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Sex-related Mortality of White Ibis (*Eudocimus albus*) Nestlings During a Starvation Event

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Abstract.—During a time of food stress, we observed sex-biased mortality during the nestling stage in a sexually size dimorphic species of wading bird, the White Ibis (*Eudocimus albus*). Over four days spread out over a week, we captured a total of 180 25-32 d old White Ibis nestlings from a colony of several thousand breeding pairs. On sequential capture dates we caught significantly fewer females than males. Through this time period male nestlings had higher body condition indices (mass/tarsus) than females, though the rates at which male and female body condition increased over the week were not significantly different. Several sources of evidence suggest that our sampling was not sex-biased and was reflective of actual changes in abundance of males and females. These data indicate that despite the greater caloric requirements of males, their larger size may have conferred a competitive advantage over female siblings in obtaining food from parents during a time of food shortage. Received 28 September 2007, accepted 3 July 2008.

Key words.—White ibis, starvation, mortality, nestling, sex ratio.

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Sexually size dimorphic (SSD) avian species have often been found to exhibit sex dependent pre-fledgling mortality during periods of food limitation (Hipkiss *et al.* 2002). This may be because larger sized nestlings have higher mortality due to greater nutritional need (Clutton-Brock 1985; Bortolotti 1986; Anderson *et al.* 1993; Arroyo 2002; Laaksonen *et al.* 2004; Kalmbach *et al.* 2005), but there are also numerous examples in which both the smaller sex has higher mortality as nestlings or juveniles (Røskaft and Slagsvold 1985; Teather and Weatherhead 1989; Torres and Drummond 1999; Nager *et al.* 2000). These differences in sex-biased mortality suggest that another mechanism may be at work, including large siblings out-competing smaller ones for food (Oddie 2000), larger individuals being better able to withstand starvation or extreme temperature resilience (Greenberg 1979) and sex-specific, size-unrelated mortality (Müller *et al.* 2005). Covariates linked to sex-related mortality that are independent of size and sex are brood size (Raberg *et al.* 2005), prey size (Anderson *et al.* 1993), prey availability (McDonald *et al.* 2005), and hatching asynchrony (Ostreiher 1997; Gonzalez-Solis *et al.* 2005); these factors influence the dynamics

of sibling competition in nests and may determine whether a population exhibits significant sex-related mortality (Maness *et al.* 2007).

Here, we report on differential sex related mortality in young of the sexually dimorphic White Ibis (*Eudocimus albus*). Adult males are larger than females in most measurements of body size by roughly 15% (Kushlan 1977a; Babbitt and Frederick 2007). A variety of selective costs and benefits to adults have been proposed for sustaining the sexual dimorphism (Kushlan 1974; Petit and Bildstein 1987; Bildstein 1993; Babbitt and Frederick 2007), but there has been little research on the costs and benefits of SSD in nestlings.

Breeding propensity and breeding success are largely limited by prey availability in White ibises (Kushlan 1974; Kushlan and Bildstein 1992; Frederick 2001). In the shallow marshes of South Florida, USA, surface water recession during the dry season is typically associated with highly available prey (fishes and crustaceans), while rising surface waters are typically associated with poor availability and abandonment of nesting (Kushlan 1974; Frederick and Collopy 1989; Frederick and Spalding 1994; Gawlik 2002).

In many years, nesting may be wholly or partly abandoned in response to unseasonable rainfall and associated water level increases (Frederick 2001). Incubation and hatching of eggs in this species is asynchronous, and a resulting size differential is typical for nestmates up to the approximate midpoint of the 40-50 d nestling stage (Kushlan 1974). A sex-related size differential is also typical of nestlings, ranging from very little at hatching to nearly adult ratios at fledging.

In this paper we document changes in secondary sex ratio and body condition in nestling White Ibises during a widespread nest abandonment event resulting from a food shortage.

