

## EFFECTS OF NESTLING HEALTH ON POSTFLEDGING SURVIVAL OF WOOD STORKS

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**Abstract.** Little is known about the period between fledging and breeding in long-lived birds, including survival rates and factors affecting survival, yet this period may be critical to population regulation. We conducted health exams on 72 nestling Wood Storks (*Mycteria americana*) aged 4–6 weeks, and monitored survival of these birds via satellite telemetry for up to two years of age. Eighty-two percent of nestlings fitted with transmitters in 2002 ( $n = 33$ ) survived to fledging. Of these fledglings ( $n = 27$ ), 44% survived their first year. Second-year survival for the same cohort ( $n = 12$ ) was 75%. In contrast, 50% of nestlings fitted with transmitters in 2003 ( $n = 34$ ) survived to fledging, and 6% of fledglings ( $n = 17$ ) survived the first year. Of the health parameters we measured in large nestlings, white blood cell count was consistently the most closely related to postfledging survival. Significantly elevated heterophil:lymphocyte ratios in 2003 coincided with the observed high colony abandonment that year. After controlling for health parameters, gender also appeared to play a significant role in predicting survival, with males at greater risk of mortality. Hematological factors and gender were both more closely associated with survival in 2003 than in 2002, suggesting these factors may play a greater role in regulating postfledging survival or, in the case of hematology, serve as indicators of poor health in less favorable years when nestling storks are exposed to multiple stressors.

**Key words:** *Ciconiiformes*, health, immune system, *Mycteria Americana*, postfledging, survival, Wood Stork.

### Efectos de la Salud de los Polluelos sobre la Supervivencia Posterior al Abandono del Nido en *Mycteria americana*

**Resumen.** Se conoce poco sobre el periodo comprendido entre el abandono del nido y la reproducción en las aves longevas, incluyendo las tasas de supervivencia y los factores que las afectan. Aún así, este periodo puede ser crítico para la regulación de las poblaciones. Realizamos exámenes para determinar la salud de 72 polluelos de *Mycteria americana* de cuatro a seis semanas de edad y monitoreamos la tasa de supervivencia de estas aves por medio de telemetría satelital hasta los dos años de edad. El 82% de los polluelos marcados en 2002 ( $n = 33$ ) sobrevivieron desde el marcaje hasta el abandono del nido. De los volantones que abandonaron la colonia ( $n = 27$ ), el 44% sobrevivieron el primer año. De estos, el 75% ( $n = 12$ ) sobrevivieron el segundo año. De manera contraria, el 50% de los polluelos marcados en 2003 ( $n = 34$ ) sobrevivieron desde el marcaje hasta el abandono del nido, y el 6% de los volantones ( $n = 17$ ) sobrevivieron el primer año. De los parámetros de salud que medimos en polluelos grandes, el conteo de glóbulos blancos fue consistentemente el que estuvo más relacionado con la supervivencia después de abandonar el nido. Proporciones significativamente elevadas de heterófilos: linfocitos en el 2003 coincidieron con las altas tasas de abandono observadas ese año. Después de controlar por los parámetros de salud, el sexo pareció jugar un papel significativo en la predicción de la supervivencia, estando los machos en mayor riesgo de mortalidad. Los factores hematológicos y el sexo estuvieron más estrechamente relacionados con la supervivencia en 2003 que en 2002, lo cual sugiere que estos factores podrían jugar un papel más importante en la regulación de la supervivencia de los volantones o, en el caso de la hematología, servir como indicadores de una salud deficiente en años desfavorables en los que las cigüeñas están expuestas a múltiples factores de estrés.

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## INTRODUCTION

Although adult survival is often considered to have the greatest effect on population regulation in long-lived species, Sæther and Bakke (2000) found considerable variability in the sensitivity of population growth rates to adult survival among long-lived species such as owls, wading birds, and seabirds. For example, in Gray Herons (*Ardea cinerea*) the size of the breeding population was more closely regulated by immature survival (North 1979). Similarly, in some long-lived ungulates (Gaillard et al. 1998) and turtles (Crowder et al. 1994), immature survival affected variation in population growth rates more than adult survival. However, there are relatively few survival estimates for the period between fledging and breeding for long-lived birds, and immature birds often spend this period away from their natal areas, making reliable survival estimates difficult to obtain.

