

Temporal and sex-specific variation in growth rates of Marabou Stork *Leptoptilos crumeniferus* chicks

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The nesting success of Marabou Storks *Leptoptilos crumeniferus* breeding in north-eastern Swaziland is closely associated with rainfall, with nests started late in the season exposed to higher rainfall and showing lower success. This may be related to lower food intake and slower growth of the chicks. This study set out to determine whether hatching date and sequence of laying affected the growth rate of chicks. Chicks were also sexed, as Marabou Storks show sexual size dimorphism—males are on average 20% larger—and this trait is often associated with differing patterns of growth between sexes. Nestlings were measured weekly from hatching until they either died or fledged. Nestling development is described in detail and photographs of different-aged chicks are presented. The nestling period was significantly shorter for female chicks, at 94 d, than for male chicks at 104 d. Male and female chicks differed in growth rate and asymptote for both mass and wing length. Unusually, females showed higher instantaneous growth rates for much of the nestling period. Chicks surpassed adult mass before fledging. Date of hatching had an effect on growth rates, with chicks at late nests having slower growth, consistent with a decline in food availability. Marabou Storks appear to be slower growing than expected for the Ciconiidae, the taxonomic family to which they belong.

Introduction

Marabou Storks are large scavenging birds associated with humans across much of Africa (Brown et al. 1982). Despite being widespread in southern Africa (Anderson and Herremans 1997, Anderson 2000) breeding colonies are restricted to just a few sites (Monadjem 2005, Monadjem et al. 2008), resulting in this species being listed as Vulnerable in Swaziland (Monadjem et al. 2003) and Near Threatened in South Africa (Barnes 2000).

The largest and most active colony of Marabou Storks south of the Limpopo River is at Hlane National Park, Swaziland, where around 30 pairs nest each year (Monadjem and Bamford 2009). Nesting success fluctuates significantly and is closely associated with rainfall both between and within seasons, as nests started late in the breeding season, when rainfall is higher, are less successful than those started early (Monadjem and Bamford 2009). The reasons for this relationship are not clear but may be related to food intake by the chicks (Pomeroy 1978). The growth of Marabou Stork chicks has been studied in captivity by Kahl (1966) who hand-raised three chicks from hatching to 65 d of age, which covered only the first half of the approximately 95–115 d nestling developmental period (Brown et al. 1982). Monadjem (2005), observing the development of two chicks in the wild, presented growth curves for nestlings of this species. However, these previous studies were of chicks of unknown sex, and Marabou Storks show a slight sexual size

dimorphism, with males being about 20% larger than females (mean weights 7.1 kg and 5.7 kg, respectively; Pomeroy 1977). Many size-dimorphic species show sexually different growth patterns (Richner 1991), with the ultimately smaller sex often having lower growth rates or shorter nestling periods.

The current study presents growth curves for Marabou Stork chicks based on a sample of chicks of known sex and hatching date. The main objective of the study was to determine whether sex, hatching date and sequence of laying affect the growth rate of Marabou Stork chicks.

Methods

Study area

This study was conducted in the 16 000 ha Hlane National Park (31°53' S, 26°18' E), Swaziland. The vegetation is dominated by knobthorn *Acacia nigrescens* woodland interspersed with riverine forest. The climate is subtropical [see Monadjem (2005) and Monadjem and Bamford (2009) for more details on topography and climate]. The Marabou Stork breeding season covers the austral winter: 2–3 eggs are laid in May or June; eggs hatch after approximately 30 d incubation, usually in June or July, which is the coldest time of year; and the chicks fledge in October (Monadjem and Garcelon 2005, Monadjem et al. 2008, Monadjem and Bamford 2009).

Data collection

Breeding Marabou Storks were monitored regularly between 2003 and 2007 (Monadjem and Bamford 2009). In the 2008 breeding season, we checked all known nest sites for activity. Additional nests were found by searching on foot and from the air using a microlight aircraft. Active nests (a nest on which eggs were found or adult activity was observed) were visited twice weekly until the chicks hatched or the nest failed. Chicks were measured once a week, from within 3 d of hatching. Mass, wing length, tarsus length, bill length and tail length were recorded and a photograph taken of each chick on each visit.

