

Sociable Weaver biometrics and primary moult

H Dieter Oschadleus

Avian Demography Unit, Department of Statistical Sciences, University of Cape Town, Rondebosch 7701, South Africa
e-mail: dieter@adu.uct.ac.za

The biometric and primary moult data housed at the South African Bird Ringing Unit (SAFRING) were analysed for the Sociable Weaver *Philetairus socius*. The average body mass and wing length was 27.9g (SD = 2.2) and 74.1mm (SD = 2.5), respectively. Variation in these parameters is not clearly correlated with region, season or climate, other than a negative correlation of body mass with average annual water deficiency. Body mass of Sociable Weavers near Kimberley showed a long-term decrease of 2.9g, probably due to stabilising selection on mass. Primary moult duration varied from 152 days to 169 days and started between 26 January and 31 December in two populations (*socius* and South African *eremnus* respectively). Individual primaries moulted mainly one at a time, each taking 20–28 days to grow fully. Prolonged moult duration in this species is probably an adaptation to reduce energy expenditure, and to grow more durable feathers due to abrasion in entering the nest. The lack of clear patterns of geographical variation in biometrics indicates that the contiguous populations of Sociable Weaver should belong to the nominate species.

Introduction

The Sociable Weaver *Philetairus socius* is a colonial, co-operatively breeding species, best known for its massive communal nests (Craig 2004). It is endemic to the semi-arid savannas of western South Africa, much of Namibia and south-eastern Botswana (Mendelsohn and Anderson 1997).

Recently, Craig (2004) considered the species monotypic. However, Clancey (1989) recognised four sub-species of the Sociable Weaver: *P. s. socius*, *geminus*, *eremnus* and *xericus*. He considered *P. s. eremnus* to have a disjunct range, being sub-divided by the central nominate sub-species (Figure 1). Clancey (1989) described complex variations in plumage colour throughout the species' range. Compared to individuals in the centre, weavers at the north and south of the range had darker upperparts and whiter ventral surfaces. These plumage variations were thought to be largely associated with substrate type. Clancey (1989) also found marginal size variation throughout the species' range, thought to be temperature-dependent: birds in the north had shorter wings than those in the south while birds in the south were larger, with a clinal east-to-west increase in wing length.

In this paper, biometric data from Sociable Weavers ringed in South Africa and Namibia are analysed to investigate whether contiguous populations should belong to the nominate species or not. A subset of the data is used to study seasonal and temporal variations in body mass. The timing and total duration of primary moult are also investigated.

Methods

Morphometric data (body mass and wing length) and primary moult data (De Beer *et al.* 2001) for adult Sociable Weavers were obtained from records submitted between 1970 and May 2004 to SAFRING. Body mass and wing length data were analysed according to the subspecies dis-

tribution map in Clancey (1989), and on a finer scale by degree grid to investigate geographic variation. A degree grid cell is 1° x 1°, e.g. 1915 is the one degree grid cell with 19°S 15°E in the north-western corner. Spearman's rank correlation co-efficient was used to compare body mass and wing length to rainfall, temperature and water deficiency (extracted from Schultze and McGee 1978) by grid cell. Water deficiency is the moisture needed by vegetation that soil water storage and rainfall cannot supply, and is an indicator of drought or aridity (Schultze and McGee 1978).

A comprehensive subset of mass data was obtained from Benfontein Game Farm, 6km south-east of Kimberley, Northern Cape, South Africa (approx. 28°53'S, 24°49'E, see Covas *et al.* 2002 for study area details). To investigate temporal variation in mass, the weighted moving average method developed by Cleveland (1979) and implemented, for example, by Summers *et al.* (1992), was used. This algorithm enables a smooth curve to be fitted to the scatterplot of mean body mass against date. This method does not have discontinuities as happens in the usual moving average or moving window smoothing methods, because individual points are included and then excluded from the moving average. Rainfall models were applied to compare with body mass, using combinations of rainfall in the current and previous months. Monthly rainfall for 1993 to 2003 was obtained from Kimberley Airport (about 15km from Benfontein Game Farm).

To determine the mass of primary feathers, individual feathers from three wings of two Sociable Weaver specimens were oven-dried at 60°C for 24 hours and then weighed on a balance (Ohaus GA200D, precision 0.0001g) (compare Underhill and Summers 1993). Underhill and Joubert (1995) have shown that small samples are adequate to determine the relative masses of primary feathers, because there is little intra-specific variation in this characteristic. The

Underhill–Zucchini moult model (Underhill and Zucchini 1988) was applied to the data sets. The data were considered to be of 'type 2' because Sociable Weavers remain near their nests and are available for capture throughout the year (Mendelsohn and Anderson 1997). The parameters of primary moult were estimated using the transformations recommended by Summers *et al.* (1980, 1983), designed to reduce the bias introduced by the fact that the individual feathers are of different masses. The moult index used was percentage feather mass grown (PFMG), calculated according to the method of Underhill and Summers (1993). The Underhill–Zucchini model was also used to estimate the parameters of moult for individual primary feathers, as done for selected species of waders by Underhill (2003).

