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Breeding seasonality and primary moult parameters of *Euplectes* species in South Africa

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The grassland biome in South Africa has a summer rainfall and Southern Red Bishops *Euplectes orix*, Fan-tailed Widows *E. axillaris*, White-winged Widow *E. albonotatus*, Red-collared Widow *E. ardens* and Long-tailed Widow *E. progne* breed from October or November to March. Primary moult starts in late March or early April. The widows with long tails (Long-tailed and Red-collared Widows) have moult durations of two months, while the widows with shorter tails (White-winged and Fan-tailed Widows) had moult durations of 1.5–1.7 months. Moult ends in late May or early June. Long-tailed Widows have rounder wings than other weaver species, possibly because their larger size affects flight aerodynamics. In the winter rainfall region, Southern Red Bishops and Yellow Bishops *E. capensis* start breeding after the winter rains, from August–November, and moult starts in early December. Primary moult duration in Yellow Bishops is relatively long, at 3.4 months. Yellow Bishops grow individual primary feathers at an average rate of 21.3 days per feather, while the other species moult primaries more quickly: White-winged Widow 8.1 days, Fan-tailed Widow 11.3 days, and Red-collared Widow 14.4 days. The number of primaries growing simultaneously is similar in the different species. The longer duration of primary moult of the Yellow Bishop may be related to food.

Introduction

There are seven breeding species of *Euplectes* bishops and widows in South Africa (Tarboton 2001). The bishops have short tails that are not replaced during the pre-nuptial moult and the widows grow long black tails in the pre-nuptial moult (Craig 1993). Species in this genus in South Africa have their distributions centred on the grassland and savanna biomes in the eastern parts of the country; Southern Red Bishops *Euplectes orix* and Yellow Bishops *E. capensis* extend into the eastern fynbos region of the Western Cape (Harrison *et al.* 1997, Figure 1). All seven South African species occur in the two easternmost provinces, KwaZulu-Natal and Mpumulanga. Six species occur in Limpopo Province, Gauteng and the Eastern Cape; five species occur in the North-west and Free State Provinces; three species occur in the Western Cape; and three species have been recorded in the Northern Cape. The Southern Red Bishop covers the greatest geographic extent, being widespread through most of South Africa.

The species are relatively uniform in their ecology and maintain mutually exclusive territories where they occur in the same area (Emlen 1957, Craig 1980). They are common birds of grassland or marshes, feeding mainly on seeds. They are sexually and seasonally dimorphic; females are dull-coloured throughout the year. Male widows have elongated black tail feathers, which are used in mate selection. Tail length in male widows in breeding plumage varies greatly between species, from 65mm in Fan-tailed Widows *E. axillaris* to 500mm in Long-tailed Widows *E. progne* (Andersson and Andersson 1994, Pryke 2003). All species feed and roost in large flocks in the non-breeding season, often in mixed-species flocks (Craig 1980).

The Southern Red and Yellow Bishops breed from August–November in the Western Cape, about three months earlier than the peak of December–March in the summer rainfall region. The other *Euplectes* species breed mainly from October–March (Harrison *et al.* 1997). All *Euplectes* species are polygynous, build a dome-shaped nest with a side entrance, and the female alone incubates eggs and feeds young (Fry and Keith 2004).

Little is known about the moult of bishops and widows. Craig and Manson (1979) found that three *Euplectes* species in KwaZulu-Natal and Zimbabwe moulted soon after breeding; the authors estimated duration of primary moult based on recaptures. Bonnevie *et al.* (2004) found that Southern Red Bishops moulted three months earlier in the Western Cape than in the predominantly summer rainfall regions. Savalli (1993) described the pre-nuptial moult in the Yellow-mantled Widowbird *E. macrourus* in western Kenya.

This paper examines the relationship between the timing of primary moult and the timing of breeding in the annual cycles of six of the seven *Euplectes* species of South Africa. We estimate the primary moult parameters of the Southern Red Bishop, the Yellow Bishop, the Fan-tailed Widow, the White-winged Widow *E. albonotatus*, the Red-collared Widow *E. ardens*, and the Long-tailed Widow. Insufficient data were available to analyse moult of the Yellow-crowned Bishop *E. afer*.

