

RESEARCH ARTICLE

Phenology of Body Mass Changes During Reproduction in a Nomadic, Tropical Waterbird, the Scarlet Ibis (*Eudocimus ruber*)

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In birds, the prereproductive buildup of endogenous energy reserves (e.g. body fat) is highly variable and is often thought to be a strategy evolving in response to either seasonal and/or unpredictable changes in breeding conditions. Nomadic behavior is also thought to be an adaptation to unpredictable resource distribution in both space and time. Because of the difficulty in obtaining a longitudinal time series of body masses for free-living individuals of highly nomadic species, the relationship between nomadism and endogenous energy storage has not been explored. In this study, we investigated prereproductive energy storage in a large free-flighted captive colony of highly nomadic waterbird, the Scarlet Ibis, *Eudocimus ruber*. We used size-corrected body mass as an index of body condition both earlier to and during breeding. We compared both breeders and nonbreeders body condition earlier to nesting. We also prevented a subsample of the birds from gaining mass earlier to nesting and compared their nesting success with a control group that was allowed to feed freely. Although significant differences were found in prereproductive body conditions of breeders and nonbreeders, we were unable to control breeding by manipulating prereproductive condition, most likely because of the ability of some birds to rapidly change body condition within several days or weeks earlier to nesting. We conclude that prereproductive energy storage is important for nesting success in both sexes of this highly nomadic species, however energy stores are highly labile

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INTRODUCTION

Breeding birds rely to varying degrees upon endogenous energy reserves, such as stored fat for reproduction. Reliance upon such reserves (“capital breeders”) is typified by migrants breeding at high latitude, often faced with predictable seasonal food shortages [Raveling, 1979; Ankey and MacInnes, 1978; Drent and Daan, 1980, but see also Meijer and Drent, 1999; Gauthier and Hobson, 2003]. Reliance on energy stores in early reproduction may also represent a strategy that evolves in animals and plants in response to breeding conditions that are unpredictable in space or time [Jonsson, 1997]. Reliance upon stored fat or protein, however, carries energetic costs of flight and storage, implying that where local resources are at least seasonally abundant, reliance upon local resources (“income breeding”) may be more efficient [Jonsson, 1997].

Many energetic strategies other than the storage of fat exist by which individuals can cope with the risk of temporal and spatial uncertainty in finding enough food to support a reproductive effort. Pre and postbreeding life history adaptations to temporally unpredictable resources include increased life span, prolonged or intermittent breeding seasons [Nur and Sydeman, 1999; Cam et al., 1998], variable clutch size [Mock and Forbes, 1995], facultative brood reduction [Amundsen and Slagsvold, 1998; Forbes and Mock, 1996], and nomadism [Brown and Hopkins, 1996]. Colonial breeding and local enhancement through social foraging also represent adaptations to spatially unpredictable resources [Brown and Brown, 1996; Clark and Mangel, 1984; Poysa, 1992]. Such strategies may allow for less reliance upon stored reserves for breeding even when reproduction is limited by resource distribution or availability [Meijer and Drent, 1999].

It is not yet clear how to predict when and to what extent birds should be reliant upon body reserves for breeding, as there seem to be multiple fitness solutions to the problem of breeding energetics. The spatial and temporal scale of resource predictability may be key in understanding these solutions. Resource use has been relatively well studied in birds that have predictable but highly seasonal environments [high latitude breeders, e.g. lesser snow goose, *Chen caerulescens*, Carey, 1996], and in situations where food is temporally predictable but spatially unpredictable [seabirds, Whittow and Rahn, 1984; Hull et al., 2002]. Nevertheless, it is less well understood for animals that face unpredictable resources at both large time and large spatial scales (e.g. will food be present at all this year or in five, and will it be here or 300 km away?).

Here, we investigate the importance of body reserves to reproduction for a nomadic, tropical breeder, the Scarlet Ibis (*Eudocimus ruber*) that typically may have large uncertainties in predictability of food resources at large spatial and temporal scales. Scarlet Ibises are considered by some to be conspecific with the White Ibis [*E. albus* see Ramo and Busto, 1987; Hancock et al., 1992] and at minimum, the two are a closely related superspecies. See the American Ornithologists Union checklist at <http://www.aou.org/checklist/index.php3>.