Results

The following analyses are based on 4 895 ringing records and 3 069 recapture records of 7 964 adult Sociable Weavers, sampled throughout most of the species' distribution range (Figure 1). The records contained at least body mass, or wing length, or primary moult information.

Geographic and seasonal variation in body mass and wing length

Mean body mass was 27.9g (SD = 2.2, range = 18–39.6, $n = 7\ 846$) and mean wing length was 74.1mm (SD = 2.5, range = 64–84, $n = 5\ 940$).

The mean body mass and wing length were calculated for each subspecies (Table 1). A one-way ANOVA on the ringing data showed that the mean masses of the five groups had a range of 2.8g, with individuals of the *eremnus* population in South Africa being the heaviest (mean mass 28.6g), and individuals of the Namibian population of this subspecies being the lightest (mean mass 25.8g) of all five groups. These differences were statistically significant ($F_{4,7841} = 416.8$, $P < 0.001$). There was a similar pattern for wing length, with *eremnus* individuals having a longer wing than individuals of other populations ($F_{4,5935} = 455.8$, $P < 0.001$) (Table 1). Wing lengths obtained from ringing data were smaller than Clancey's (1989) museum specimen data (Table 1).

To investigate geographic variation in body mass in more

detail, and independently of Clancey's subspecies, the mean masses per degree grid cell were calculated (Table 2). A one-way ANOVA showed significant variation ($F_{15,7286} = 131.2$, $P < 0.001$), with individuals in grid 2824 (part of the *eremnus* population in South Africa) being the heaviest (mean mass 28.7g), and individuals in grid 2315 (part of the *eremnus* population in Namibia) being the lightest (mean mass 24.1g). Similarly, significant variation was obtained for wing length ($F_{8,5400} = 222.7$, $P < 0.001$), although the largest wing length was in grid 2821 (part of the *socius* population). Tabulating the difference of the mean mass or wing length per grid from the overall mean did not, however, show any obvious pattern (Table 2).

Mean body mass, wing length, annual rainfall, temperature and annual water deficiency were averaged for each grid cell (14 in total) to determine whether there is a change in body mass or wing length with increasing aridity. There was no significant correlation between wing length and mean annual rainfall ($r_s = 0.36$, $P < 0.05$), mean annual tem-

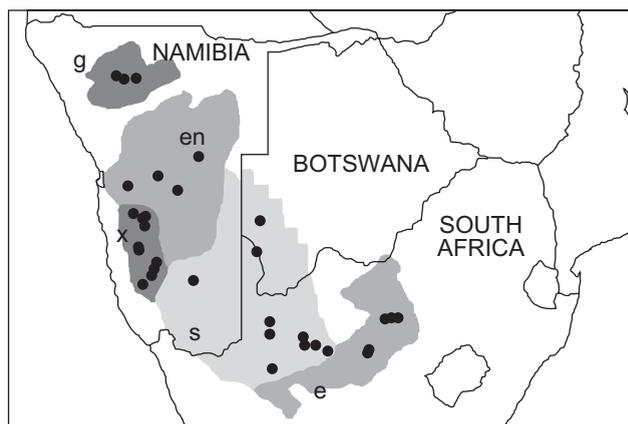


Figure 1: Distribution of Sociable Weavers, showing the races described by Clancey (1989) where *s* = *P. s. socius*, *g* = *geminus*, *e* = *eremnus* (South African population), *en* = *eremnus* (Namibian population) and *x* = *xericus*; dots indicate ringing sites with at least mass or wing or primary moult data

Table 1: Mass (g) and wing measurements (mm) of adult Sociable Weavers, from ringers' data by population, compared to Clancey (1989)

	<i>eremnus</i> (S Africa)	<i>eremnus</i> (Namibia)	<i>geminus</i>	<i>socius</i>	<i>xericus</i>
Mass (g)					
Mean	28.6	25.8	26.7	27.1	27.4
Range	20.5–39.6	20.0–33.0	20.7–39.0	18.0–36.0	20.5–33.7
SD	2.0	1.7	2.0	2.3	1.8
n	4 915	514	991	1 087	339
Wing (mm)					
Mean	75.0	72.9	72.0	73.0	74.1
Range	68–81.5	66–78	64–84	65–80	69–82
SD	2.2	2.3	2.0	2.2	1.9
n	3 644	239	931	991	135
Wing (mm), summarised from Clancey (1989)					
Mean	75.6	73.7	73.7	75.4	78.5
Range	72.5–79	71–75.5	72–75.5	71.5–80	75.5–81
SD		1.43	1.28		1.94
n	34	10	8	55	6

