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**Phenology of body mass changes during reproduction in a nomadic,
tropical waterbird, the Scarlet Ibis (*Eudocimus ruber*)**

GREGORY A. BABBITT^{1,2} AND PETER C. FREDERICK³

¹Center of Evolutionary Functional Genomics, The Biodesign Institute,
Arizona State University, Tempe, AZ 85287-5001

²Corresponding Author: Gregory.Babbitt@asu.edu

³Department of Wildlife Ecology and Conservation, University of Florida, Gainesville,
FL 32605

Running head – Reproduction and Nutrition in Scarlet Ibis

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5 In birds, the pre-reproductive buildup of endogenous energy reserves (e.g. body
6 fat) is highly variable and is often thought to be a strategy evolving in response to either
7 seasonal and/or unpredictable changes in breeding conditions. Nomadic behavior is also
8 thought to be an adaptation to unpredictable resource distribution in both space and time.
9 Because of the difficulty in obtaining a longitudinal time series of body masses for free-
10 living individuals of highly nomadic species, the relationship between nomadism and
11 endogenous energy storage has not been explored. In this study, we investigated pre-
12 reproductive energy storage in a large free-flighted captive colony of highly nomadic
13 waterbird, the Scarlet Ibis, *Eudocimus ruber*. We used size-corrected body mass as an
14 index of body condition both prior to and during breeding. We compared both breeders
15 and non-breeders body condition prior to nesting. We also prevented a sub-sample of the
16 birds from gaining mass prior to nesting and compared their nesting success with a
17 control group that was allowed to feed freely. While significant differences were found
18 in pre-reproductive body conditions of breeders and non-breeders, we were unable to
19 control breeding by manipulating pre-reproductive condition, most likely because of the
20 ability of some birds to rapidly change body condition within several days or weeks prior
21 to nesting. We conclude that pre-reproductive energy storage is important for nesting
22 success in both sexes of this highly nomadic species, however energy stores are highly
23 labile and can be rapidly obtained through pre-nesting hyperphagia.
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KEYWORDS – avian, nutrition, reproduction, nomadism

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 post-breeding 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, since 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). But it is less well understood for animals that face

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3 unpredictable resources at both large time and large spatial scales (eg, will food be
4 present at all this year or in five, and will it be here or three hundred km away?).
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7 Here, we investigate the importance of body reserves to reproduction for a
8 nomadic, tropical breeder, the Scarlet Ibis (*Eudocimus ruber*) that typically may have
9 large uncertainties in predictability of food resources at large spatial and temporal scales.
10 Scarlet Ibises are considered by some to be conspecific with the White Ibis (*Eudocimus*
11 *albus* see Ramo and Busto 1987, Hancock et al. 1992) and at minimum, the two are a
12 closely related superspecies. See the American Ornithologists Union checklist at
13 <http://www.aou.org/checklist/index.php3> .
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19 Both Scarlet and White ibises show adaptations to unpredictable breeding and
20 feeding conditions, including central place foraging, colonial breeding, regional
21 nomadism, low breeding site fidelity, hatching asynchrony and brood reduction, and wide
22 postbreeding wandering (Kushlan and Bildstein, 1992, Bildstein 1993, Frederick et al.
23 1996, Martinez and Rodrigues 1999). The amount of energy White Ibises consume
24 during breeding has been estimated (Kushlan 1977), but there is no information about the
25 relative use of fat reserves vs local resources during the breeding cycle. The nomadic
26 behavior of the White Ibis makes the long term study of marked birds nearly impossible,
27 therefore information relating pre-nesting energetics to reproductive success is difficult to
28 obtain. In this study, we rely upon a large breeding captive population to address basic
29 questions about energetic strategies used by a nomadic species such as this.
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39 We report on the relationship between ibis body condition and reproduction in a
40 large free-flighted captive colony where the birds breed regularly, where birds are
41 individually marked, where age and sex were known, and where we could control food
42 type and amount. We hypothesized that fat levels and body condition prior to breeding
43 may be related to the initiation and success of breeding. To test this prediction we used
44 two approaches. First, we attempted to manipulate body condition through a
45 supplemental feeding program and compared reproduction (initiation rate and success) of
46 supplemented and unsupplemented birds. Second, we compared body condition indices
47 of successful and unsuccessful breeders. Because reproductive performance can also be
48 influenced by other factors such as age (Saether 1990), experience (Ratcliffe et al. 1998),
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3 time of season (Wilson and Cooper 1998), and mate quality (Otter et al. 1999), we
4 monitored these conditions either directly or indirectly.
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8 9 **METHODS**