Both Scarlet and White ibises show adaptations to unpredictable breeding and feeding conditions, including central place foraging, colonial breeding, regional nomadism, low breeding site fidelity, hatching asynchrony and brood reduction, and wide postbreeding wandering [Kushlan and Bildstein, 1992; Bildstein, 1993; Frederick et al., 1996; Martinez and Rodrigues, 1999]. The amount of energy White Ibises consume during breeding has been estimated [Kushlan, 1977], but there is no information about the relative use of fat reserves vs local resources during the breeding cycle. The nomadic behavior of the White Ibis makes the long-term study of marked birds nearly impossible, therefore information relating prenesting energetics to reproductive success is difficult to obtain. In this study, we rely upon a large breeding captive population to address basic questions about energetic strategies used by a nomadic species such as this.

We report on the relationship between ibis body condition and reproduction in a large free-flighted captive colony where the birds breed regularly, where birds are individually marked, where age and sex were known, and where we could control food type and amount. We hypothesized that fat levels and body condition earlier to breeding may be related to the initiation and success of breeding. To test this prediction we used two approaches. First, we attempted to manipulate body condition through a supplemental feeding program and compared reproduction (initiation rate and success) of supplemented and unsupplemented birds. Second, we compared body condition indices of successful and unsuccessful breeders. Because reproductive performance can also be influenced by other factors such as age [Saether, 1990], experience [Ratcliffe et al., 1998], time of season [Wilson and Cooper, 1998], and mate quality [Otter et al., 1999], we monitored these conditions either directly or indirectly.

METHODS

The Study Site

During the spring breeding seasons of 1998 and 1999, we studied the reproduction of over 400 individually color-banded Scarlet Ibises in a 3,082 m² mixed species aviary at Disney's Animal Kingdom in Lake Buena Vista, Florida. Other species housed there included Caribbean Flamingo (*Phoenicopterus ruber*), Roseate Spoonbills, (*Platalea ajaja*), and several species of small heron. The enclosure was nearly 20 m high at some points and included some mature trees. The flock was composed of birds predominantly under 6 years of age, with a few individuals as old as their early twenties. The sex ratio was 60/40 male to female, and past breeding had been recorded only during March–July, typical for both White and Scarlet Ibises breeding in the wild in the United States [Kushlan and Bildstein, 1992].

The birds were fed free choice on a commercial flamingo diet (Mazuri Flamingo Complete 5644, 19% protein, 5% fat <http://www.mazuri.com/Index.asp>), supplemented with partially thawed Atlantic Silversides (*Menidia menidia*, averaging 38 g/d per bird). These fish have variable lipid content ranging from about 8 to 32% of their mass depending on time of season in which they are harvested [Schultz and Conover, 1997]. Although the commercial diet was continuously available, the ibises fed only in small groups and rarely alone. This nearly obligate social feeding

behavior resulted in strong dominance interactions over food. Typical feeding bouts involved subordinate birds feeding only when they were not supplanted by more dominant birds, resulting in very short bouts and decreased food intake for subordinate birds (Babbitt and Frederick, unpublished data). Thus, a gradient existed in food intake.

Morphometrics and Preseason Body Condition

Of the >400 ibises, 226(56%) in the 1998 season and 378 (83%) in the 1999 season were lured by food and trapped into in six large flight pens measuring $15 \times 15 \times 3$ m, adjacent to the aviary. The birds were held for as long as 5 weeks in both the years during February and March, though the actual amount of time held varied depending on when the individual was caught ($\bar{x} = 13.2 \pm 8.1$ days). These birds were handled, weighed, and measured once between mid-February and mid-March, just earlier to the initiation of nesting. We measured mass, bill chord, bill length, bill depth at the base of the nares, wing chord (1999 only) and tarsometatarsal length. We used a body condition index calculated as the difference between observed and expected mass predicted from body size [Brown, 1996; Jakob et al., 1996]. Expected mass was predicted through a linear regression of body mass on a body size factor score (separate for males and females). The body size component was derived through principal components analysis of all the linear body measurements taken earlier to nesting. The first principal component that represents body size variation (all positive loadings) accounted for 82% of the morphologic variation in the birds. Of the remaining variation, 12% was owing to shape differences largely related to bill curvature and the rest (6%) was not significantly reduced by the analysis. We estimated the body condition of 226 and 378 birds using this function during the 2 months earlier to nesting in both seasons.