A total of 24 nests with eggs was found during the 2008 breeding season. Of the 69 eggs that were laid in these nests, 48 hatched and 26 chicks successfully fledged. Complete growth curves were available for 22 chicks, 21 of which were sexed. Chicks were categorised as first or second hatched depending on their hatching sequence. Although three chicks may be present in a nest, we have only ever recorded a maximum of two chicks fledging in over seven years of observing Marabou Storks at nests. Nests were defined as being early or late according to whether the laying date was before or after the median laying date (Monadjem and Bamford 2009) – in the 2008 season this was the 12th of June. Fledging date was taken as the date of the last visit on which the chick was still on the nest.

Sexing

Genomic DNA was isolated from blood collected in EDTA tubes at the National Zoological Gardens, Pretoria, using the QIAGEN DNeasy Blood and Tissue Kit[®]. Amplification of the *CHD1* gene was conducted using the 2550F/2718R (Fridolfsson and Ellegren 1999) primer set. PCR amplification was carried out in a total volume of 25 μ L and included a no template control as well as positive controls for a male and female bird of known sex. PCR was conducted with Promega GoTaq[®] DNA polymerase, which has a 1 \times buffer containing 10 mM Tris-HCl (pH 9.0), 50 mM potassium chloride (KCl) and 0.1% Triton[®] X100. The final reaction conditions were as follows: 1 \times PCR buffer, 1.5 mM MgCl₂, 200 μ M of 2'-deoxynucleotide triphosphates (dNTPs), 5 pmol each of the forward and reverse primer, 0.25 U Taq DNA polymerase and 10 ng genomic DNA template. The conditions for PCR amplification were as follows: 2 min at 94 °C denaturation, 30 cycles for 30 s at 94 °C, 30 s at 50 °C and 2 min at 72 °C, followed by extension at 72 °C for 10 min. PCR products were added to tracking dye and were separated by electrophoresis in a 2% agarose gel for 45 min at 100 V in 1 \times Tris-borate-EDTA buffer.

Statistical analyses

Statistical analyses were carried out in R 2.8.1 (R Development Core Team, Vienna; <http://www.r-project.org>). Growth curves for chick mass and wing length were modelled using non-linear regressions. For both measurements several models were tested, and the best fit was given by logistic curves of the form:

$$y = c / (1 + e^{-K \times (\text{Age} - m)})$$

where y is the chick measurement to be modelled, c is the asymptotic size of the chick, K is the logistic constant growth rate, which is proportional to the time required for growth, and m is the inflection point (the point at which the instantaneous growth rate is greatest). Instantaneous growth rates (g) are obtained by differentiation of this equation, and the maximum growth rate (g_{max}) is the instantaneous rate at the inflection point (Richner 1991). Other models tested included the Gompertz curves, and the model as above but with fixed asymptotes.

Growth curves were fitted, and values for c , K and m recorded, for each chick individually. Analysis of variance was used to compare the values of the constants between male and female (sex), 1st hatched and 2nd hatched (hatching order) and early and late nests (laying date). Akaike's information criterion (AIC) was used to select the best model in each case.

Results

Nestling development

The mean mass \pm SD of recently hatched (0 and 1 d old) chicks was 102.3 ± 6.8 g ($n = 12$). When chicks hatch they are sparsely covered in light down with the skin clearly showing through (Figure 1a). There is little visible change in the first 10 d other than an increase in size (Figure 1b). By 21 d (three weeks) of age, the chick is almost entirely covered by white down (Figure 1c). By 35 d (five weeks) the chick is completely covered in thick, white down, but no black feathers are yet showing as the remiges have not yet erupted (Figure 1d). By the age of 50 d (seven weeks), black is clearly showing through the white down as the remiges, coverts and tail feathers start erupting (Figure 1e). This process continues rapidly over the next two to three weeks so that by the age of 65 d (just over nine weeks) the birds are predominantly black, but with white down still showing (Figure 1f). By 80 d of age (11.5 weeks), the chicks resemble adults in plumage and size (Figure 1g) and there is little change between now and fledging at around 90–110 days of age (Figure 1h). Mean mass \pm SD at fledging was 7.6 ± 0.7 kg for males and 6.3 ± 0.8 kg for females, and mean wing length \pm SD was 661 ± 32 mm for males and 579 ± 40 mm for females. Mean fledging times were significantly different between the sexes: 94 d for females and 104 d for males (t -test: $t = -3.14$, $df = 19$, $p = 0.006$).

