing pelicans. Estimates on intake may be useful for wild pelican conservation or determining costs related to captive rearing. There are also numerous conservation and wild and captive management implications of these growth data, such as combining predictive models to create daily maintenance energy formulas (Kendeigh et al. 1977) and formulas to estimate pelican age (Palacio 2001).

All applicable ethical guidelines for the use of birds in research have been followed, including those presented in the Ornithological Council's "Guidelines to the Use of Wild Birds in Research" (Fair et al. 2010). This research was conducted under U.S. Department of Agriculture, National Wildlife Research Center, Institutional Animal Care and Use Committee (IACUC) study protocol QA-1794. All experiments were performed with applicable Federal and State permits (e.g., U.S. Fish and Wildlife Service Scientific Collecting Permit MB019065-2). Funding for this research was provided by USDA, Wildlife Services, National Wildlife Research Center and Mississippi State University (Department of Wildlife, Fisheries, and Aquaculture; Forest and Wildlife Research Center or Mississippi Agricultural and Forestry Experiment Station - Aquaculture Unit; Berryman Institute; College of Veterinary Medicine; Department of Animal and Dairy Science; Department of Biochemistry). We thank the graduate students, USDA employees and volunteers who helped during this study for their hard work and time: F. Cunningham, B. Leopold, L. Pote, C. Huston, C. Aultman, C. Brown, N. Alberson, S. Easley, G. Rosser, M. Assenmacher, M. Sovada, S. Lemons, P. Fioranelli, K. Dorr, R. Middleton, J. Cooley, A. Bartos and S. Willard. We also thank two anonymous reviewers for constructive criticisms of previous versions of this manuscript.

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