Survival during nonbreeding periods is known to significantly influence population fluctuations for all age groups of birds, but is typically difficult to quantify (Sæther et al. 1996, Cézilly 1997). Survival and population trends for birds breeding in temperate zones (particularly first-year birds) have often been linked to conditions at wintering sites (Cézilly 1997).

The life history of birds is also strongly influenced by the immune system and its competency (Ricklefs and Wikelski 2002). Health during the nestling stage is known to have a significant effect on postfledging survival in birds (Gaston 1997, Naef-Daenzer et al. 2001). Body condition, defined here as body mass corrected for variation in body size (Johnson et al. 1985), has been shown to affect survival in many avian taxa (Haramis et al. 1986, Naef-Daenzer et al. 2001, Hill et al. 2003). Hematological analysis is commonly used to characterize the health of wild birds, and blood composition can be strongly influenced by a bird's nutritional state (Latshaw 1991).

Here, we report on survival, and correlates of survival, during the first two years of life in Wood Storks (*Mycteria americana*), a long-lived species with delayed reproduction. Immature birds (1–3 years of age) are likely to face the highest mortality in ciconiiform birds (2–3

times that of adult mortality; Cézilly 1997, Frederick 2001), but there are no measurements of immature survival for Wood Storks (Coulter et al. 1999). Among the reported sources of mortality for fledged Wood Storks, collisions with power lines and vehicles are the most common (Forrester and Spalding 2003), though this may be due to a sampling bias.

Storks are tactile feeders and are highly dependent on shallow, declining surface water conditions, which concentrate prey (Ogden 1994, Gawlik 2002). Water levels are dependent both upon weather patterns and human management, and in many years can play an important role as an indirect stressor for individuals, particularly during nesting (Ogden 1994, Coulter et al. 1999). Another possible stressor for storks in southern Florida is exposure to mercury (Frederick 2000). The detrimental effects of mercury on the health of waterbirds are extensive and are summarized in Frederick et al. (2002).

We predicted that the highest levels of mortality in immature storks would occur during the first six months after fledging, when young storks are learning to forage for themselves and are moving across unfamiliar landscapes. By the same reasoning, we also predicted that survival would be higher in the second than in the first year of life. Hypothesizing that variation in the development of the immune system would play a strong role in fledgling survival, we predicted that nestlings with abnormal hematological parameters, higher stress indices, higher mercury levels, and lower body condition indices would have lower postfledging survival.

## METHODS

### SURVIVAL

We followed the nestling and postfledging survival of Wood Storks hatched in the Tamiami West colony (25°45'N, 80°32'W), a mixed-species wading bird colony located in Everglades National Park, Miami-Dade County, Florida. Nests in the colony were almost entirely built in the canopy (2–5 m above ground) of Pond Apple (*Annona glabra*) trees. We monitored nest contents every 4–7 days for 120 of 400 and 108 of 350 nests initiated in 2002 and 2003, respectively. These were selected as

all nests within 5 m of two roughly north–south transects that crossed the entire colony. Transects were separated by a canal approximately 10 m wide. This design produced a sample with both edge and center-located nests, which are known to have different characteristics and risks associated with survival (Coulson 1968, Simpson et al. 1987, Brunton 1997).

One nestling between four and five weeks of age from 33 and 34 randomly selected nests was included in the health and telemetry studies between late April and early June in 2002 and 2003, respectively. We selected the earliest-hatched chick from each nest to avoid problems in analysis with nonindependence of siblings and to control for biases related to hatching order (Mock 1984). In one case in 2002, the earliest-hatched chick was too mobile for capture, and its later-hatched sibling was chosen instead. Hatching order was determined by visually assessing relative culmen lengths among siblings. In cases where hatching date was unknown, storks were considered to be at least four weeks of age when they had visible white contour feathers on the back and coverts, and primaries 15 cm or greater in length (Kahl 1962).