Growth curves

The data compiled on the different morphometric measurements (Figure 2) showed that the relationship between growth of tarsus and mass was approximately linear, whereas wing growth was more rapid than that of other measurements made and bill growth lagged that of tarsus and mass. Among chicks less than 3 d old there was no difference in mass between males and females (t -test: $t = -0.336$, $df = 10$, $p = 0.70$). The AIC values for the effect of sex, hatching order and laying date on growth parameters are shown in Table 1. Most parameters differed between males and females. Males showed larger asymptotes for both mass (1.24 times larger, $F_{1,19} = 22.2$,



Figure 1: Photographs of eight Marabou Stork chicks of known age: (a) 1 d old, (b) 10 d old, (c) 21 d old, (d) 35 d old, (e) 50 d old, (f) 65 d old, (g) 80 d old, and (h) 105 d old.

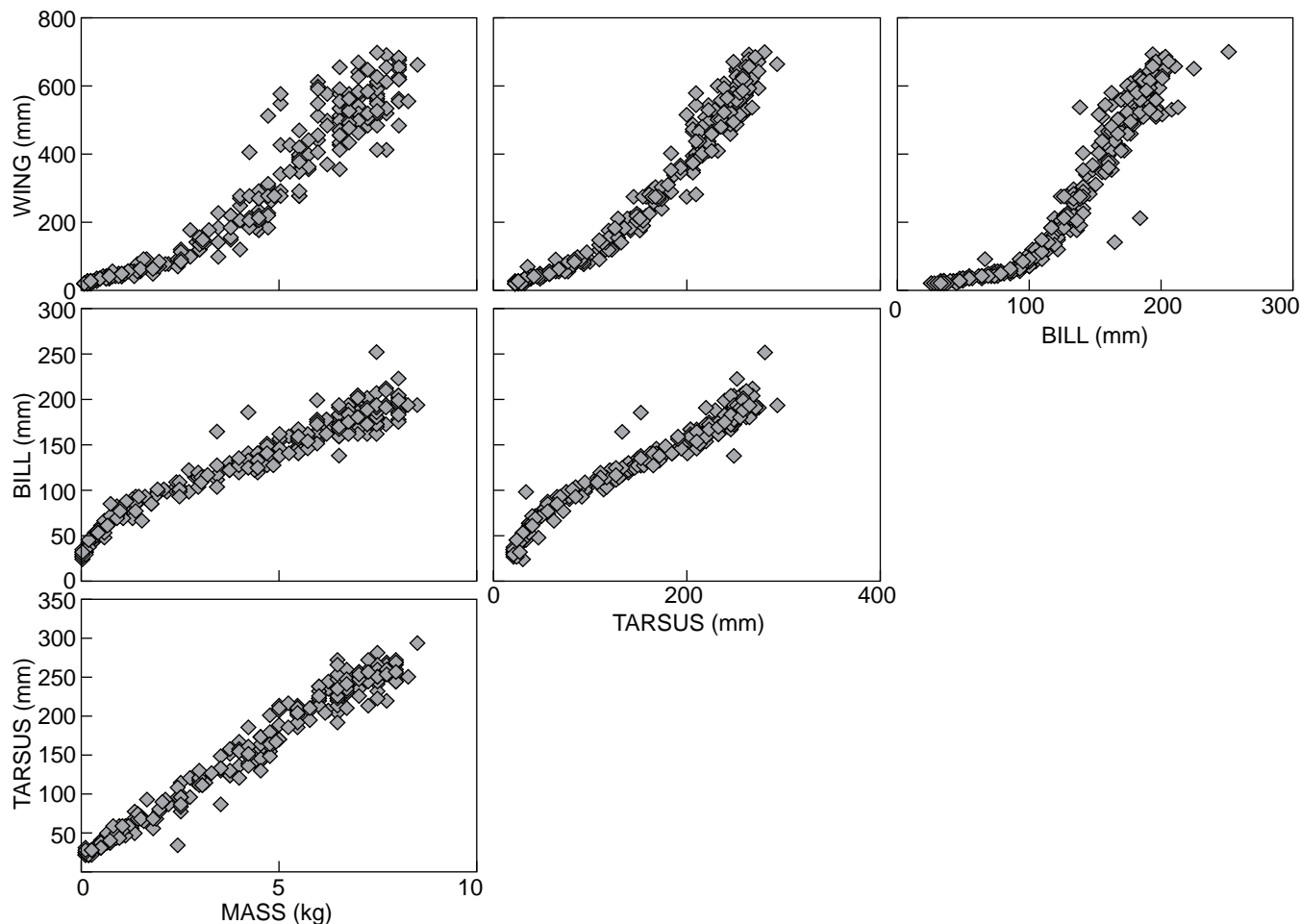


Figure 2: Bivariate plots of morphometric variables measured from 21 Marabou Stork chicks

Table 1: Akaike's information criterion values for models fitted to explain variation between individual Marabou Storks in parameters in logistic growth equations. In each case the best model is in bold. Sex = male or female; order = hatching order, first or second; date = laying date, early or late; c = asymptote; K = logistic growth rate; m = inflection point; g_{\max} = maximum instantaneous growth rate

Model	Mass				Wing length			
	c	K	m	g_{\max}	c	K	m	g_{\max}
Sex+order+date	343.8	-134.3	141.0	183.8	219.2	-153.5	147.7	42.2
Sex+date	341.9	-135.3	142.5	182.5	217.2	-155.3	147.8	41.3
Sex+order	343.8	-131.8	139.6	182.6	228.8	-144.1	146.1	43.4