Methods

Breeding seasonality data were obtained from the BirdLife South Africa Nest Record Card Scheme (NRC): Avian

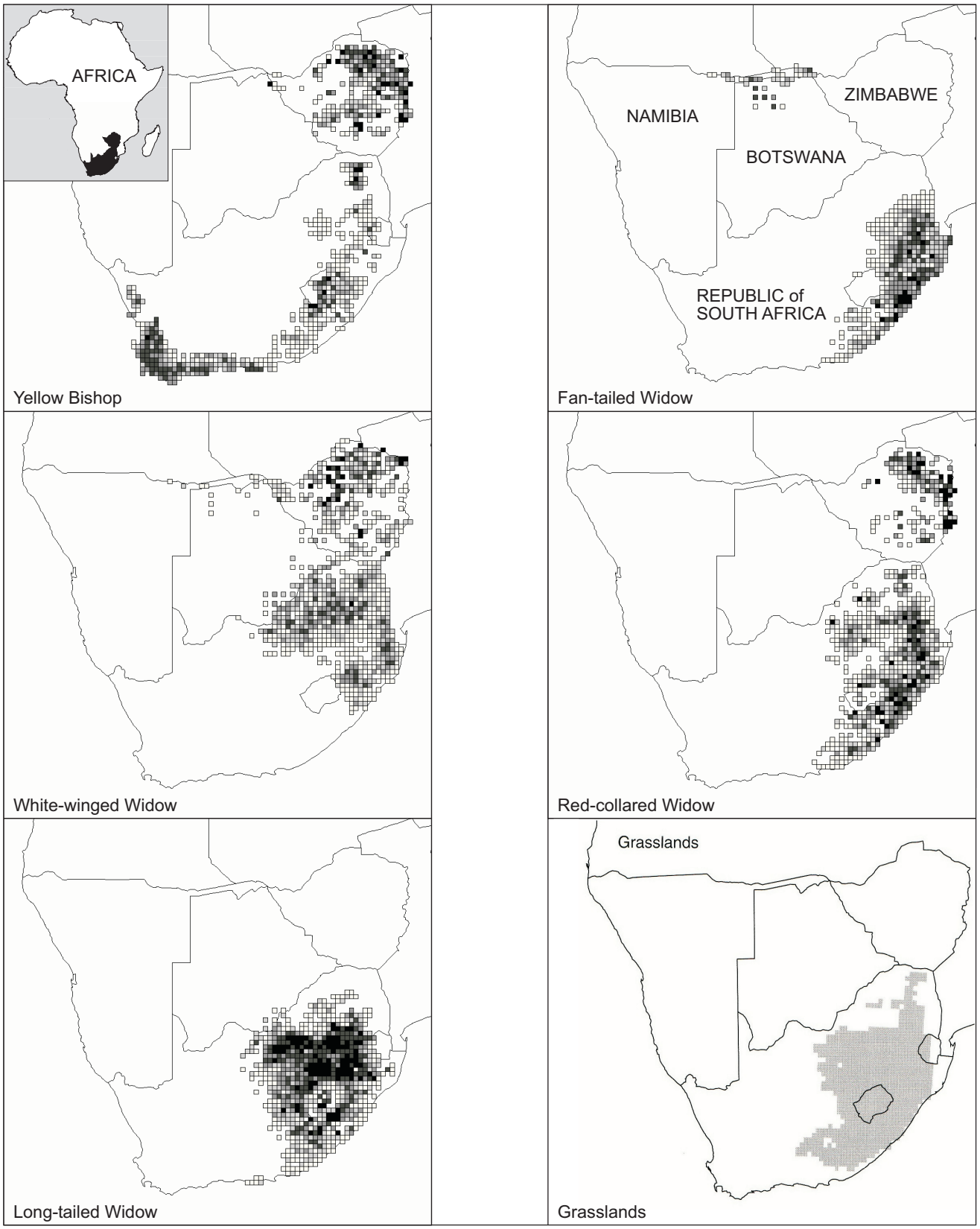

Figure 1: Distributions, in southern Africa, of five *Euplectes* species that occur in South Africa. Darker shading indicates higher reporting rates (from Harrison *et al*. 1997); the Southern Red Bishop occurs throughout South Africa. The figure at the bottom right-hand side of the page shows the grassland biome (from Allan *et al*. 1997)

Table 1: Months of egg laying (percentages) for *Euplectes* species in South Africa (from Prys-Jones and Newton 1987). The percentages are summarised as 5th percentile (represents start of breeding), 95th percentile (end of breeding), range (90% range of egg laying) and median egg-laying month. Numbers represent parts of months, e.g. 12.4 = 40% through December (see text). Localities are abbreviations for South African provinces: WC = Western Cape, EC = Eastern Cape, NC = Northern Cape, KZN = KwaZulu-Natal, FS = Free State, Tvl = former Transvaal (includes Gauteng)