Body Condition and Reproductive Behavior

All nesting was observed by the first author and one assistant observing the breeding birds for 5 hr every weekday throughout the nesting season. Because the nests were located high in the aviary, we could not handle eggs to determine egg or clutch size or quality. Despite this, reproductive success could be defined by progression through nesting stages, which is actually a better indicator of reproductive success for ibises and other nomadic species that often abandon nesting attempts when encountering suboptimal resource abundance. Each individual was identified with colored and number leg bands and was classified progressively through the following stages of nesting as follows. In 1998, nesting attempts were ranked as “no attempt to breed,” “courting or nest building with no egg production,” “nesting with egg production,” and “successful hatching.” In 1999, the nesting stage categories were the same, but the “courting with no egg production” category was split three ways: (A) birds that were observed courting and copulating over several days but were not observed nest building, (B) birds that were observed nest building, and (C) birds that were observed copulating but never courting or nest building. Preseason body condition was compared with outcome of nesting using an ANOVA, with age, nest density, and male morphologic traits (bill length and body size factor score) as co-dependent variables. Post hoc pairwise comparisons were made using *t*-test with Bonferroni adjustment. Nest density was determined as the ratio of the number of other nests present when a pair started nest

building, to the ground area covered by the whole colony during its maximum size. Although we looked for evidence of re-pairing with the same mate in the second year of study, we found little evidence of re-pairing. To track changes in body condition during the breeding season, we weighed individuals repeatedly during the 1999 nesting season using feeding dishes attached to remotely read electronic balances. The proportion of nesting by the aviary population in 1998 and 1999 was compared statistically to assess presence of any season specific differences in nesting. Other possible correlates to reproductive success of pairs such as size, age, and bill length, a measure of male dominance [Babbitt and Frederick, 2007] were also analyzed separately within each sex.

Supplemental Feeding Experiment

We manipulated prenesting body condition of a random sample of birds from the aviary through supplemental feeding. We anticipated that the random selection of individuals into different treatment groups would control for possible effects of dominance or health status. Earlier to nesting, which began in March of both seasons, two groups of 30 birds were isolated from the rest of the flock on 24 January 1999, and held for 54 days in identical adjacent flighted pens ($15 \times 15 \times 3$ m). We recorded body masses both before and after treatment. We supplemented the normal pelleted diet of one group of birds with as many fish (Atlantic Silversides) as they would eat once per day, whereas keeping a control group on the normal diet without supplemental fish. The increased lipid content of the fish fed to supplemental group was expected to increase available lipids in the diet. We compared the timing and ultimate fate of breeding attempts of individuals in these two groups after their release on March 19, 1999. All birds in the flock were trapped, weighed, and measured during the same period and were held approximately 3 weeks (depending on date of capture) before release back into the aviary on March 19. These birds were fed similarly to when they were back in the aviary. The two groups were compared regarding body mass on release to ensure that the diet treatment created differences in the body conditions of the birds and later, after the nesting season, with regards to nesting success and timing of nesting.

RESULTS

Body Condition and Reproduction

The proportion of birds that produced eggs or young in the aviary did not differ significantly between 1998 and 1999 (males, $\chi^2 = 1.26$, $P = 0.15$; females $\chi^2 = 0.329$, $P = 0.64$, mean clutch = 2.4 ± 0.7 eggs). Forty-three percent of the males and 34% of the females in the aviary successfully produced eggs or young in 1998 and 34% of males and 30% of females did so in 1999. In 1998, we found lower levels of prebreeding body condition in individuals of both sexes who did not attempt to nest or whose nests did not produce eggs, compared with those whose nests did produce eggs. This difference was significant for females but not males (females: $t = -2.551$, $P = 0.023$). No distinction was made in 1998 between pairs that made no attempt to court or nest and those that courted but did not produce eggs.

In 1999, closer observations from the top of the aviary allowed us to better distinguish between nonbreeding, courting, and egg-laying birds in the nesting colony, and we found a significantly lower prebreeding body condition in both males and females observed only courting or never attempting to build a nest, compared with those that built nests or laid eggs (males, $t = -2.239$, $P = 0.026$; females, $t = -2.34$, $P = 0.021$) (Fig. 1). However, males observed copulating but not nesting later in the season had much lower prebreeding body condition than females in the same category, possibly reflecting typical sex differences in investment in gamete production. Mean differences in body weight between successful and unsuccessful breeding groups were +18.92 g (2.0%) for males and +31.42 g (4.2%) for females in 1998, and +16.81 g (1.8%) for males and +16.88 g (2.3%) for females in 1999, indicating in each sex of each year, successful breeders were heavier than unsuccessful birds. In 1999, 22 males and 20 females were observed copulating with each other but were not observed courting as is typical when a pair bond is formed. These noncourting males were on average 16.95 g (2.5%) below their expected mass, whereas the females were on average 14.83 g (1.5%) above their expected mass.