Table 2: Mass (g) and wing measurements (mm) of adult Sociable Weavers, from ringers' data, averaged by degree grids (e.g. 1915 = refers to the one degree grid cell with 19°S 15°E in the north-western corner)

Degree grid	Population	Mean	Range	SD	n	Difference from overall mean
(a) Mass (g)						
2725	<i>eremnus</i> (SA)	27.5	22–36	1.8	525	–0.4
2824	<i>eremnus</i> (SA)	28.7	20.5–39.6	2.0	4 390	0.8
2118	<i>eremnus</i> (Namibia)	26.1	25–27	0.8	8	–1.8
2216	<i>eremnus</i> (Namibia)	25.9	20–33	1.7	338	–2.0
2315	<i>eremnus</i> (Namibia)	24.1	22–29	1.6	26	–3.8
2317	<i>eremnus</i> (Namibia)	26.1	22.7–31	1.5	142	–1.8
1915	<i>geminus</i>	26.7	20.7–39	2.0	991	–1.2
2420	<i>socius</i>	24.5	23–26.2	1.1	10	–3.4
2520	<i>socius</i>	26.4			1	–1.5
2618	<i>socius</i>	25.9	23–29	1.3	29	–2.0
2721	<i>socius</i>	24.2	18–30	1.7	117	–3.7
2821	<i>socius</i>	27.2	26–28.5	1.3	3	–0.7
2822	<i>socius</i>	27.5	19.2–36	2.2	840	–0.4
2823	<i>socius</i>	28.5	26.5–30	1.8	3	0.6
2921	<i>socius</i>	28.2	26–31	1.3	84	0.3
2415	<i>xericus</i>	27.4	26–30	1.2	15	–0.5
2416	<i>xericus</i>	27.4	23–32	1.8	88	–0.5
2516	<i>xericus</i>	27.5	20.5–33.7	1.9	191	–0.4
2616	<i>xericus</i>	26.8	21–29	1.5	45	–1.1
All mass		27.9	18–39.6	2.2	7 846	
(b) Wing length (mm)						
2725	<i>eremnus</i> (SA)	73.8	71–78	1.8	16	–0.3
2824	<i>eremnus</i> (SA)	75.0	68–81.5	2.2	3 628	0.9
2118	<i>eremnus</i> (Namibia)	75.4	73–77	1.3	8	1.3
2216	<i>eremnus</i> (Namibia)	72.8	68–76	1.9	56	–1.3
2315	<i>eremnus</i> (Namibia)	69.4	66–73	1.3	28	–4.7
2317	<i>eremnus</i> (Namibia)	73.4	68–78	2.0	147	–0.7
1915	<i>geminus</i>	72.0	64–84	2.0	931	–2.1
2618	<i>socius</i>	71.6	67–76	1.9	30	–2.5
2721	<i>socius</i>	71.4	68–76	1.3	113	–2.7
2821	<i>socius</i>	76.8	76–77	0.5	4	2.7
2822	<i>socius</i>	73.2	65–80	2.2	841	–0.9
2823	<i>socius</i>	76.0	72–79	3.6	3	1.9
2516	<i>xericus</i>	74.0	69–82	2.1	94	–0.1
2616	<i>xericus</i>	74.3	72–77	1.5	41	0.2
All wing		74.1	64–84	2.5	5 940	

perature ($r_s = 0.13$, $P < 0.05$), or average annual water deficiency ($r_s = -0.26$, $P < 0.05$). Similarly, there was no significant correlation between body mass (number of grid cells = 19) and mean annual rainfall ($r_s = 0.14$, $P < 0.05$) or mean annual temperature ($r_s = -0.24$, $P < 0.05$). There was, however, a significant negative correlation between body mass and average annual water deficiency ($r_s = -0.43$, $P < 0.05$).

For *eremnus* (South Africa), body mass varied from 28g to 30g and no clear seasonal pattern was evident (Figure 2). Full sets of monthly data were not available for the other subspecies. However, mean monthly masses of *P. s. eremnus* (Namibia) were generally lower than those of *eremnus* (South Africa) (Figure 2). The incomplete data sets available for the other subspecies indicated wide fluctuations in mean monthly mass, and this was greatest for *P. s. socius* (24–28g) (Figure 2).