Date+order	357.3	-130.2	149.5	184.1	232.9	-149.2	150.4	41.3
Sex	341.8	-132.9	141.1	181.3	226.8	-146.0	146.2	42.2
Date	357.8	-132.2	147.7	184.4	232.7	-148.9	148.7	39.7
Order	355.8	-129.4	147.6	183.1	236.0	-143.1	148.6	42.6
Null	435.8	-47.3	221.6	267.8	335.1	-53.1	234.1	161.4

$P < 0.001$) and wing (1.18 times larger, $F_{1,19} = 12.0$, $P = 0.003$) and also had faster maximum growth rates (Table 2, Figures 3 and 4) but took longer to become fully grown, as shown by the larger values for m , due to their larger size. There was more variability between growth curves for male than female chicks (Figure 3a and 4a). Instantaneous growth rates for mass were greater for

females for the first 38 d after hatching (Figure 3b) and throughout this period females had a greater mean mass, although the larger variance of the male chicks meant that the largest individual was usually male. Second-laid eggs generally hatched 1 d later than first-laid eggs. A possible bias in the sex ratios of first- and second-laid eggs—the majority of first-laid eggs (11/16) were male, the majority of

Table 2: Average growth parameters for male and female Marabou Stork chicks. Each parameter is presented as mean ± SD. Sample sizes were: males = 12, females = 9. *c* = Asymptote; *K* = logistic growth rate; *m* = inflection point; *g_{max}* = maximum instantaneous growth rate

Variable	Mass (g)		Wing length (mm)	
	Male	Female	Male	Female
<i>c</i>	8001 ± 759	6434 ± 750	702 ± 50	628 ± 47
<i>K</i>	0.0709 ± 0.0103	0.0785 ± 0.0078	0.0621 ± 0.0060	0.0682 ± 0.0078
<i>m</i>	47.8 ± 7.8	40.3 ± 3.5	62.5 ± 7.8	57.4 ± 6.1
<i>g_{max}</i>	141 ± 16	126 ± 17	10.8 ± 0.5	10.6 ± 0.7