Species	Locality	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	n	5th	95th	Range	Median
Southern	WC	<1	18	47	25	10	<1							1 109	8.3	11.5	3.2	9.7
Red Bishop	FS					3	36	56	4	<1	<1			240	12.1	2.0	1.9	1.2
	Karoo		2	6	34	4		1	6	43	3			96	9.5	4.0	6.5	2.3
	NC				5	86	9							22	11.0	12.5	1.4	11.5
	EC			1	3	15	58	14	8	2				160	11.1	2.6	3.5	12.6
	KZN				6	12	67	13	1	1				1 276	10.8	1.8	2.9	12.5
	Tvl				2	20	34	30	10	4				1 043	11.2	2.9	3.7	12.8
Yellow	WC	<1	23	44	26	5	1							239	8.2	11.2	3.0	9.6
Bishop	EC			9	18		45	18	9					11	9.6	2.5	4.9	12.5
	KZN					10	80	10						10	11.5	1.5	2.0	12.5
Fan-tailed	EC					25	50		25					16	11.2	2.8	3.6	12.5
Widow	KZN			4	5	24	40	18	7	1				148	10.2	2.5	4.3	12.4
White-winged	KZN					13	41	38	6		3			32	11.4	2.7	3.3	12.9
Widow	Tvl				1	4	37	26	29	3				70	11.8	2.9	3.1	1.3
Red-collared	EC			14	25	32	7	4	18					28	9.4	2.7	5.4	11.3
Widow	KZN				17	31	36	13	2	2				64	10.3	1.9	3.6	12.0
	Tvl				4	18	46	25	4	4				28	11.1	2.6	3.5	12.6
Long-tailed	EC			20	45	25		10						20	9.3	1.5	4.3	10.7
Widow	FS				9	45	26	6	13	1				152	10.5	2.7	4.2	11.9
	KZN			3		38	25	22	13					32	11.1	2.6	3.6	12.4
	Tvl				7	17	30	31	13	2				87	10.7	2.8	4.1	12.9

Table 2: Individual primary feather masses (g) of two Long-tailed Widow specimens from Mpumulanga and one White-winged Widow specimen from North-west Province, and the mean relative mass of each primary (information used in the calculation of Percentage Feather Mass Grown)

Primary	Feather mass (g)			Mean feather masses	
	Long-tailed Widow male, left wing	Long-tailed Widow male, right wing	White-winged Widow male, left wing	Long-tailed Widow	White-winged Widow
1	0.0235	0.0356	0.0108	9.4	9.3
2	0.0234	0.0372	0.0112	9.5	9.6
3	0.0250	0.0400	0.0114	10.2	9.8
4	0.0275	0.0440	0.0121	11.3	10.4
5	0.0289	0.0466	0.0135	11.9	11.6
6	0.0305	0.0484	0.0138	12.4	11.8
7	0.0314	0.0468	0.0140	12.4	12.0
8	0.0304	0.0433	0.0146	11.7	12.5
9	0.0295	0.0378	0.0152	10.8	13.0
10	0.0009	0.0014	<0.0001	0.4	0.0
Total	0.2510	0.3811	0.1166	100.0	100.0

Demography Unit, University of Cape Town) (Prŷs-Jones and Newton 1987, Underhill *et al.* 1991). Prŷs-Jones and Newton (1987) estimated the month of laying of the first egg for each record. They then summarised breeding seasonality for all birds in South Africa by presenting monthly totals of clutches laid per species per region. One of the regions they used was the former Transvaal province: this region incorporates the current Gauteng Province, from where most of the records originate. To compare breeding seasonality of weavers, the tabulated data of Prŷs-Jones and Newton were used to estimate the median and the 5th and 95th percentiles for each species and region. The median was calculated by finding the cumulative monthly sums of the percentage of nest records. The median month was the month in which the cumulative sum first exceeded 50%. The values of the sums of the previous and successive months were used to assign a relative distance into the month. For example, if there were 47% of cumulative records by the end of October, and 64% by the end of November, the median clearly is during November. Then, using proportions (50–47)/(64–47) gives 17.7%, the relative distance into November. Thus, the median lies 17.7% into November (Month 11), calculated as 11.177 (and rounded to 11.2 for presentation, i.e. a precision of about three days). The 5th and 95th percentiles were interpolated in a similar fashion. Dates in January were recorded as being in Month 1 (not Month 0).