Temporal changes in body mass at Benfontein Game Farm

Plotting the means of the mass data for adult Sociable Weavers at Benfontein over 10-day intervals showed a long-

term decline (Figure 3) from a mean mass 29.1g (SD = 1.9, $n = 3 039$) between August 1992 and June 1998, to 27.9g (SD = 1.8, $n = 1 214$) between November 1998 and September 2001, to 26.3g (SD = 1.9, $n = 365$) between September 2002 and December 2003. This represented a reduction in mean mass of 2.9g (9.9%) between the first and last periods considered here. Two ringers were involved during the first two periods, but inter-observer difference in mean mass (29.2g and 28.7g) was only 0.5g. During the third period a third ringer was involved with no recaptures so it is not possible to check for inter-observer differences.

The influence of monthly rainfall on mean monthly mass at Benfontein was investigated. Several models were tested, each using the change in mean mass in the current month m_i and the next month m_{i+1} . Mass changes ($m_{i+1} - m_i$) relative to rainfall were modelled using four rainfall indices: (a) rain in current month r_i (b) rain in previous month r_{i-1} (c) sum of rain in current month and previous month $r_i + r_{i-1}$ and (d) rain in current month $r_i > 0$ and rain in previous month $r_{i-1} = 0$, to see the effect of rain after a dry month. In each model, the linear regression was not significant. A second order polynomial fit

gave a curve starting near zero and dropping slightly below zero with increasing rainfall, before increasing at very high rainfall (example of model (a) in Figure 4; the quadratic equation shown is not significant).

Timing and duration of primary moult

Individual primaries from two Sociable Weaver museum specimens were weighed (Table 3). The Sociable Weaver has 10 primary feathers, but the 10th primary is vestigial. This outermost primary had a mass less than 0.0001g, and was thus not considered in moult calculations. The innermost primaries accounted for 8.5–11.6% each of the total mass of the primary feathers. Primaries 6–8 were the largest, and similar in size, accounting for 12.4–12.7% of the relative primary mass. 1 733 ringing and recapture records with primary moult information were extracted. 18 records

showed irregular moult, i.e. a pattern not ascendant, e.g. 155553000. 128 records (7.4% of total) showed apparent suspended moult, e.g. 555555000. By subspecies, the numbers of birds showing suspended moult were *P. s. eremnus* 18 (1.0%), *geminus* 38 (2.2%) and *socius* 70 (4.0%). One bird (BH00041) had apparently suspended moult after its fourth primary was renewed, and had recommenced moult from the fifth primary (score 888855520). Unlike birds that moult more than one primary simultaneously, it was not apparent if moult was suspended or recorded just before the next primary was dropped. The irregular and suspended moult data were not included in further analyses.

50.0% of 1 586 remaining records indicated active moult (i.e. at least one feather with a score between 1 and 4). 22 records had at least three feathers scored as 4, e.g. 444441000, and one record with three feathers scored as 3. Frequency of number of growing primaries of those in moult was one (82.1%), two (13.2%), three (1.3%) and four (0.3%) feathers. Thus 82.2% of Sociable Weavers have one primary in active moult when moulting, with less than 15% of birds growing more than one primary feather at a time.

Three recaptures at Benfontein within the same year with capture dates near start and end of moult gave the following extrapolated results: 136 days duration starting on 16 February, 281 days duration starting on 9 November and 337 days duration starting on 4 December. For the South African *eremnus* population (Benfontein data, plus two records from Sandveld Nature Reserve; Figure 5) moult duration was 169 days (5.6 months) and the average starting date was 31 December. 83% of records were from 1996 and 2000. There were sufficient data to analyse moult in a single year for *eremnus* at Benfontein in 1996 and this was similar for the moult analysis with the data from all years (Table 4). In *socius* (Northern Cape, 13 sites in degree grid 2821), moult duration was 152 days (5.1 months) and started on 26 January. 88% of records were from 2000 and 2002 (Table 4). In *geminus* (northern Namibia), moult duration was 216 days (7.2 months) and started on 28 January; however, most of these data were collected at the start of the

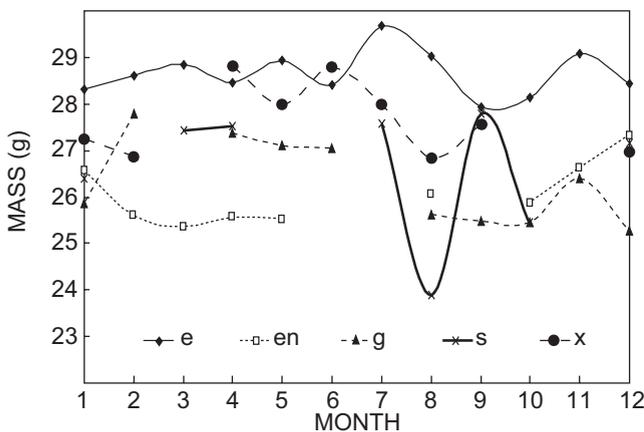


Figure 2: Mean mass per month for five populations of Sociable Weavers, all years combined; subspecies as described by Clancey (1989) where s = *P. s. socius*, g = *geminus*, e = *eremnus* (South African population), en = *eremnus* (Namibian population) and x = *xericus*