Table 3: Average growth parameters for Marabou Stork chicks from early and late nests. Each parameter is presented as mean ± SD. Sample sizes were: early = 13, late = 9. *c* = Asymptote; *K* = logistic growth rate; *m* = inflection point; *g_{max}* = maximum instantaneous growth rate

Variable	Mass (g)		Wing length (mm)	
	Early	Late	Early	Late
<i>c</i>	7281 ± 943	7628 ± 1293	651 ± 57	708 ± 50
<i>K</i>	0.0772 ± 0.0084	0.0678 ± 0.0117	0.0676 ± 0.0065	0.0593 ± 0.0054
<i>m</i>	44.0 ± 6.1	46.6 ± 9.2	59.6 ± 6.6	62.0 ± 8.6
<i>g_{max}</i>	139 ± 14	127 ± 23	10.9 ± 0.5	10.5 ± 0.5

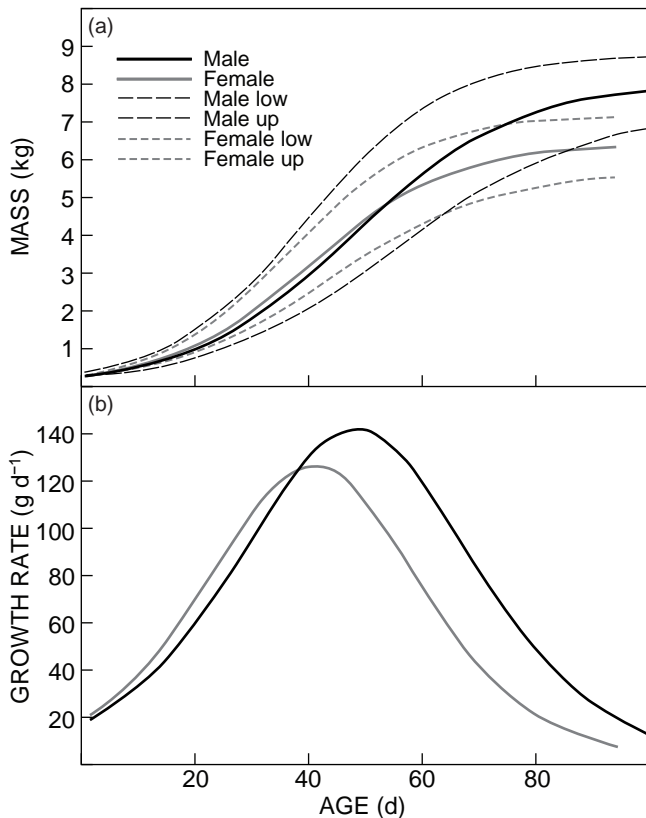


Figure 3: (a) Mean growth curves for mass of male and female Marabou Storks. For each sex, the range of curves generated using the standard deviations in Table 2 is shown in dashed lines. (b) Instantaneous growth rates