Ringing data were collected by ringers in the standard SAFRING (South African Bird Ringing Unit) electronic format. This includes standard ringing information (such as location and date) and data on bird body mass, wing length and primary moult (de Beer *et al.* 2001). Primary moult records until mid-January 2005 were extracted from SAFRING's database for adult *Euplectes* species. For each species, a geographic area was chosen, so that sufficient records could be obtained for the analysis of moult: generally, 200 records spread over a year are adequate to enable the moult model of Underhill and Zucchini (1988) to converge. In bishops and widows, the moult of the primaries is descendant, with the nine flight feathers being renewed outwards.

Capture sites are illustrated in Figure 2.

Masses of primary feathers were obtained from road kills. The White-winged Widow specimen was a male found at Skeerpoort, North-west Province, and the Long-tailed Widows were found in Wakkerstroom (non-breeding male) and Leandra (breeding male), both in Mpumulanga. Masses of primary feathers for Southern Red Bishops are from Craig *et al*. (2001). The primaries were dried in an oven at 60°C for 24h to eliminate moisture and then weighed (Ohaus GA200D balance, precision 0.0001g). These values were averaged and used to calculate the relative mass of each primary (Underhill and Summers 1993). Underhill and Joubert (1995) showed that small samples are adequate to determine the relative masses of primary feathers, because there is little intraspecific variation in this characteristic. As recommended by Summers *et al.* (1980, 1983), the moult record for each bird was transformed to Percentage Feather Mass Grown (PFMG), calculated from the moult scores for the individual primary feathers and their relative masses, according to the method of Underhill and Summers (1993). The Underhill-Zucchini moult model (Underhill and Zucchini 1988) was used to estimate the parameters of primary moult. The data were considered to be of 'Type 2' of Underhill and Zucchini (1988), because full moult scores were recorded for each bird and all birds were considered to be available for sampling throughout the moult period. The use of Type 2 data assumes that the sample of birds handled on each day is representative of the stages of primary moult in the population on that day. This analysis was then repeated, to provide estimates of the parameters of moult of each individual primary (Underhill 2003, Underhill *et al.* in press). Underhill and Joubert (1995) showed that within the Charadriiformes, the relative masses of the primary feathers were so similar that the average value for the species for which data were available could safely be used for species for which data were unavailable. The same principle appears to apply within the Ploceidae (Oschadleus 2005), and the relative primary masses for White-winged Widows were used to calculate

PFMG for the Red-collared Widow, the Fan-tailed Widow and the Yellow Bishop. These species have similar overall wing shapes (HDO pers. obs.).

Presentation in tables of the statistical results of the Underhill-Zucchini moult model includes the following information: mean starting date, standard deviation of the start date, mean duration of moult, and mean completion date. The Underhill-Zucchini moult model assumes that the distribution of starting dates has a normal distribution, which has two parameters: mean and standard deviation. The mean of this distribution is interpreted as the mean starting date of moult in the population and the standard deviation measures the extent of variability about the mean. If the standard deviation is small, then moult is synchronised, and *vice versa*. Thus, 95% of birds are estimated to start moult during the period from 1.96 standard deviations below the mean to 1.96 standard deviations above the mean. The third parameter of the Underhill-Zucchini moult model is the duration of moult of the average bird. For each of the parameters, its standard error is also estimated; 95% confidence intervals for each parameter are given by the parameter estimate plus and minus 1.96 times the standard error of the parameter estimate. The moult records are plotted as feather mass *versus* date for different individuals. Ringing data was chosen from grids as shown in Figure 2 where grids are latitude and longitude, e. g. 3318 = the grid 33°–34° and 18°–19°.

Results

Within South Africa, breeding by *Euplectes* species began earliest in the Western Cape; the median date of egg laying in this province was September (Table 1). In the grassland biome, breeding was in summer: in KwaZulu-Natal the median date of egg laying was in December for all species and in the former Transvaal it was December or January (Table 1). Median date for onset of egg laying was variable in the other regions.

For the Long-tailed Widow the sixth and seventh primaries were the largest, giving the species a rounded wing shape, whereas for the White-winged Widow the ninth primary was largest (Table 2), in common with the more pointed wing shapes of most ploceids (Oschadleus 2005), as exemplified in Figure 3.