Nonbreeding males had significantly higher body condition index than nonbreeding females ($t = 2.363$, $df = 100$, $P = 0.02$). This result may be related to the male biased sex ratio (60/40 m/f) in the colony and suggests that some males may have not been able to nest owing to a lack of potential mates, despite having high body condition.

Changes in Body Condition Associated With Reproduction

In 1999, body masses of both males and females in the general flock increased an average of 107 g in the period after their release (March 19) and earlier to nesting with no significant differences in the amount of increase between successful (= laid eggs) and unsuccessful breeders. During incubation, males lost an average of 43.21 g (4.6%) ($n = 14$) whereas females lost an average of 21.67 g (2.9%) ($n = 3$). Females varied significantly in body condition throughout the nesting stages ($F = 6.78$, $P < 0.001$) whereas male condition followed a similar trend but did not vary significantly. In both seasons, the highest body conditions in both sexes were observed during courtship (Fig. 2).

Other Correlates to Reproductive Success

There were no significant differences in mean age of successful and unsuccessful breeders, in either sex. However, failure to progress beyond the courtship stage was common when old males were paired with young females. There were no obvious male morphologic traits, such as size, that were associated with nesting success. However, male bill length (both years) (1998: $r = -0.395$, $P = 0.036$; 1999: $r = -0.485$, $P = 0.049$) was significantly correlated with hatch date, indicating that longer-billed males nested earlier. This was expected owing to the primary role of bill length in establishing male dominance in this species [Babbitt and Frederick, 2007]. Successfully nesting females had significantly larger body size factor scores ($t = -2.868$, $P = 0.005$ in 1999 and $t = -2.321$, $P = 0.027$ in 1998) than unsuccessful females. Because we found no birds re-nesting in 1999 with the same mates, there