METHODS

As part of a study of captive ibis behavior and reproduction, we collected young ibises from 1) the Alley North colony in Water Conservation Area 3 (WCA3) in the Florida Everglades (Broward County, FL, N 26°11.179, W-80°31.431) and 2) a colony in White Springs, Hamilton County, FL (N 30°19.900, W-82°45.367). Alley North is one of the largest multi-species wading bird colonies in North America and is composed of a 4-km long willow tree island/cattail complex in the northeast corner of WCA3. We banded 300 nestlings (largest in each nest) before they could leave the nest (about 10 d of age) in order to be able to later identify the first hatched young at the time of collection when chicks are mobile and not associated with siblings or nests (De Santo et al. 1990). The bands were individually numbered plastic spirals (National Band and Tag Co., Lexington, KY, USA).

Some of the banded birds were re-captured at 25-32 d on 14, 17, 19, and 21 April 2005. We collected birds using a combination of herding techniques to concentrate them, followed by capture by hand or using hand nets. All 21 birds collected on 14 April 2005 were banded, first-hatched nestlings. After this date we were able to discover no other banded birds, and so we collected any birds we were able to capture. All birds were transported overnight to a free-flight aviary. The following morning, prior to any feeding, all birds were weighed, had both the culmen and tarsus measured, and blood samples (about 50 μ L) were drawn from the brachial

vein. We used blood for DNA sexing (Fridolfsson and Ellegren 1999) at Avian Biotech (Tallahassee, FL, USA).

The White Springs colony was on an island within a dredge-spoil lake. Here, we banded chicks between ca. 2 and 7 d of age and identified the first-hatched chicks by relative size and development. We sexed 60 first-hatched chicks by blood DNA, and returned a week later (ca. 10 d of age) to collect only female chicks.

We used an ANOVA to examine size and mass corrected size (culmen length/total mass) by collection date and sex. The binomial test (expected value = 0.5) was used to test a departure from random for each collection period. All analyses were conducted using JMP IN v. 5.1.

RESULTS

Prior to our first collection date there was evidence of colony-wide nest abandonment at the Alley North colony. Dead chicks were a common sight in and around nests beginning in early April and continuing through the collection dates. Circling vultures were observed during the first pre-collection foray into the colony where we banded first-hatched chicks. However, adults were still attending many nests. The abandonments occurred following sharp increases in water level resulting from heavy rains in middle and late March and again in early April (Cook and Call 2005). Between the middle of March and 21 April, local water levels increased by 22.9 cm, as measured by long term gauging stations in the marsh.

Over the course of the week-long collections of ibises at the Alley North colony, the ratio of male to female chicks captured increased dramatically (Table 1). We found marginally significant or significant departures from a 50:50 male/female ratio on both the third and fourth collection dates ($P = 0.057$ and 0.043 , respectively, binomial test) while birds collected from the first and second collection did not significantly differ

Table 1. Number of male and female White Ibis (*Eudocimus albus*) nestlings captured during a colony-wide starvation event in the central Everglades on four dates in April 2005, male:female displayed in parentheses.

Sex	Collection date				Total
	4/14/2005	4/17/2005	4/19/2005	4/21/2005	
Males	10	21	41	31	103
Females	11	18	27	18	74
Total	21 (0.476)	39 (0.538)	68 (0.603)	49 (0.633)	177 (0.582)

from 0.5 (binomial test, $P = 0.66$ and $P = 0.37$, respectively). The sex ratio of first-hatched birds from the White Springs, FL colony, also did not differ significantly from 0.5 ($P = 0.84$, $n = 59$, binomial test). The first collection in Alley North and the single collection at White Springs only included first-hatched nestlings and we found no evidence of sex ratio bias in the samples of 21 and 69 birds, respectively.

Body condition—as quantified by the ratio of weight (g) to tarsus length (cm)—changed during the course of the one-week collections and was different between the sexes (Fig. 1). We found a significant effect of collection date and sex on mass/tarsus ratio (ANCOVA, $P < 0.001$ for both tests), but found no significant interaction ($P = 0.66$). Both sexes increased in body condition index over time. While males had significantly higher condition indices than females, the rate of condition increase was virtually identical between the sexes.