For Long-tailed Widows, 279 moult records were available (166 records for Mpumulanga, 55 for the Free State, 53 for Gauteng, and five records from other provinces). Moult records for the remaining species are based on higher sample sizes and are confined to a province or smaller grid (Table 3, Figure 2). Moulting birds were captured throughout the moulting season (Figure 4), sometimes in large numbers, enabling moult parameters to be estimated reliably. Widow species breeding in summer rainfall areas (Long-tailed Widow, White-winged Widow, Red-collared Widow and Fan-tailed Widow) had primary moult durations of about two months, starting in late March or early April and ending in late May or early June (Table 3). In the winter rainfall region the Southern Red Bishop and Yellow Bishop showed a longer moult duration of 3.0–3.4 months, with moult starting in early or mid-December

Table 3: Estimates of the primary moult parameters of adults of five species of widow birds (Long-tailed Widow, White-winged Widow, Red-collared Widow, Fan-tailed Widow, and Yellow Bishop) in South Africa; values for the Southern Red Bishop are from Oschadleus (2005) and Craig *et al.* (2001). Localities are abbreviations for South African provinces (Figure 2): WC = Western Cape; GP = Gauteng Province; KZN = KwaZulu-Natal; and area in which the data were collected. Gauteng is included in the Transvaal region of Table 2. PFMG model: * indicates that the PFMG data of White-winged Widows were used, as wings of the species concerned were not available; blank means that wings of the species concerned were used

Species	Locality	PFMG model	Mean starting date	Standard error (days)	Standard deviation (days)	Standard error (days)	Mean duration (days)	Mean duration (months)	Standard error (days)	Mean completion date	Standard error (days)	n
Southern Red Bishop	WC grid 3318		13 Dec	1.1	25.3	0.6	88.6	3.0	1.7	12 Mar	1.2	3 154
	EC		28 Apr	4	47.3	2.9	89	3.0	7	26 Jul	6.1	622
	GP		23 Mar	1.5	35.1	1.1	71.9	2.4	2.5	3 Jun	2.3	4 808
Yellow Bishop	WC grids 3318 and 3418	*	4 Dec	2.0	23.3	1.0	103.4	3.4	3.0	17 Mar	1.8	777
Fan-tailed Widow	KZN grid 2930	*	2 Apr	1.9	18.1	0.9	50.5	1.7	2.8	23 May	2.0	1 002
White-winged Widow	GP		18 Apr	2.5	26.3	1.6	46.5	1.5	3.3	3 Jun	2.6	685
Red-collared Widow	GP	*	5 Apr	2.5	30.8	1.6	59.9	2.0	3.5	3 Jun	2.6	667
Long-tailed Widow	All		26 Mar	4.8	20.6	2.9	60.7	2.0	8.7	25 May	7.1	279