Young were typically capable of flying and had become independent of their nest sites by 55 days after hatching. However, young storks remained associated with the colony and continued to be fed by their parents until at least 80 days of age. Nestlings were considered fledged when they permanently left the colony.

#### SATELLITE TELEMETRY

Each nestling was fitted with a Teflon ribbon backpack harness that carried a 10 g VHF radio-transmitter with a motion-mortality detector (2002: American Wildlife Enterprises, Monticello, FL; 2003: Model A1120, Advanced Telemetry Systems, Isanti, MN) and a 35 g solar-powered Argos-certified satellite transmitter (PTT; Microwave Telemetry, Inc., Columbia, MD) on a duty cycle of 10 hr on per 34 hr. Total package weight was 48 g (2.0%–2.5% of nestling and adult mass). Birds were fitted with the additional radio-transmitter with an estimated lifespan of two years to facilitate recovery of the expensive PTTs. Although daily location information for all PTTs was obtained by e-mail from Service Argos, Inc. (Landover, MD), we often did not receive a location

accurate within 1 km for all individuals every day. For this reason, a bird may have died quite some distance from its last known location, especially during periods of migration.

We determined the survival of birds fitted with transmitters prior to fledging by monitoring VHF frequencies daily from a position near the colony, and after fledging by monitoring satellite transmitter information. Birds were categorized as dead when either the mortality signal from the VHF was activated, or when the PTT signal was lost or stationary for more than one week.

#### NESTLING HEALTH

Nestlings were examined for several health parameters at the same time they were fitted with transmitters. All nestlings were caught by hand on the nest and were immediately hooded to reduce stress. All birds received numbered aluminum bands, and were measured for culmen and tarsometatarsal lengths (mm) and mass (g). We also collected 4–6 growing scapular feathers for mercury analysis (method detailed in Frederick et al. 2004).

We collected up to 2 mL of blood from the brachial vein. We used 1–3 drops to determine sex, stored either in ethanol (2002) or as a blood smear across a prepared card (2003). Blood was analyzed for sex by Zoogen Services, Inc., Davis, California. Remaining blood was stored in lithium heparin tubes (100 units  $\text{cc}^{-1}$ ) and put on ice.

Within 4 hr, whole blood was transferred to heparinized microcapillary tubes and centrifuged at 12 000 rpm for 5 min to obtain packed cell volume, measured with a ruler as the percent cellular fraction of total volume. Total white blood cell counts were performed by counting the average number of leucocytes observed within five fields under 50 $\times$  power (Campbell 1995) using an eosinophil Unopette (Becton-Dickinson, Rutherford, NJ).

Within four months of preparation, blood smears were stained with Wright-Geisma stain (ACROS Organics, Morris Plains, NJ) to look for hemoparasites and to estimate the proportion of different types of leucocytes. The differential leukocyte count was determined for each bird by multiplying the white blood cell count by the relative percentages of lymphocytes, heterophils, monocytes, basophils and eosinophils based on descriptions by Hawkey

and Dennett (1989). The number of heterophils compared to the number of lymphocytes (H:L) is frequently used as an index of stress among birds, with higher ratios indicative of greater stress (McFarlane and Curtis 1989, Carsia and Harvey 2000). Means and ranges of the hematological values are reported in Hylton (2004).

#### STATISTICAL ANALYSES

We used the Cox proportional hazards model (Cox 1972, 1975, Yoder et al. 2004) to determine the effects of nestling health variables on the survival of postfledging storks (Lee and Wang 2003). Explanatory variables included packed cell volume, white blood cell counts, eosinophil counts, lymphocyte counts, basophil counts, heterophil counts, monocyte counts, H:L ratio, body condition, and gender. Although we examined blood for the presence of blood parasites and diseases, both critical factors in the health of an individual, none were found and thus were not used in this analysis. We fit independent models for each year of study because survival was significantly different between years.

We derived an index of body condition (body mass corrected for variation in body size) using principal components analysis (PROC PRINCOMP; SAS Institute 1990) of tarsus and culmen lengths (Alisauskas and Ankney 1987). The first principal component (PC1) accounted for 71% of the overall variation. We then regressed body mass on PC1 to give an index of body condition (PROC GLM; SAS Institute 1990).