DISCUSSION

Our data suggest that there were sex-related differences in mortality and body condition in 25–32 d White Ibis nestlings during an interruption in food availability, and that this pattern was not a result of sex bias in the hatch order. Water level had been increasing for about a month previous to our collection and

such increases are typically associated with nest abandonment and limited prey availability in White Ibises (Frederick 1987; Frederick and Collopy 1989; Bildstein *et al.* 1990; Russell *et al.* 2002; Gawlik 2002). We found no evidence of predation or disease at the colony; in fact, most dead ibis chicks were untouched by predators or scavengers. Although disease seems unlikely because no adult birds were found dead, it is sometimes difficult to determine if disease or parasites are causing nest abandonments and colony failure (Frederick and Spalding 1994) and some SSD birds have been found to have sex-related differences in immunity (Fargello *et al.* 2002). However, the repeated examples of co-occurrence of food shortage and abandonment under very similar hydrological conditions (Frederick and Collopy 1989; Frederick and Spalding 1994) lend strong support to our interpretation of food shortage as a causative factor.

There are multiple forms of bias inherent in many of the patterns that have been described in this work. First, capture technique could be hypothesized to be sex-biased. This appears to be unlikely as capture methods were not altered over the collection period. The population was sampled without replacement; because we collected more males than females, this would only increase our probability of collecting females in the subsequent weeks rather than the observed decrease. Despite the statistical difficulties with hypothesis testing in sex ratio studies due to small sample size when the expected values of a ratio is 0.5 (Ewen *et al.* 2002), our data showed biologically and statistically significant trends toward a male bias.

Second, there may be bias in the estimates of body condition. Sex-specific allometric scaling may account for differences size-corrected mass implying that females and males may be of equal condition despite differences in density. Allometric scaling is generally correlated with body size in adult (Fairbairn 1997) and nestling (Teather and Weatherhead 1994) birds. In breeding adults and in juvenile White Ibises in captive conditions, males have higher size-corrected mass than females (Kushlan 1977a; Kushlan 1977b; Kushlan and Bildstein 1992; unpub-

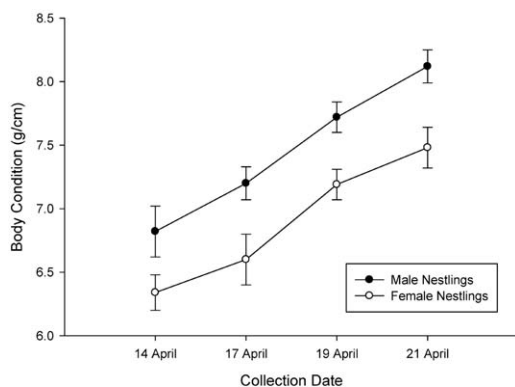


Figure 1. Increase in mean mass (with standard error bars) corrected for tarsus length in male and female White Ibis (*Eudocimus albus*) nestlings collected around middle of April 2005 in the central Everglades. For N of each date and sex see Table 1.

lished data). The apparent lack of difference in rate of increase in body condition between male and female nestlings that we found is consistent with the allometric scaling hypothesis, preventing the rejection of this competing hypothesis. Alternatively, females may have been in consistently worse condition throughout the recorded period. Hydrological evidence suggests that the worst foraging conditions occurred before our collections and that conditions began to improve during our study. Evidence for both these competing hypotheses remains equivocal as anecdotal evidence was found to support both.

We suggest three possible mechanisms by which females might obtain less food than males when food is scarce. First, male nestlings may out-compete their female counterparts for food given by parents. Older and larger ibis nestlings typically are fed first by parents (Rudegeair 1975; Bildstein 1993); if food is limited then the smaller sex may get fewer or smaller regurgitated boluses. There is some evidence to suggest that among birds there is higher mortality in the smaller sex when prey items are small (Anderson *et al.* 1993) and the size of the brood is small (Raberg *et al.* 2005). Using relative definitions supplied by these studies, White Ibises deliver small prey and have small brood sizes. Males may also be better equipped to deal with long intervals between feedings. Poor foraging is associated with longer intervals between chick feedings (Rudegeair 1975; Bildstein *et al.* 1990; Frederick 2001). A larger animal may be better able to survive longer periods between food deliveries. This explanation is not necessarily in competition with or exclusive of the food dominance hypothesis. Finally, parent birds could be investing more food in male offspring during times of food limitation. It is not clear that there would be a benefit to doing so, but the decision would presumably be affected by increased parental fitness caused by producing males over females (e.g., a female biased adult sex ratio).