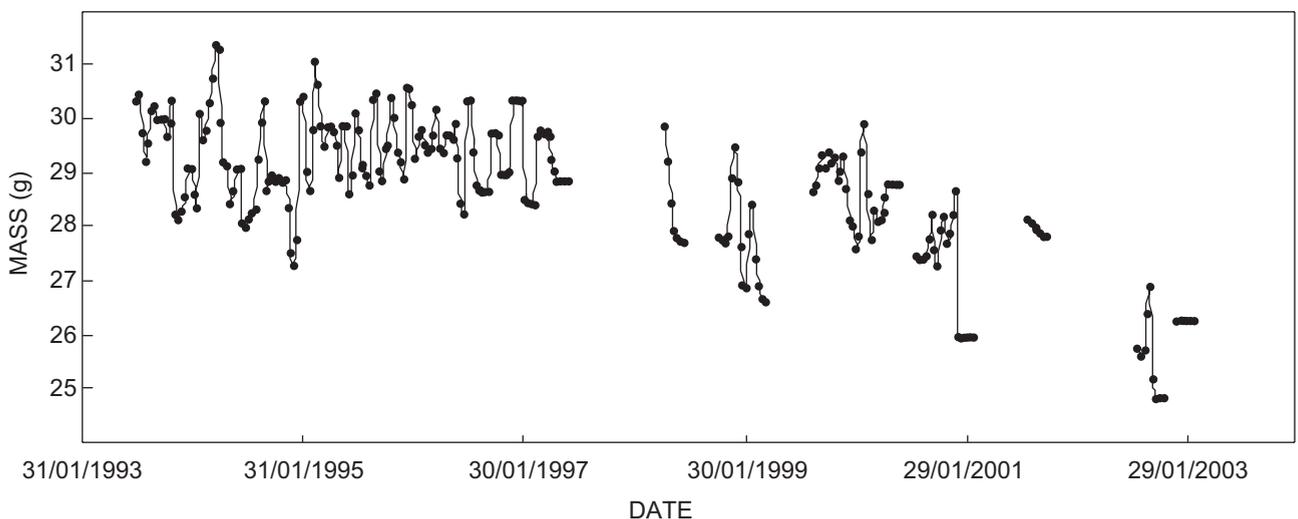


Figure 3: Mean mass per 10-day period for adult Sociable Weavers at Benfontein, Northern Cape

moult so that the duration and end dates have larger standard errors and are less reliable than the start date (Table 4).

Applying the Underhill–Zucchini model to individual primary feathers gave results for primaries 3–9; there were insufficient data for primaries 1 and 2 for the algorithm to converge. Individual feathers took 20–28 days to grow

(Table 5). The timing of moult for primaries 3–6 showed no or little overlap, i.e. only one feather growing at a time. Later primaries showed increasing overlap (Figure 6), rather than speeding up individual growth feather rates.

Discussion

Geographic and seasonal variation in body mass and wing length

Clancey (1989) considered complicated patterns of size variation, based on small sample sizes of museum specimens of Sociable Weavers. He considered wing length to increase from north to south, and east to west. Analysing ringing data by subspecies indicates that body mass and wing length are smaller in *eremnus* (Namibia) and *geminus*, lending possible support for a north-to-south increase in size. There is no clear pattern from east to west (Table 1): based on ringing data, the largest individuals belong to *eremnus* (South Africa) rather than *xericus*, as suggested by Clancey (1989). Analysis by degree grids also shows geographical variability in body size. However, this variation may be an artefact of data collection methods. For example, some grid cells were represented by small sample sizes, data from some samples were collected on only one day and measurements were per-

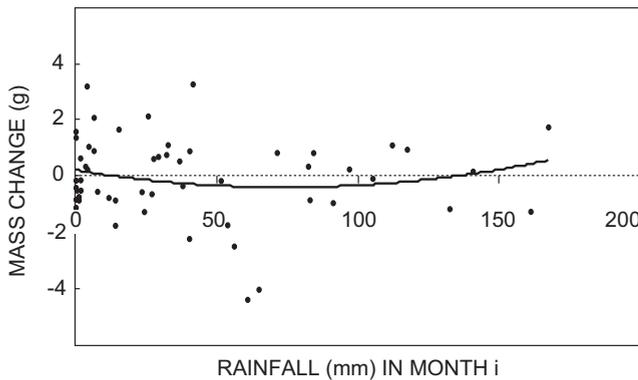


Figure 4: Mass change versus rainfall for adult Sociable Weavers at Benfontein, Northern Cape; model (a) — see text

Table 3: Individual primary feather masses (g) of two Sociable Weaver specimens, and the mean relative mass of each primary, used in the calculation of Percentage Feather Mass Grown (PFMG)