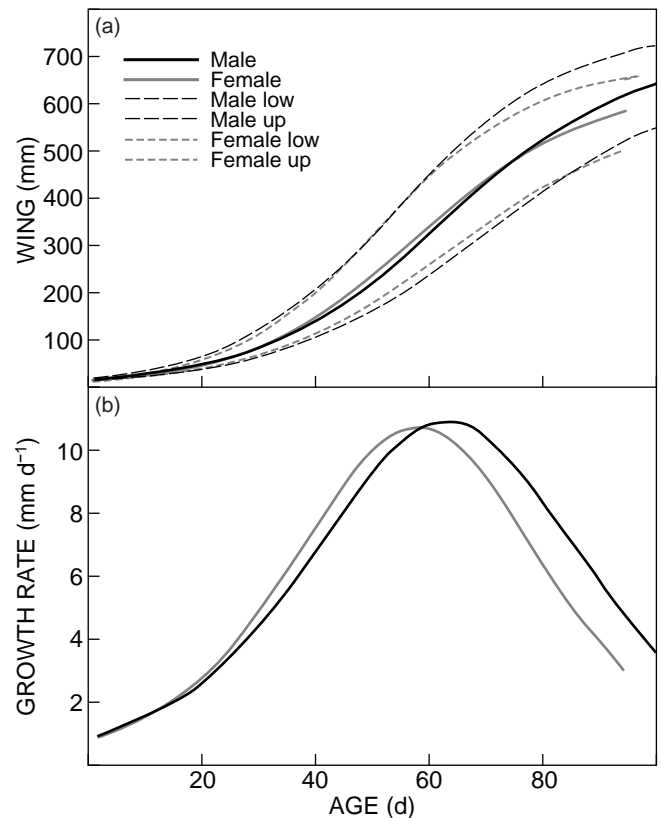


Figure 4: (a) Mean growth curves for wing length of male and female Marabou Storks. For each sex, the range of curves generated using the standard deviations in Table 2 is shown in dashed lines. (b) Instantaneous growth rates

second-laid eggs (6/9) were female—was not significantly different from a random expectation (two-tailed Fisher’s exact test, *p* = 0.19).

Laying date explained some of the differences in asymptote and logistic growth rate between individual

Marabou Storks (Table 1). Chicks of both sexes on late nests showed slower growth rates (0.88 of the rate of early chicks for both mass and wing), with lower values for *K* for both mass and wing, and larger values for *m* (Table 3). Chicks of both sexes on late nests showed larger

asymptotes for wing length. Order of hatching was not well supported in any model, showing only a slight effect on the inflection point in both growth curves.

Discussion

Marabou Storks nesting late in the breeding season generally show lower breeding success than those nesting early (Monadjem and Bamford 2009). This decreased success of late nests is related to increased rainfall late in the season, and may be mediated through a decline in food availability (Monadjem and Bamford 2009). The analyses presented here show that chick growth rates were generally slower among chicks of late-nesting parents, which is consistent with declining food availability. For example, among captive-reared *Gyps* vultures, Houston (1976) showed that chick growth rates were affected by food intake. Similar effects on chicks have been reported for birds in the wild (Jodice et al. 2008). The influence of late nesting on growth patterns was evident even after taking into account the considerable differences in growth between the sexes.

Sex-specific growth patterns have been recorded in various species that show sexual size dimorphism (Richner 1991). In general, the smaller sex shows equal or smaller maximum growth rates, equal or larger logistic growth constants, less variation in growth parameters (but see Schaadt and Bird 1993, Velando et al. 2000) and fledges either at the same time or earlier than the larger sex (Richner 1991). In these respects the Marabou Storks observed here are typical of size-dimorphic species. The Marabou Storks are unusual, however, in that the smaller sex, the female, on average showed larger instantaneous growth rates for mass for the first third of the nestling period (Figure 3b). This was an average difference; the large variation between males meant that the fastest-growing individual was male, as indeed was the slowest-growing individual. Faster instantaneous growth rates in the smaller sex have only been recorded in one other avian species, the Hooded Crow *Corvus cornix* (Richner 1991), although in that case the smaller sex also showed larger maximum growth rates. Earlier fledging in the smaller sex has been recorded in various species (Richner 1991), although not in all size-dimorphic species (Richner 1991, Schaadt and Bird 1993, Weimerskirch et al. 2000). Among blackbirds, females fledge approximately 5% earlier than males (Richner 1991), while in raptors, males, which are smaller, fledge between 7% and 13% earlier (Newton 1979). Female Marabou Storks fledged 10% earlier than males.