The Cox proportional hazards model (PROC PHREG; SAS Institute 1990) yielded estimated regression coefficients for the hazard function using a partial likelihood function that only included probabilities for birds that died within six months of fledging. All birds that were alive on a given day were considered the at-risk population in the model. The threshold for stepwise inclusion of a specific variable into the model was arbitrarily set at  $P < 0.20$ . The Wald test statistic, which uses a chi-square distribution, was used to determine if the estimated regression coefficients were significantly different from zero.

Chi-square and Mann-Whitney  $U$ -tests were used for bivariate analyses. A significance level of  $P \leq 0.05$  was set *a priori* for all statistical tests, unless otherwise noted.

## RESULTS

### SURVIVAL

Of the 33 birds fitted with satellite transmitters in 2002, six died prior to fledging (82% survival). Of the 34 birds monitored in 2003, 17 died prior to fledging (50% survival). The following six-month, first-year, and second-year survival data cover only postfledging survival, and do not include likelihood of surviving the nestling period. Survival of the 27 birds marked in 2002 was 63% for the first six months (Jun–Nov, Fig. 1, Table 1). First-year survival (44%,  $n = 27$ , June 2002–February 2003) was not significantly lower than second-year survival (75%,  $n = 12$ , March 2003–February 2004) for the 2002 cohort ( $\chi^2_1 = 3.1$ ,  $P = 0.08$ ). Overall, 31% of fledglings in the 2002 cohort survived to 24 months of age.

Seventeen birds fitted with satellite transmitters in 2003 fledged. Survival for the first six months was significantly lower for the 2003 cohort (24%) than for the 2002 cohort (63%,  $\chi^2_1 = 6.5$ ,  $P = 0.01$ ; Fig. 1). Only one of the 17 fledglings in the 2003 cohort was still alive after 12 months, resulting in 6% first-year survival. First-year survival of the 2003 cohort was thus also significantly lower than that of the 2002 cohort ( $\chi^2_1 = 7.4$ ,  $P = 0.001$ ). We could not compare second-year survival for the 2003 cohort with the 2002 cohort due to the limited sample size.

We were able to confirm only three and four mortalities from the 2002 and 2003 cohorts, respectively, by actually recovering transmitters. While this is not surprising given the dense, aquatic habitat and low confidence in actual

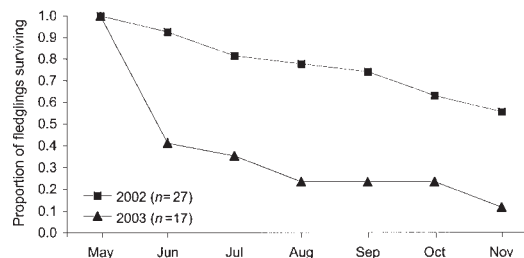


FIGURE 1. Survival curves of Wood Storks fitted with transmitters in the 2002 and 2003 cohorts for the first six months after fledging. As survivorship is based on known outcomes, not estimates, error bars are not available. Fledging occurred in late May in both years.

TABLE 1. Analysis (Cox proportional hazards model) of the risk factors we hypothesized to affect postfledging survival in immature Wood Storks. Explanatory variables included year, total white blood cell counts, counts of two specific types of white blood cells (lymphocytes and eosinophils), gender, heterophil:lymphocyte ratio (a commonly used indicator of stress), body condition (body mass corrected for variation in body size), and mercury levels. A dash (—) indicates the variable did not meet the  $P < 0.20$  threshold for entry into the model. Model fit in 2003 was not significant at the 0.05 level. The signs (+ or -) indicate the direction of the variable's relationship to survival.