10 11 The Study Site

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15 During the spring breeding seasons of 1998 and 1999, we studied the
16 reproduction of over 400 individually color-banded Scarlet Ibises in a 3,082m² mixed
17 species aviary at Disney's Animal Kingdom in Lake Beuna Vista, Florida. Other species
18 housed there included Caribbean Flamingo (*Phoenicopterus ruber*), Roseate Spoonbills,
19 (*Platalea ajaja*) and several species of small heron. The enclosure was nearly 20m high
20 at some points and included some mature trees. The flock was composed of birds
21 predominantly under 6 years of age, with a few individuals as old as their early twenties.
22 The sex ratio was 60/40 male to female, and past breeding had been recorded only during
23 March – July, typical for both White and Scarlet Ibises breeding in the wild in the United
24 States (Kushlan and Bildstein 1992).
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33 The birds were fed free choice on a commercial flamingo diet (Mazuri Flamingo
34 Complete #5644, 19 % protein, 5 % fat <http://www.mazuri.com/Index.asp>),
35 supplemented with partially thawed Atlantic Silversides (*Menidia menidia*, averaging 38
36 g/d per bird). These fish have variable lipid content ranging from about 8% to 32% of
37 their mass depending on time of season in which they are harvested (Schultz and Conover
38 1997). Although the commercial diet was continuously available, the ibises fed only in
39 small groups, and rarely alone. This nearly obligate social feeding behavior resulted in
40 strong dominance interactions over food. Typical feeding bouts involved subordinate
41 birds feeding only when they were not supplanted by more dominant birds, resulting in
42 very short bouts and decreased food intake for subordinate birds (Babbitt and Frederick
43 unpub data). Thus a gradient existed in food intake.
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54 Morphometrics and Pre-season Body Condition

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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 6 large flight pens measuring 15x15x3 meters, adjacent to the aviary. The birds were held for as long as 5 weeks in both 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 prior 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 upon 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 prior to nesting. The first principal component which represents body size variation (all positive loadings) accounted for 82% of the morphologic variation in the birds. Of the remaining variation, 12% was due 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 two months prior 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 five hours 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 which often abandon nesting attempts when encountering sub-optimal 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

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3 production” and “successful hatching”. In 1999, the nesting stage categories were the
4 same, but the “courting with no egg production” category was split three ways: A) birds
5 that were observed courting and copulating over several days but were not observed nest
6 building, B) birds that were observed nest building, and C) birds that were observed
7 copulating but never courting or nest building. Pre-season body condition was compared
8 with outcome of nesting using an ANOVA, with age, nest density, and male morphologic
9 traits (bill length and body size factor score) as co-dependent variables. Post-hoc pairwise
10 comparisons were made using t-test with Bonferroni adjustment. Nest density was
11 determined as the ratio of the number of other nests present when a pair started nest
12 building, to the ground area covered by the whole colony during its maximum size.
13 Although we looked for evidence of re-pairing with the same mate in the second year of
14 study, we found little evidence of re-pairing. In order to track changes in body condition
15 during the breeding season, we weighed individuals repeatedly during the 1999 nesting
16 season using feeding dishes attached to remotely read electronic balances. The proportion
17 of nesting by the aviary population in 1998 and 1999 was compared statistically to assess
18 presence of any season specific differences in nesting. Other possible correlates to
19 reproductive success of pairs such as size, age and bill length, a measure of male
20 dominance (Babbitt and Frederick 2007) were also analyzed separately within each sex.
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37 Supplemental Feeding Experiment