Primary	Feather mass (g)			Mean PFMG
	Bird 1 left wing	Bird 2 left wing	Bird 2 right wing	
1	0.0098	0.0101	0.0100	8.54
2	0.0103	0.0110	0.0107	9.14
3	0.0113	0.0117	0.0120	9.99
4	0.0127	0.0127	0.0128	10.90
5	0.0136	0.0133	0.0136	11.57
6	0.0139	0.0147	0.0154	12.56
7	0.0142	0.0145	0.0148	12.42
8	0.0147	0.0147	0.0151	12.71
9	0.0136	0.0142	0.0149	12.19
10	<0.0001	<0.0001	<0.0001	0.00
Total				100.00

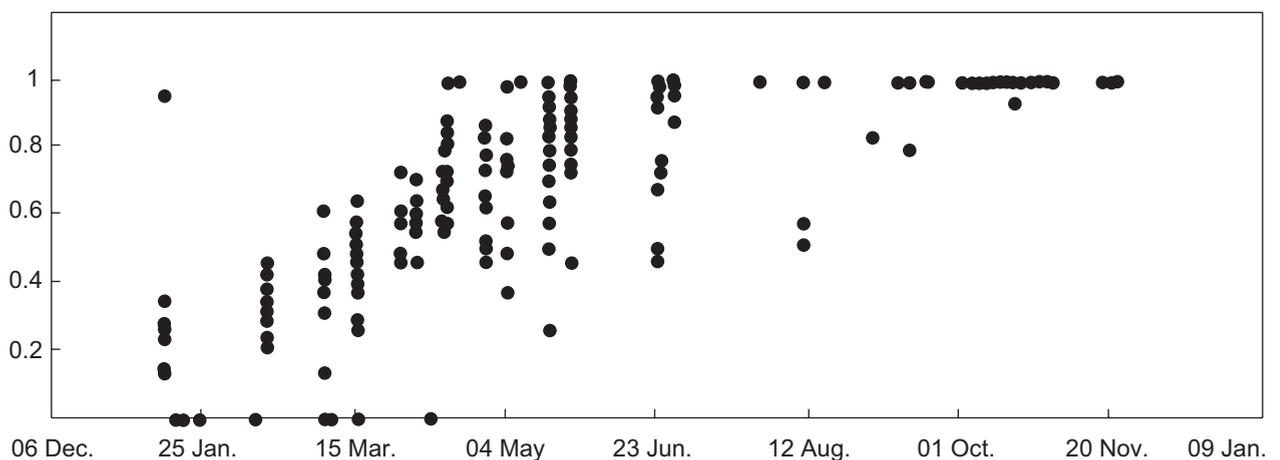


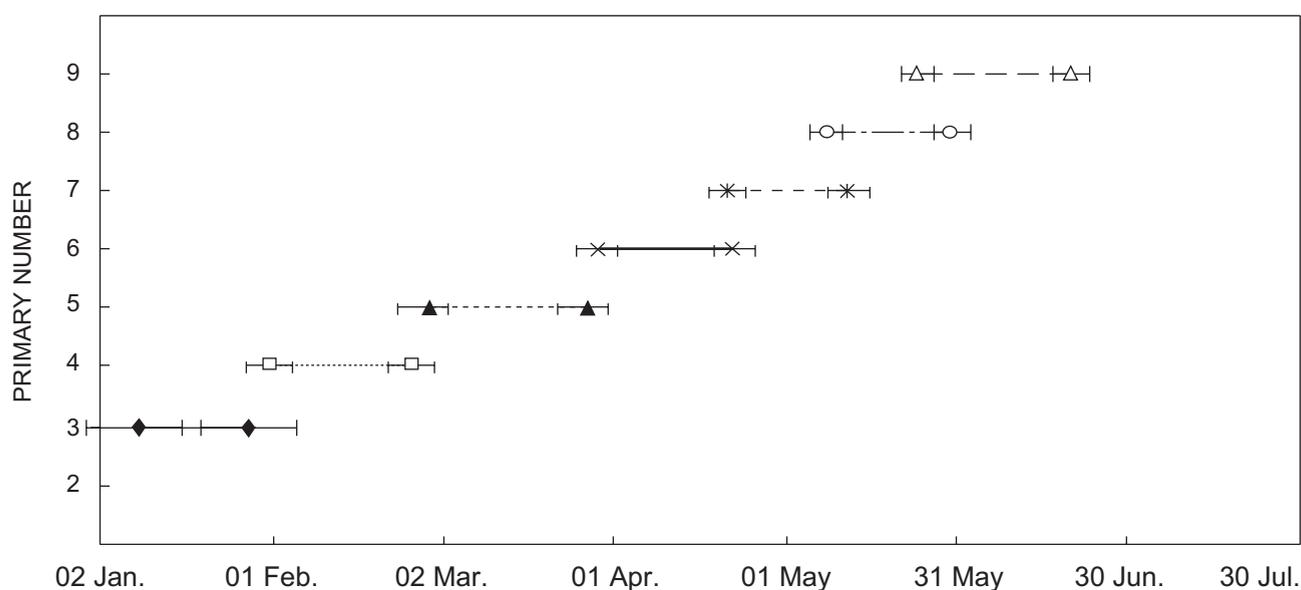
Figure 5: Primary moult scores by date for adult Sociable Weavers of the *eremnus* (South Africa) population