Variable	Model		
	Years combined <i>P</i>	2002 cohort <i>P</i>	2003 cohort <i>P</i>
Year	0.001 (-)	—	—
White blood cell count	0.004 (-)	0.007 (+)	0.04 (-)
Lymphocyte	—	0.07 (-)	0.03 (+)
Eosinophil	—	0.03 (-)	0.12 (+)
Gender (F)	—	0.10 (+)	0.03 (+)
Heterophil:lymphocyte ratio	—	—	0.02 (+)
Body condition	—	—	0.11 (-)
Mercury	—	—	0.18 (-)

last locations, it introduces some uncertainty about actual versus perceived mortality. Within the fledged 2002 cohort, first-year survival of marked birds using only fully confirmed mortalities was 75% ( $n = 16$ ), as compared to 44% ( $n = 27$ ) when including all assumed mortalities. Within the fledged 2003 cohort, first-year survival was 29% ( $n = 7$ ), as compared to 6% ( $n = 17$ ) when including all assumed mortalities.

#### NESTLING HEALTH

Regression analysis using the Cox proportional hazards model revealed that year ( $P = 0.001$ ) and white blood cell counts ( $P = 0.004$ ) were significantly correlated with six-month survival of immature storks (Table 1). For the 2002 cohort, increased white blood cell counts ( $P = 0.007$ ) and decreased eosinophil counts ( $P = 0.03$ ) were significantly correlated with survival. Both decreased lymphocyte counts ( $P = 0.07$ ) and gender ( $P = 0.10$ ) were also marginally associated with 2002 cohort survival.

Survival for the 2003 cohort was not consistent throughout the six-month period, with a large decline in survival during the first month after fledging, followed by a survival curve similar to that of the 2002 cohort thereafter (Fig. 1). Including time-dependent covariates in the model did not allow for a better model fit. Although this inconsistency in survival over the six-month period resulted in a less accurate fit to the Cox proportional hazards model

( $\chi^2_7 = 9.8$ ,  $P = 0.20$ ), the model for the 2003 cohort still has explanatory value.

Three additional variables were included in the model in 2003 as compared to 2002 (Table 1). Survival of the 2003 cohort was strongly associated with an elevated H:L ratio ( $P = 0.02$ ), gender ( $P = 0.03$ ), elevated lymphocyte counts ( $P = 0.03$ ), and decreased white blood cell counts ( $P = 0.04$ ; Table 1). In contrast to the 2002 cohort, eosinophil counts ( $P = 0.12$ ) were not related to survival risk in the 2003 cohort. Neither variation in mercury levels ( $P = 0.18$ ) nor body condition ( $P = 0.11$ ) was associated with survival in the 2003 cohort. Total mercury concentration in feathers ranged from 3.4–27.0 mg kg<sup>-1</sup> ( $\bar{x} = 7.9$  mg kg<sup>-1</sup>) in 2002 and 0.5–4.3 mg kg<sup>-1</sup> ( $\bar{x} = 1.9$  mg kg<sup>-1</sup>) in 2003.

While gender was only marginally associated with survival in 2002, it was significantly correlated with survival in 2003. Controlling for health factors, females were  $2.0 \pm 1.2$  and  $5.0 \pm 2.3$  times as likely as males to survive to six months of age in 2002 and 2003, respectively.

The only statistical difference between years for any of the health parameters was in mercury levels, which were significantly lower in 2003 ( $P < 0.01$ ). There was also some evidence that H:L ratios were greater in 2003 ( $P < 0.06$ ), suggesting higher stress levels. Descriptive statistics for body measurements, mass, mercury levels, and health factors are given in Hylton (2004).



## DISCUSSION

Although there were large, significant differences in the survival of immature storks between the two cohorts of our study, the general patterns that emerged largely matched our predictions. The highest levels of mortality occurred during the first six months after fledging, and second-year survival was greater than first-year survival. Although mercury levels and body condition were not good predictors of survival, hematological parameters, gender, and stress levels were all closely associated with postfledging survival in at least one year of the study.

The wide range in survival values exhibited by immature Wood Storks is fairly typical for wading birds, with high productivity and survival in some years and little to none in others (Freeman and North 1990, Hafner et al. 1998, Barbraud et al. 1999). For example, annual survival of banded immature White Storks (*Ciconia ciconia*) has been shown to be highly variable across years (0%–100%), although adult survival during the same time period was relatively constant, averaging 78% (Barbraud et al. 1999). Little Egrets (*Egretta garzetta*) have also been estimated to have a higher, less variable adult survival rate of 71% (range = 69%–86%) compared to first-year birds (range 7%–55%) (Hafner et al. 1998).