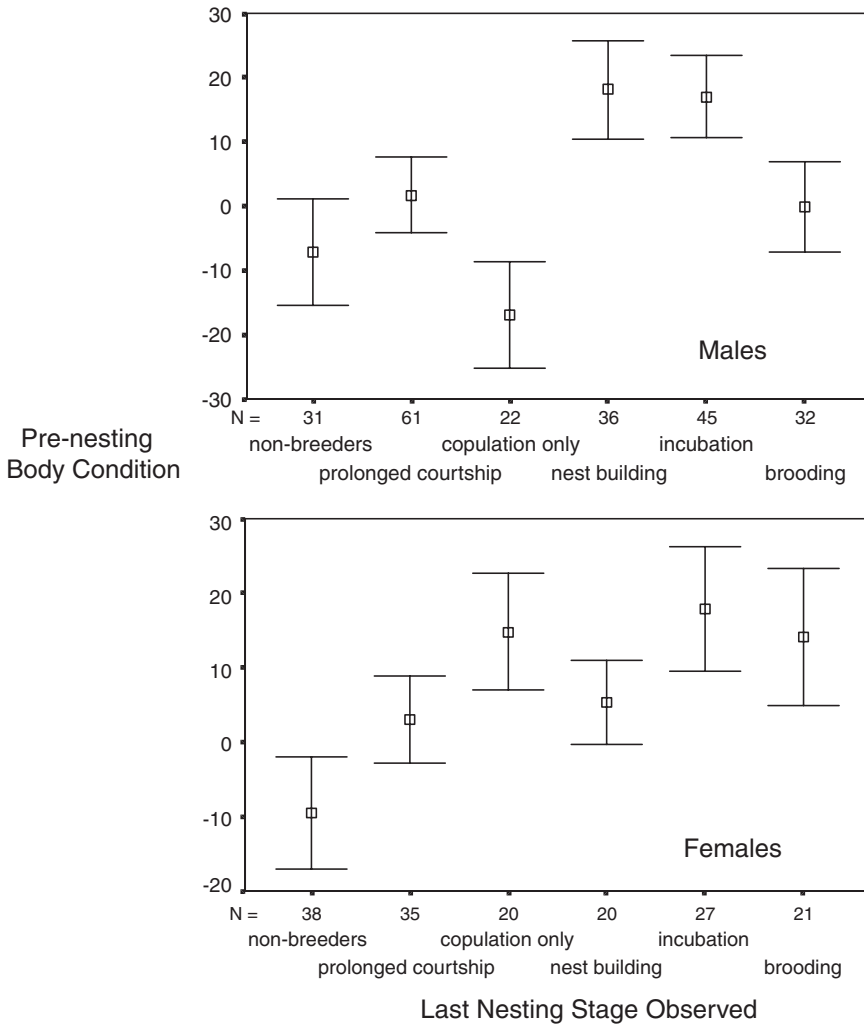


Fig. 1. Average prenesting body condition (size-corrected mass), recorded in late February and early March, compared with the last completed nesting stage in captive Scarlet Ibises during the 1999 nesting season at Disney's Discovery Island in Lake Buena Vista, Florida.

was no evidence that previous nesting experience with particular individuals contributes to nesting success in this species. Nesting success was not significantly associated with nest density.

Supplemental Feeding Experiment

During the 5 weeks that the experimental groups were held separately from the rest of the aviary, the supplemented group gained significantly more mass (and prenesting body condition) than the control group (mean difference of 149 g, $t = -11.5$, $P < 0.001$). However, we found no significant differences between supplemented birds and controls in either nesting success or timing of breeding.

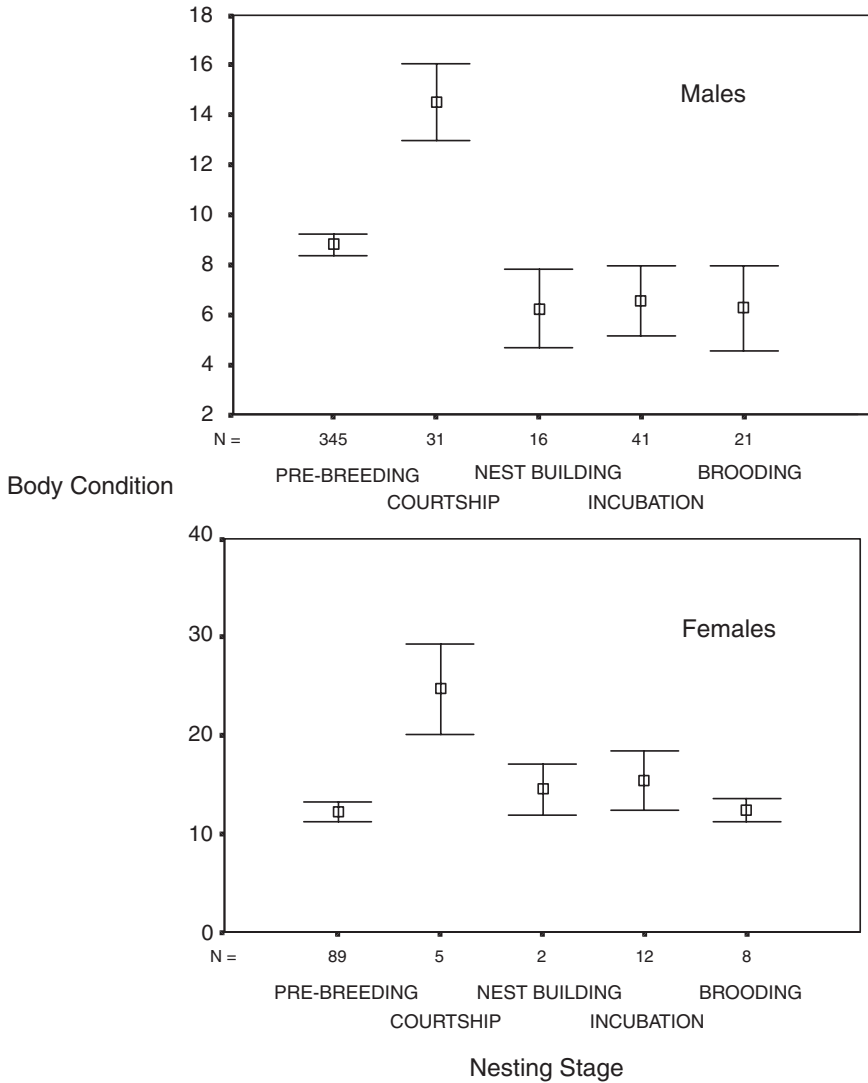


Fig. 2. Average body condition during each nesting stage in captive Scarlet Ibises during the 1998 and 1999 nesting seasons at Disney’s Discovery Island in Lake Beuna Vista, Florida.