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40 We manipulated pre-nesting body condition of a random sample of birds from the
41 aviary through supplemental feeding. We anticipated that the random selection of
42 individuals into different treatment groups would control for possible effects of
43 dominance or health status. Prior to nesting, which began in March of both seasons, two
44 groups of 30 birds were isolated from the rest of the flock on 24 January 1999, and held
45 for 54 days in identical adjacent flighted pens (15x15x3 meters). We recorded body
46 masses both before and after treatment. We supplemented the normal pelleted diet of one
47 group of birds with as many fish (Atlantic Silversides) as they would eat once per day,
48 while keeping a control group on the normal diet without supplemental fish. The
49 increased lipid content of the fish fed to supplemental group was expected to increase
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3 available lipids in the diet. We compared the timing and ultimate fate of breeding
4 attempts of individuals in these two groups after their release on March 19, 1999. All
5 birds in the flock were trapped, weighed and measured during the same period, and were
6 held approximately 3 weeks (depending on date of capture) before release back into the
7 aviary on March 19. These birds were fed similarly to when they were back in the
8 aviary. The two groups were compared regarding body mass upon release to ensure that
9 the diet treatment created differences in the body conditions of the birds and later, after
10 the nesting season, with regards to nesting success and timing of nesting.
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18 19 RESULTS

20 21 Body Condition and Reproduction

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26 The proportion of birds that produced eggs or young in the aviary did not differ
27 significantly between 1998 and 1999 (males, $\chi^2 = 1.26$, $p = 0.15$; females $\chi^2 = 0.329$, $p =$
28 0.64 , mean clutch = 2.4 ± 0.7 eggs). Forty-three percent of the males and 34% of the
29 females in the aviary successfully produced eggs or young in 1998 and 34% of males and
30 30% of females did so in 1999. In 1998, we found lower levels of pre-breeding body
31 condition in individuals of both sexes who did not attempt to nest or whose nests did not
32 produce eggs, compared to those whose nests did produce eggs. This difference was
33 significant for females but not males (females: $t = -2.551$, $p=0.023$). No distinction was
34 made in 1998 between pairs that made no attempt to court or nest, and those that courted
35 but did not produce eggs.
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44 In 1999, closer observations from the top of the aviary allowed us to better
45 distinguish between non-breeding, courting, and egg-laying birds in the nesting colony,
46 and we found a significantly lower pre-breeding body condition in both males and
47 females observed only courting or never attempting to build a nest, compared to those
48 that built nests or laid eggs (males, $t = -2.239$, $p = 0.026$; females, $t = -2.34$, $p = 0.021$)
49 (Figure 1). However, males observed copulating but not nesting later in the season had
50 much lower pre-breeding body condition than females in the same category, possibly
51 reflecting typical sex differences in investment in gamete production. Mean differences
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3 in body weight between successful and non-successful breeding groups were +18.92 g
4 (2.0%) for males and +31.42 g (4.2%) for females in 1998, and +16.81 g (1.8%) for
5 males and +16.88 g (2.3%) for females in 1999, indicating in each sex of each year,
6 successful breeders were heavier than unsuccessful birds. In 1999, 22 males and 20
7 females were observed copulating with each other but were not observed courting as is
8 typical when a pair bond is formed. These non-courting males were on average 16.95 g
9 (2.5%) below their expected mass, while the females were on average 14.83 g (1.5 %)
10 above their expected mass.
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18 Non-breeding males had significantly higher body condition index than non-
19 breeding females ($t = 2.363$, $df = 100$, $p = 0.02$). This result may be related to the male
20 biased sex ratio (60/40 m/f) in the colony and suggests that some males may have not
21 been able to nest due to a lack of potential mates, despite having high body condition.
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24 25 26 Changes in Body Condition Associated with Reproduction

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30 In 1999, body masses of both males and females in the general flock increased an
31 average of 107 grams in the period after their release (March 19) and prior to nesting with
32 no significant differences in the amount of increase between successful (=laid eggs) and
33 unsuccessful breeders. During incubation, males lost an average of 43.21 grams (4.6%)
34 ($n = 14$;) while females lost an average of 21.67 grams (2.9%) ($n = 3$). Females varied
35 significantly in body condition throughout the nesting stages ($F = 6.78$, $p < 0.001$) while
36 male condition followed a similar trend but did not vary significantly. In both seasons,
37 the highest body conditions in both sexes were observed during courtship (Figure 2).
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45 46 Other Correlates to Reproductive Success