Lower survival in first-year birds compared to older birds is also a common pattern that is generally attributed to relative experience levels (Lack 1954). The greatest mortality in Wood Storks occurred during the first six months after fledging in both years. This is the period when birds are presumably developing their foraging skills and making decisions regarding habitat selection and predator avoidance. Immature storks often initially forage at inappropriate sites where adults are not present and prey are unavailable, such as flooded lawns and rainwater depressions (Coulter et al. 1999). Limited prey availability, when coupled with inexperience, could have a strong negative effect on survival of immature birds in some years.

The survival estimates of immature Wood Storks in our study were based on several assumptions: 1) losses of telemetry devices from living birds were negligible, 2) failure of the telemetry devices on living birds was negligible, and 3) carrying a transmitter package did not

affect survival. There was no evidence to suggest harness failure or detachment of transmitter from the harness, as all of the harnesses recovered during the nestling ( $n = 18$ ) and postfledging ( $n = 7$ ) periods were intact and neither torn nor frayed (Hylton 2004). The only visible wear on recovered harnesses was faded color from exposure to sunlight and weather. There was also no evidence that satellite transmitters (PTTs) simply stopped working, as all PTTs were working upon recovery. Nine deployed PTTs were still operating after 2.25 years as of 1 July 2004. However, because there was probably some small loss of transmitters overall, our survival estimates should be considered conservative.

Assumption 3 was not tested in our study, but there is evidence from other studies to support this assumption. Survival estimates of 42 Peregrines (*Falco peregrinus*) with PTTs were not significantly different from previous survival estimates based on a mark-resighting study of banded Peregrines (Britten et al. 1999). K. Meyer (Avian Research and Conservation Institute, unpubl. data) found no significant difference between survival estimates of Swallow-tailed Kites (*Elanoides forficatus*) from birds fitted with PTTs and those fitted with VHF radio-transmitters, even though PTTs were almost twice as heavy as radio-transmitters. Transmitter loads for these raptors were <3% of the bird's mass, as they were in our study. Phillips et al. (2003) found that negative effects of transmitters on behavior recorded in albatrosses and petrels generally occurred only in studies where transmitter loads exceeded 3% of adult mass, or where adults were fitted with transmitters during sensitive nesting periods. We fitted nestling storks with transmitters 3–5 weeks prior to fledging, which allowed for a lengthy period of recovery from handling and habituation to the transmitter package prior to flight and fledging. In light of existing knowledge about transmitter effects, it seems unlikely that bird handling and transmitter attachment had a large effect on postfledging survival in our study.

The poor postfledging survival in 2003 was probably linked to the significantly lower nestling survival that same year (Hylton 2004). Heavy rains in early March 2003 preceded nest abandonment by approximately half the nesting storks in the Tamiami West colony. The

synchrony of abandonments coincided with rapid water level increases throughout the nestling period. It seems unlikely that our own activities in the colony resulted in the abandonments, especially since synchronous abandonment during this period was seen in other stork colonies in the Everglades ecosystem in which we did not work (Gawlik and Crozier 2003). In addition, rising water levels are known to strongly affect abandonment rates through decreased foraging success in Wood Storks (Kahl 1964, Ramo and Busto 1992). It seems likely, therefore, that storks reached the fledging stage in a less favorable environment in 2003 than in 2002.

Our results regarding the effect of nestling health on postfledging survival were varied between the two years, but did suggest a link between the immune system and survival. White blood cell count, an indicator of an organism's response to infection, was consistently the best health-related predictor of survival. White blood cell counts were negatively correlated with survival in 2003, while they were positively correlated in 2002. Eosinophil levels were also negatively correlated with survival in 2002. High white blood cell and eosinophil counts are often indicative of infections or blood disorders, while low white blood cell counts may indicate poor immunocompetency (Campbell 1988, Svensson and Merilä 1996). Thus, it seems consistent that poor survival was associated with white blood cell counts at both extremes.