DISCUSSION

In both years of study, we found a significant association between prebreeding body condition and the stage of reproduction achieved. The mean difference in prebreeding body condition between breeders and nonbreeders, (16–18 g for males and 16–30 g for females), represents about 44% of the typical estimated fat component in the body of an 800 g bird [based on allometry of Calder, 1984]. We observed large individual variation in prebreeding body condition, ranging 30% above and below expected mass for males and females. This might suggest that the fat/lipid component in the body of a Scarlet Ibis may be more than what is predicted

by allometric comparisons across taxa. Or conversely, not all of size-corrected mass may be owing to fat and there could be significant muscle mass differences, particularly in a captive flock where long distance flying is not mandatory.

We were unable to influence breeding status or success by supplemental feeding, even though we were able to achieve marked differences in body condition by the time the birds were released back into the aviary. This result seems to contradict the evidence (above) that body condition influences breeding success. However, it seems quite likely that even in the short time between release and breeding, the birds were able to increase body mass and condition by feeding. Body condition in the rest of the aviary (nonexperimental birds) increased overall in both males and females just earlier to nesting. Both control and experimental birds began nesting on average 5 weeks after their release into the aviary, suggesting that this amount of time was not limiting for increasing body condition to the point of reproduction. We observed some individuals increase in mass by 100 g in as little as 2 weeks. Thus, the differences in body condition we established through supplemental feeding were apparently overwhelmed by prebreeding hyperphagia. Taken as a whole, the evidence suggests that increased body condition was a precursor to breeding, and that mass gain can be accomplished in a short period immediately earlier to breeding when new sources of food are discovered.

The magnitude and speed of body mass change in both sexes of our ibises was similar to that of female wood ducks (*Aix sponsa*), an income breeder that relies upon prelaying hyperphagia to acquire lipids necessary for egg production [Drobney, 1980]. However, unlike wood ducks, the ibises in our study peaked in body mass during the prenesting period rather than the laying period. This latter characteristic is similar to high latitude "capital" breeders. Male and female Cackling Canada Geese (*Branta canadensis minima*) exhibit a peak of a 20–30% increase in mass during the prelaying period [Raveling, 1979]. However, the ibises exhibited at most a 10–12% increase in mass. Unlike the female Lesser Snow Goose, another high latitude capital breeder [Ankey and MacInnes, 1978], the mass loss in male and female ibises does not continue steadily throughout the nesting cycle. For the ibises in our study, this lack of decline in mass may be an artifact of continuously available food and very reduced energetic costs in the captive situation. The relevance of these results to wild populations of this species must therefore be gauged cautiously. However, the ability to gain mass rapidly just earlier to breeding does not appear to be an artifact of captivity and is probably significant in characterizing the reproductive energetics of this species. Therefore, the spatially and temporally heterogeneous food supply experienced by nomadic tropical birds may favor an intermediate energetic strategy that exists midway on the continuum from capital to income breeders. The acute peak and subsequent drop in body reserves observed in both sexes during courtship (Fig. 2) is suggestive that energetic demand is greatest at this time. Apparently, energy gained just earlier to courtship is also mostly spent during courtship and energetic demands of later stages of reproduction are met by dietary incomes. Male ibises may have to rely upon their larger size and greater fasting endurance during courtship to mate-guard during the female's most fertile period. Extra-pair copulations and nearly continuous mate guarding are evident in wild populations of White Ibises [Frederick, 1987], and we observed in this study that 24% of copulations did occur outside of socially bonded pairs.

CONCLUSION

We conclude that in Scarlet Ibises, (1) an increase in body mass is a precursor to breeding, and that the increase in body mass may be achieved in a fairly short period by prebreeding hyperphagia. This is logical for a bird that has very little philopatry [Frederick and Ogden, 1997] and that breeds somewhat spontaneously [Bildstein, 1993]. (2) The reliance upon body reserves during courtship is probably related to nearly continuous nest attendance required of males and also, to a lesser extent, females. There may also be a large energetic cost of accumulating large fat reserves for both White and Scarlet ibises during breeding as distance to food resources is highly unpredictable and flight distances may be long [cf 20–60 km one way, Kushlan and Bildstein, 1992].

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