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50 There were no significant differences in mean age of successful and unsuccessful
51 breeders, in either sex. However, failure to progress beyond the courtship stage was
52 common when old males were paired with young females. There were no obvious male
53 morphologic traits, such as size, that were associated with nesting success. However,
54 male bill length (both years) (1998: $r = -0.395$, $p = 0.036$; 1999: $r = -0.485$, $p = 0.049$)
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3 was significantly correlated with hatch date, indicating that longer-billed males nested
4 earlier. This was expected due to the primary role of bill length in establishing male
5 dominance in this species (Babbitt and Frederick 2007). Successfully nesting females
6 had significantly larger body size factor scores ($t = -2.868$, $p = 0.005$ in 1999 and $t = -$
7 2.321 $p = 0.027$ in 1998) than non-successful females. Because we found no birds re-
8 nesting in 1999 with the same mates, there was no evidence that previous nesting
9 experience with particular individuals contributes to nesting success in this species.
10 Nesting success was not significantly associated with nest density.
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18 19 Supplemental Feeding Experiment

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23 During the 5 weeks that the experimental groups were held separately from the
24 rest of the aviary, the supplemented group gained significantly more mass (and pre-
25 nesting body condition) than the control group (mean difference of 149 grams, $t = -11.5$,
26 $p < 0.001$). However, we found no significant differences between supplemented birds and
27 controls in either nesting success or timing of breeding.
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33 **DISCUSSION**

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37 In both years of study, we found a significant association between pre-breeding
38 body condition and the stage of reproduction achieved. The mean difference in pre-
39 breeding body condition between breeders and non-breeders, (16-18 grams for males and
40 16-30 grams for females), represents about 44% of the typical estimated fat component in
41 the body of an 800 gram bird (based on allometry of Calder 1984). We observed large
42 individual variation in pre-breeding body condition, ranging 30% above and below
43 expected mass for males and females. This might suggest that the fat/lipid component in
44 the body of a Scarlet Ibis may be more than what is predicted by allometric comparisons
45 across taxa. Or conversely, not all of size-corrected mass may be due to fat and there
46 could be significant muscle mass differences, particularly in a captive flock where long
47 distance flying is not mandatory.
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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 (non-experimental birds) increased overall in both males and females just prior to nesting. Both control and experimental birds began nesting on average five 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 grams in as little as two weeks. Thus the differences in body condition we established through supplemental feeding were apparently overwhelmed by pre-breeding 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 prior 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 pre-laying 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 pre-nesting 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 pre-laying period (Raveling 1979). However, the ibises exhibited at most a 10-12% increase in mass. And, 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 prior 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 (Figure 2) is suggestive that energetic demand is greatest at this time. Apparently, energy gained just prior 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 in order 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 pre-breeding 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 since 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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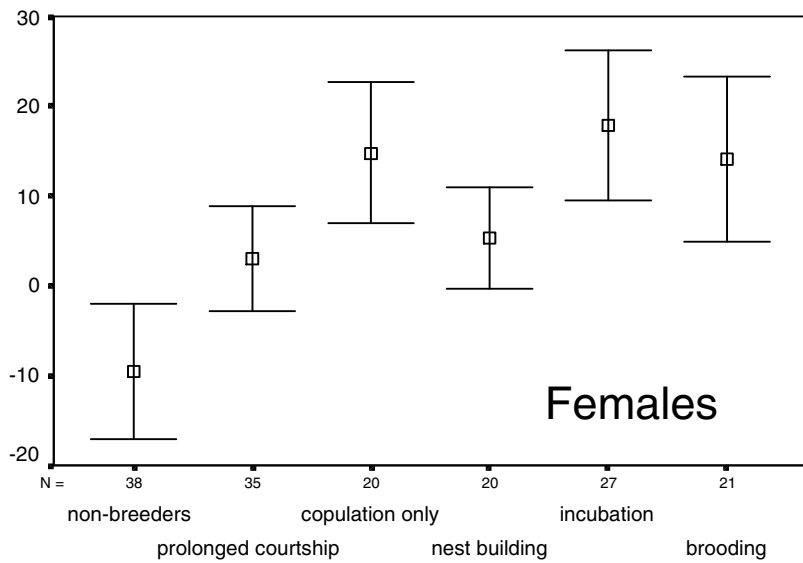
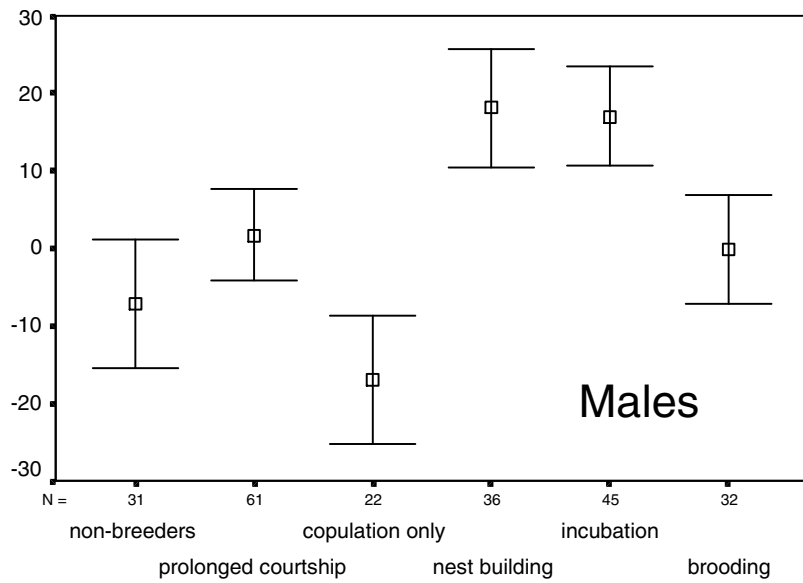
Figure Headings