Similarly, the H:L ratio, a commonly used estimator of stress levels (Gross and Siegel 1983, Mazerolle and Hobson 2002, Ruiz et al. 2002), was a significant predictor of survival in 2003, with high ratios negatively correlated with postfledging survival. The significantly higher H:L ratios observed during the nestling period in 2003 compared to 2002 coincided with high nest abandonment observed in 2003 (Hylton 2004). Although there is some controversy in interpreting H:L ratios in wild birds (Ots et al. 1998, Clinchy et al. 2004), our results indicate that higher H:L ratios during the nestling period may provide an indication of health problems that are associated with reduced survival.

Body condition is also often used as a measure of bird health. In our study, we found that stork body condition measured at the time of

transmitter attachment was not significantly different between years, despite very different survival during the nestling (Hylton 2004) and postfledging periods. In addition, body condition of nestlings was not associated with survival in either year, as we had predicted. This result was unexpected since H:L ratios were generally higher in 2003, which we would have predicted to be correlated with lower body condition. This result indicates that body condition was not related to the immune response at the time of sampling. One explanation for this is that higher H:L ratios in 2003 were unrelated to food availability, but instead linked to other environmental stressors such as weather or disease.

One potential problem with our analysis is that body condition at 4–5 weeks of age may not have been indicative of body condition 3–4 weeks later at fledging, or during the postfledging period. While nestling body condition did not appear to be related to immature survival, this test of the hypothesis may have been confounded by our inability to monitor body condition during the late nestling period.

Although a bias in survival related to sex was not apparent from the raw data (Hylton 2004), females were twice as likely as males to survive in 2002 and five times more likely to survive in 2003 after controlling for other model parameters. In many vertebrates, males are more often negatively affected than females by adverse conditions during growth (Clutton-Brock 1991). Male Wood Storks are slightly larger than females, and may have greater energy requirements (Coulter et al. 1999) and thus greater sensitivity to adverse conditions (Clutton-Brock et al. 1985, Slagsvold et al. 1986).

Contrary to our prediction, mercury levels did not appear to be associated with survival of storks in our study in a dose-dependent fashion. However, our methodology may not have resulted in an adequate test of the effect. Mercury bonds strongly to growing feather tissue, and rapid feather growth can temporarily reduce the amount of mercury in the body (Honda et al. 1986, Spalding et al. 2000). Because we measured mercury during a period of extremely rapid feather growth, the contaminant levels we measured may not have been representative of the mercury burdens at fledging. In addition, the birds may have been exposed to widely varying levels of mercury

during the postfledging period (Spalding et al. 2000).

Overall, results supported our prediction that nestling health is associated with survival of immature birds. In particular, hematological factors and gender were more closely associated with survival in 2003 than in 2002, suggesting these factors may play a greater role in regulating, or acting as an indicator for, survival in years when nesting storks are exposed to multiple stressors such as inclement weather, lowered food availability, or disease.

We also emphasize that mortality is usually the result of effects of both proximate and ultimate factors, of which health during early development is just one; in the case of Wood Storks, we believe that nestling and postfledging foraging opportunities are probably also very important for survival, and in determining health.

Wood Storks appear to follow a "bet-hedging" life history strategy, in which long-lived species tend to inhabit generally favorable habitats, but in which the quality of the habitat may vary annually (Sæther et al. 1996). The bet-hedging life-history strategy may be an adaptation to living in variable wetland environments, allowing for high productivity in the occasional favorable years. Bet-hedging strategies are most common in waders, owls, and terns with large clutch sizes and maturation within three years (Sæther et al. 1996). Sæther and Baake (2000) found the contribution of adult survival to population growth rate varied widely in these same species. For this reason, survival of immature Wood Storks may be important for predicting population growth rates of this species.

The high initial mortality of immature storks is probably an important limiting factor for recruitment to the breeding population, even in successful years. As revealed in this study, survival during the first year can be extremely variable, making survival during the immature period difficult to predict. The large variation in survival among years and age classes underscores the caution that should be observed when making assumptions about trends in demography and population dynamics of this species.

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