It is generally assumed that the larger sex is more costly to the parents (Margath et al. 2007). Differences in body mass of chicks can provide fairly accurate estimates of the increased energetic cost to the parents of rearing those chicks (Margath et al. 2007). This would mean that, although male Marabou Storks are more costly to raise overall, females are more costly for the first 38 d after hatching, perhaps indicating that initially parents devote more resources to the females. Similar results have been found in American Kestrels *Falco sparverius* (Anderson et al. 1997) and Brown Skylarks *Cinclorhamphus cruralis* (Margath et al. 2003), where the ultimately smaller and thus

less costly sex hatches from larger eggs, thereby providing an initial size advantage. A hypothesis to explain this is that in years with high food abundance the initial disadvantage to the larger sex does not affect fledgling quality, and so does not impair production of high-quality sons. When food is scarce, however, the initial size disadvantage results in mortality biased towards the larger sex, skewing brood sex ratios towards the less costly sex (Margath et al. 2003). The nest success recorded here, of 1.08 chicks per pair, is relatively high compared with previous years in the same colony (Monadjem and Bamford 2009), suggesting that food was more abundant. The sex ratio was male biased, albeit not significantly – out of 24 chicks, including three that were sexed but which were excluded from the analysis as complete growth curves were not available, 14 were male. The bias was more pronounced in early nests (10 males out of 16 chicks) and not observed in late nests (four males out of nine chicks). This is also consistent with declining food availability throughout the breeding season. However, the sample sizes in these data are too small for any meaningful statistical analysis of sex ratios among Marabou Storks; a clearer picture may emerge as more data are collected.

The logistic growth curves provided a good fit to the observed growth when compared with other potential models. With the exception of female mass, the estimated asymptotes were higher than the recorded values at fledging. Non-linear regression can overestimate the asymptote if the asymptote is not reached in the observations (Ricklefs et al. 1986). For mass, only four out of 12 males had reached a clear asymptote by the time they fledged, compared to five out of nine females. None of the males that reached an asymptote were in late nests perhaps explaining why late males showed larger estimated asymptotes. The recorded mean weights at fledging (male 7.6 kg, female 6.3 kg) were higher than the mean weights for adults (male 7.1 kg, female 5.7 kg) given by Pomeroy (1977). A single male adult bird in breeding plumage captured in Swaziland weighed 7 kg, comparing well with Pomeroy's (1977) mean mass. It appears that Marabou Storks fledge about 0.5 kg heavier than the average mass of adults. Among non-passerine birds most species are heavier than adult weight at fledging, although the magnitude of the difference varies considerably between species (Ricklefs 1985).

Pomeroy (1978) noted that the nestling period for Marabou Storks is exceptionally long compared with other members of the family Ciconiidae. However, large birds in general have slower growth rates than smaller birds (Ricklefs 1968), and the Marabou Stork is large compared to other storks. When considering a wide range of taxa, Ricklefs (1968) estimated that the growth rate for a species was approximately the power to -0.278 of the adult body weight. Using Pomeroy's (1977) data, this gives an expected growth rate of 0.085 d^{-1} for males and 0.090 d^{-1} for females, slightly larger than the estimates from our data. Starck and Ricklefs (1998) note that comparisons across many taxa have drawbacks and that comparison within a family may be more useful. From the literature, they estimate that within the Ciconiidae the growth rate approximates the power to -0.25 of adult weight. This estimate included Kahl's (1966)

data on Marabou Storks, which were noticeably below the fitted line. The Starck and Ricklefs (1998) estimate was based on data for only five species, although recent data for the White Stork *Ciconia ciconia* (Tsachalidis et al. 2005) fit the relationship well. Based on Pomeroy's (1977) weight data, Starck and Ricklefs (1998) estimate gives an expected growth rate of 0.109 d^{-1} for male Marabou Storks and 0.115 d^{-1} for females. Therefore, Marabou Storks in Swaziland do appear to be slower growing than expected for the Ciconiidae, although the reasons for this are unknown.

Acknowledgements — This is the 14th publication of the All Out Africa Research Unit (www.alloutAfrica.org). We thank Mickey Reilly for permission to study Marabou Storks at Hlane National Park and for logistical support. Mduduzi Ngwenya and various All Out Africa volunteers assisted with the finding of nests and processing of the chicks. Dave Ducasse skilfully flew AM over the study area in a microlight. AM is supported by a British Ecological Society Overseas Bursary.

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