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LITERATURE CITED

- Anderson, D. J., C. Budde, V. Apanius, J. E. Martinez Gomez, D. M. Bird and W. W. Weathers. 1993. Prey size influences female competitive dominance in nestling American Kestrels (*Falco sparverius*). *Ecology* 74: 367-376.
- Arroyo, B. E. 2002. Fledgling sex ratio variation and future reproduction probability in Montagu's Harrier, *Circus pygargus*. *Behavioral Ecology and Sociobiology* 52: 109-116.
- Babbitt, G. A. and P. C. Frederick. 2007. Selection for bill dimorphism in ibises: an evaluation of hypotheses. *Waterbirds* 30: 199-206.
- Bildstein, K. L., W. Post, J. Johnson and P. Frederick. 1990. Freshwater wetlands, rainfall, and the breeding ecology of white ibises of coastal South Carolina. *Wilson Bulletin* 102: 84-98.
- Bildstein, K. L. 1993. *The Wetland Wanderer*. Smithsonian Institution Press, Washington and London.
- Bortolotti, G. R. 1986. Influence of sibling competition on nestling sex ratios of sexually dimorphic birds. *American Naturalist* 127: 495-507.
- Clutton-Brock, T. H., S. D. Albon and F. E. Guinness. 1985. Parental investment and sex-differences in juvenile mortality in birds and mammals. *Nature* 313: 131-133.
- Cook, M. I. and E. M. Call. 2005. *South Florida Wading Birds Report*. South Florida Water Management District, Volume 11, West Palm Beach, Florida.
- De Santo, T. L., S. G. McDowell and K. L. Bildstein. 1990. Plumage and behavioral development of nestling White Ibises. *Wilson Bulletin* 1990: 226-238.
- Ewen, J. G., P. Cassey and R. A. R. King. 2002. Assessment of the randomization test for binomial sex-ratio distribution in birds. *Auk* 12: 62-68.
- Fairbairn, D. J. 1997. Allometry for sexual size dimorphism: pattern and process for coevolution of body size in males and females. *Annual Review of Ecology and Systematics* 28: 659-687.
- Fargello, J. A., T. Laaksonen, V. Pöyri and E. Korpimäki. 2002. Inter-sexual differences in the immune response of Eurasian Kestrel nestlings under food shortage. *Ecology Letters* 5: 95-101.
- Frederick, P. C. 1987. Chronic tidally-induced nest failure in a colony of White Ibises. *Condor* 89: 413-419.
- Frederick, P. C. 2001. Wading birds in the marine environment. Pages 617-655 *in* The biology of marine birds (B. A. Schreiber and J. Burger, Eds.). CRC, St. Lucie, Florida.
- Frederick, P. C. and M. W. Collopy. 1989. Nesting success of five ciconiiform species in relation to water conditions in the Florida Everglades. *Auk* 106: 625-634.
- Frederick, P. C. and M. S. Spalding. 1994. Factors affecting reproductive success in wading birds (Ciconiiformes) in the Everglades ecosystem. Pages 659-691 *in*: Everglades: the ecosystem in its restoration (S. Davis and J. C. Ogden, Eds.) St. Lucie Press, Delray Beach, Florida.