Table 4: Primary moult parameters for adult Sociable Weavers

Subspecies	Mean starting date	SE	SD (days)	SE	Duration (days)	Duration (months)	SE	Mean completing date	SE	n
<i>eremnus</i> (SA)	31 December	6.1	38.0	2.2	168.9	5.6	8.1	17 June	3.7	481
<i>eremnus</i> (SA), 1996	24 December	7.9	28.4	2.1	176.4	5.9	10.0	17 June	3.4	204
<i>geminus</i>	28 January	5.9	67.5	5.0	215.8	7.2	13.8	31 August	12.0	231
<i>socius</i>	26 January	4.1	37.7	1.9	151.7	5.1	7.2	26 June	3.8	838

Table 5: Molt parameters of individual primary feathers for adult Sociable Weavers

Primary	Mean starting date	SE	SD (days)	SE	Duration (days)	SE	Mean completing date	SE
3	09 January	9.5	33.8	5.6	20.4	6.4	29 January	7.2
4	01 February	4.8	22.5	2.7	25.7	4.8	26 February	3.7
5	28 February	4.8	32.2	3.4	27.7	4.6	27 March	3.7
6	29 March	3.9	33.1	3.2	24.3	3.9	22 April	3.6
7	21 April	3.3	28.2	2.6	21.2	3.5	12 May	3.4
8	08 May	3.0	23.4	2.1	22.6	3.5	30 May	3.2
9	24 May	2.9	20.1	1.9	26.9	3.7	20 June	3.0

**Figure 6:** Individual primary growth of adult Sociable Weavers; start and end of primary growth (and standard deviation) for primaries 3–9 are shown (insufficient data for primaries 1 and 2); data in Table 5

formed by different ringers. One grid cell had 4 816 records and it was thus inevitable that high levels of statistical significance would result although these would not necessarily be biologically meaningful (Underhill 1999).

Surprisingly Clancey's (1989) wing lengths are longer than those calculated from the ringing data (Table 1). Museum specimens shrink, giving shorter measurements than from live birds (Herremans *et al.* 1999, and references therein). Ringers use maximum wing chord measurement (De Beer *et al.* 2001), so Clancey's longer wing measurements are not readily explained. Herremans *et al.* (1999) obtained a similar result for Levallant's Cisticola *Cisticola tinniens* and considered biometrics based on small samples of museum specimens to be misleading. They recommend-

ed that large samples of measurements of live birds should be used.

The only significant correlation between biometric measurements and environmental indices was the negative correlation of body mass with average annual water deficiency. Bergmann's rule states that warm-blooded vertebrates from cooler climates tend to be larger than congeners from warmer climates, but evaporation should be included in the climatic variable (see Meiri and Dayan 2003), which could explain why a correlation was found with water deficiency and not the other variables.

There was variation in mean monthly body mass of adult Sociable Weavers in different regions of southern Africa. These were not clearly correlated with season and were

probably attributable to the underlying data being collected in different years and months in different localities.

Temporal changes in body mass at Benfontein

For Benfontein there were sufficient data to look at body mass changes in more detail, over seasons and years. After rainfall events, breeding is initiated as a result of the increased availability of invertebrates that are fed to the chicks (Maclean 1973). The lack of correlation between mean monthly body mass and rainfall in this study indicates that Sociable Weavers at Benfontein expend energy on reproduction rather than increasing adult body mass when food increases.

There was a long-term decline in mean mass of 2.9g (<10%). This might be an artefact of sampling effort, with birds during the latter years only being weighed during the breeding season. This seems unlikely since there was little seasonal variation in mass. Inter-observer differences in weighing the birds does not explain the slight decline between the first two periods, but cannot be tested for the last period. Sociable Weavers differ in mass by about 3g (11%) between evening and morning (Spottiswoode *in litt.*), which is similar to the overnight mass loss of 6–13% recorded for three other weaver species (Oschadleus 2001). Time of capture or ringing is not recorded in the SAFRING database but most Sociable Weavers at Benfontein were captured at sunrise (Covas 2002: 44). Thus the effect of daily mass loss is minimised, except where large numbers of birds were captured, resulting in delay between capture and processing and thus possible changes in body mass. Other possibilities for temporal mass changes are due to global warming (e.g. Yom-Tov 2001), but the change recorded here is probably over too short a term for this explanation to apply. Covas *et al.* (2002) showed that there is a strong stabilising selection on body mass, verifying the prediction that body mass probably results from a trade-off between the risks of starvation at low mass and predation at high mass (Gosler and Greenwood 1995). While the data may be affected to some extent by the biases noted, the consistent long-term decline in mass of Sociable Weavers at Benfontein is more likely due to stabilising selection. Whether this is due to changes in food supply or in predation rates requires further investigation.