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

Figure 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 .

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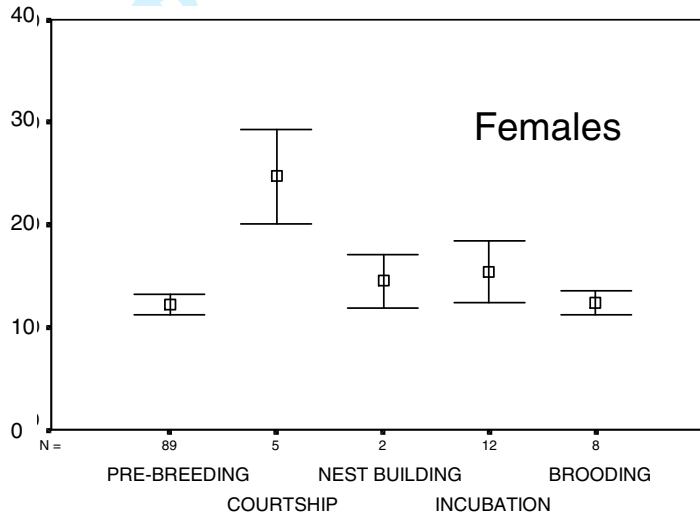
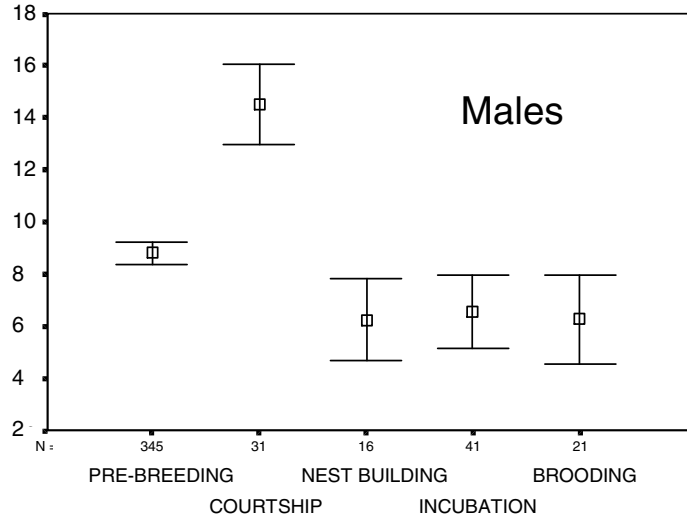
Pre-nesting
Body Condition



Last Nesting Stage Observed

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

Body Condition



Nesting Stage

Figure 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 .