- Fridolfsson, A. K. and H. Ellegren. 1999. A simple and universal method for molecular sexing of non-ratite birds. *Journal of Avian Biology* 30: 116-121.
- Gawlik, D. E. 2002. The effects of prey availability on the numerical response of wading birds. *Ecological Monographs* 72: 329-346.
- Gonzalez-Solis, J., P. H. Becker, H. Wendeln and M. Wink. 2005. Hatching sex ratio and sex specific chick mortality in Common Terns *Sterna hirundo*. *Journal of Ornithology* 146: 235-243.
- Greenberg, R. 1979. Body size, breeding habitat, and winter exploitation systems in *Dendroica*. *Auk* 96: 756-766.
- Hipkiss, T., B. Hornfeldt, U. Eklund and S. Berlin. 2002. Year-dependent sex-biased mortality in supplementary-fed Tengmalm's Owl nestlings. *Journal of Animal Ecology* 71: 693-699.
- Kalmbach, E., R. W. Furness and R. Griffiths. 2005. Sex-biased environmental sensitivity: natural and experimental evidence for a bird species with larger females. *Behavioral Ecology* 16: 442-449.
- Kushlan, J. A. 1974. The ecology of the White Ibis in southern Florida, a regional study. Ph. D. Dissertation, The University of Miami, Miami, Florida.
- Kushlan, J. A. 1977a. Differential growth of body parts in the White Ibis. *Auk* 94: 164-167.
- Kushlan, J. A. 1977b. Sexual dimorphism in the White Ibis. *Wilson Bulletin* 89: 92-98.
- Kushlan, J. A. and K. L. Bildstein. 1992. White Ibis. *In* The Birds of North America, No. 9 (A. Poole, P. Stettenheim and F. Gill, Eds.). Philadelphia: The Academy of Natural Sciences; Washington, D.C.: American Ornithologists' Union.
- Laaksonen, T., S. Lyytinen and E. Korpimäki. 2004. Sex-specific recruitment and brood sex ratios of Eurasian Kestrels in a seasonally and annually fluctuating northern environment. *Evolutionary Ecology* 18: 215-230.
- Maness, T. J., M. A. Westbrook and D. J. Anderson. 2007. Ontogenic sex ratio variation in Nazca Boobies ends in male-biased adult sex ratio. *Waterbirds* 30: 10-16.
- McDonald, P. G., P. D. Olsen and A. Cockburn. 2005. Sex allocation and nestling survival in a dimorphic raptor: does size matter? *Behavioral Ecology* 16: 922-930.
- Müller, W., T. G. G. Groothuis, C. M. Eising and C. Dijkstra. 2005. An experimental study on the causes of sex-biased mortality in the Black-headed Gull—the possible role of testosterone. *Journal of Animal Ecology* 74: 735-741.
- Nager, R. G., P. Monaghan, D. C. Houston and M. Genovart. 2000. Parental conditional, brood sex ratio and differential young survival: an experimental study in gulls (*Larus fuscus*). *Behavioral Ecology and Sociobiology* 48: 452-457.
- Oddie, K. R. 2000. Size matters: sibling competition between male and female Great Tit offspring. *Journal of Animal Ecology* 69: 903-912.
- Ostreiher, R. 1997. Food division in the Arabian Babbler nest: adult choice or nestling competition? *Behavioral Ecology* 8: 233-238.
- Petit, D. R. and K. L. Bildstein. 1987. Effect of group size and location with the group on the foraging behavior of White Ibises. *Condor* 89: 602-609.
- Raberg, L., M. Stjernman and J. A. Nilsson. 2005. Sex and environmental sensitivity in Blue Tit nestlings. *Oecologia* 145: 496-503.
- Røskoft, E. and T. Slagsvold. 1985. Differential mortality of male and female offspring in experimentally manipulated broods of rook. *Journal of Animal Ecology* 54: 261-266.
- Rudegair, T. J. 1975. The reproductive behavior and ecology of the White Ibis (*Eudocimus albus*). Unpublished Ph.D. Dissertation, University of Florida, Gainesville, Florida.
- Russell, G. J., O. L. Bass, Jr. and S. L. Pimm. 2002. The effect of hydrological patterns and breeding-season flooding on the numbers and distribution of wading birds in Everglades National Park. *Animal Conservation* 5: 185-199.
- Teather, K. L. and P. J. Weatherhead. 1989. Sex-specific mortality in nestling Great-tailed Grackles. *Ecology* 70: 1485-1493.
- Teather, K. L. and P. J. Weatherhead. 1994. Allometry, adaptation, and the growth and development of sexually dimorphic birds. *Oikos* 71: 515-525.
- Torres, R. and H. Drummond. 1999. Variably male-biased sex ratio in a marine bird with females larger than males. *Oecologia* 118: 16-22.