Timing and duration of primary moult

The life history of Sociable Weavers is largely influenced by a benign climate, which leads to reduced mortality; this should favour reduced fecundity (Covas 2002). Food availability determines if breeding can occur (Covas 2002). Individuals should thus optimise energy requirements between breeding and moult by breeding when sufficient food is available and by moulting flight feathers at a relatively slow rate.

In some species of Ploceidae, e.g. Chestnut Weavers *Ploceus rubiginosus*, timing of moult is fairly consistent between years despite variations in rainfall and thus breeding season (Komen and Buys 1990). On the eastern margin of the Sociable Weavers' range, the breeding period generally begins in spring (late August–September) (Covas 2002), although its onset depends on rainfall and varies considerably between years (Maclean 1973). Breeding may be

entirely absent during drought years (Maclean 1973) but may continue for nine months in wet years (Maclean 1973, Covas 2002). Moult in this species appears to commence between the end of December and January. Breeding may thus overlap with an extended moult season (Spottiswoode *in litt.*), and primary moult may be interrupted during intense breeding periods (Maclean 1973).

Ploceidae in semi-arid environments have widely varying moult durations, although data have not been analysed rigorously. Adult Chestnut Weavers in northern Namibia moult their primaries from June to September, i.e. in about 120 days (Komen and Buys 1990). The duration of primary moult in White-browed Sparrow-weavers *Plocepasser mahali* is 183 days (Jones 1978). Primary moult in Scaly-feathered Finches *Sporopipes squamifrons* is slow, with an estimated duration of c. 200–350 days (Tyler 2001). Other avian taxa in arid areas also have prolonged primary moult periods, e.g. sandgrouse moult over eight months in Tanzania (Kalchreuter 1979). The moult in most of 20 species of arid-zone birds studied in Australia lasted 4–4.5 months (Keast 1968). Dean (2004) reviewed moult duration in arid nomadic species, concluding that duration is highly variable.

For Sociable Weavers, Maclean (1973) noted that about one primary was replaced per month, with the shortest recorded time being three weeks. Individual primaries moult mainly one at a time and need 20–28 days to grow, but the last three primaries show increasing overlap in their growing period, reducing the total duration of primary moult. Maclean's (1996) estimate of nine months for primary moult is thus exaggerated. The present study indicated moult durations of 5.1–7.2 months, longer than the moult durations of weavers in the moister eastern parts of southern Africa where moult lasts from three to four months (Craig *et al.* 2001). The three recapture estimates for moult duration varied widely but could have been due to suspended moult. A long primary moult may be an adaptation to reduce energy expenditure since primary productivity is low in semi-arid environments (Tieleman 2002). In addition, slow-growing primaries are more resistant to abrasion than fast-growing ones (Dawson *et al.* 2000). Sociable Weaver feathers may experience high rates of feather abrasion when entering and leaving their nests, as their aluminium rings wear away relatively quickly compared to stainless steel rings (Nuttall 2001). Slow-growing high-quality primaries would then reduce the abrasive effect of the stiff grasses projecting along the nest entrances. Using individual primary feather analyses gives additional insights into duration of moult. For example, it was not previously known that Sociable Weavers overlap in the moult of the last three primaries. The only comparable analysis of the moult of individual primary feathers is for waders, where several feathers frequently grow simultaneously (Underhill 2003).

The relative primary feather masses measured in this study, each ranging between 8.5–12.7% of the total primary feather mass, are typical of a non-migratory species and are similar to that of other weavers (Underhill and Joubert 1995, Craig *et al.* 2001).

Subspecies of the Sociable Weaver

Clancey (1957) described *eremnus* as a new subspecies in the Northern Cape. Later, Clancey (1989) included a

Namibian population within the range of *eremnus*, without adequate justification. In fact, he admits that a long series taken in Namibia 'contain many specimens intermediate between nominate *socius* and *eremnus*...' (Clancey 1989: 231). Although differences do exist, for instance the smaller birds in northern Namibia, it is best to consider the contiguous Sociable Weaver populations to be monotypic. Craig (2004) also considered the species monotypic, as regional differences are not consistent.

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