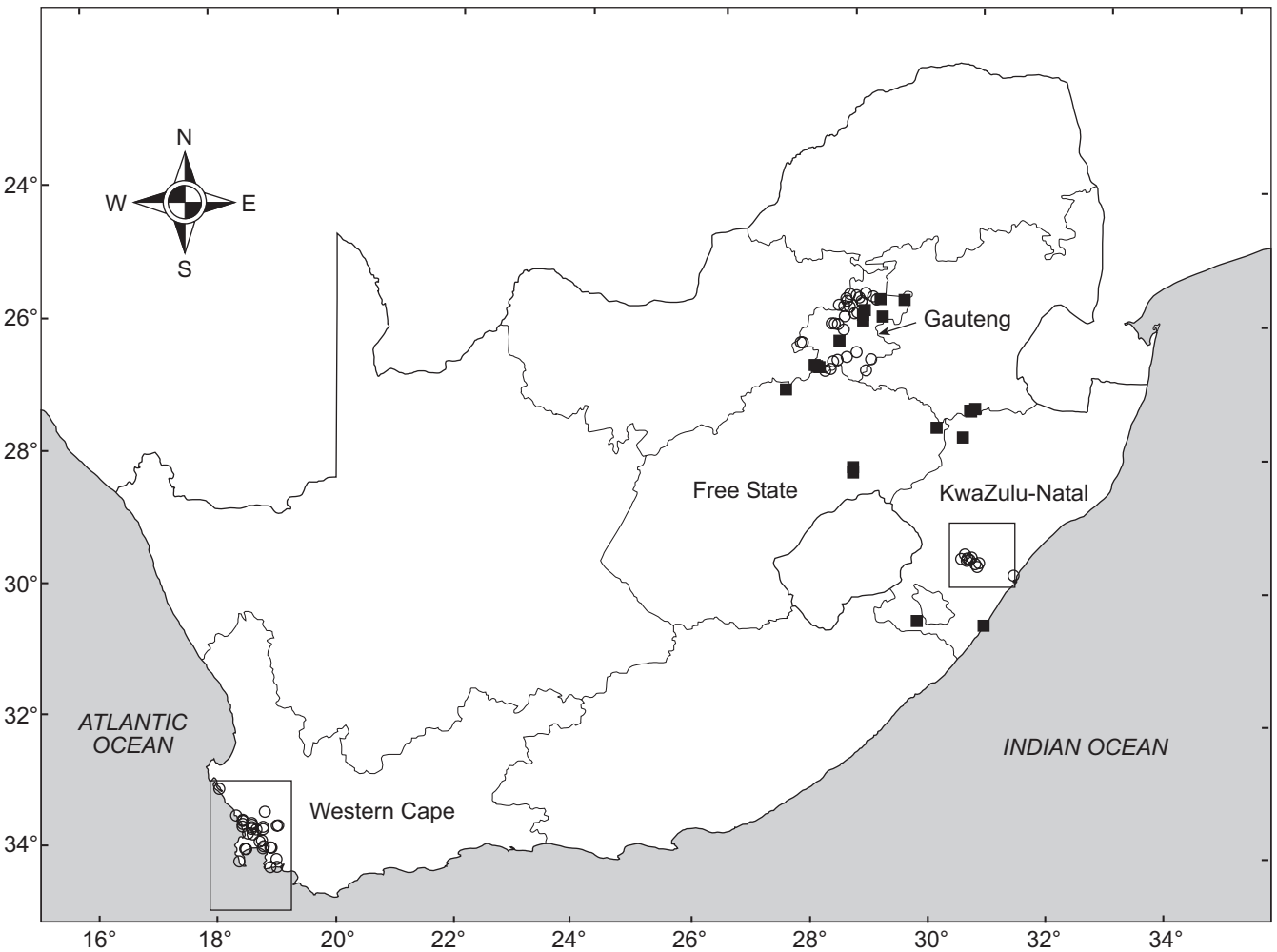

Figure 2: Capture sites for adult widow birds in South Africa, showing sites from which primary moult data were obtained. Open circles in the Western Cape represent Yellow Bishop records; open circles in KwaZulu-Natal are for Fan-tailed Widow records; open circles in Gauteng are for White-winged Widow and Red-collared Widow records; closed squares are Long-tailed Widow records. Southern Red Bishop ringing sites are not shown (for clarity), but overlap with the ringing sites shown in Gauteng, Kwazulu-Natal and the Western Cape.

(Table 3). Southern Red Bishops in the Eastern Cape showed a moult duration of 3.0 months, with moult starting in late April (Craig *et al*. 2001, Table 3).

The estimated time for individual feathers to grow varied considerably (Table 4): the Yellow Bishop, 14–29 days; the Fan-tailed Widow, 6–18 days; the White-winged Widow, 5–13 days; and the Red-collared Widow, 9–18 days (Table 3). For the Long-tailed Widow, the sample sizes were too small to allow individual feather growth durations to be estimated. Numbers of primaries growing simultaneously were similar in the five species: Southern Red Bishop 1.7, Yellow Bishop 2.0, Fan-tailed Widow 2.2, White-winged Widow 1.9, Red-collared Widow 2.3, and Long-tailed Widow 2.2. A comparison of the estimated starting and completion dates of primary moult for the wing as a whole (Table 3) and the earliest starting date and latest completion date for individual primaries (Table 4) reveals a close match, with a maximum discrepancy of seven days in the starting date of moult of the Yellow Bishop.

In the six *Euplectes* species considered, the mean starting date of primary moult was 2.5–4.3 months after the median egg laying date and 0.9–2.3 months after the 95th percentile of egg laying (Table 5). One breeding cycle, consisting of the incubation and nestling periods, is 3–4 weeks in the *Euplectes* species (Tarboton 2001). It is therefore clear that primary moult took place immediately after breeding in the annual cycles of all these species at all localities for which observations were available.

Discussion

The rounded wing shapes of the Long-tailed Widow, compared to the Southern Red Bishop and White-winged Widow (Figure 3), are probably due to adaptation rather than phylogeny (Dawson 2005). For a range of European passerines, Dawson (2005) considered that the greater relative mass of the outer primaries in some species reflected a protective function against physical abrasion, or an aerodynamic function, in that these feathers provide the leading edge to the wing. Scaling relationships (log

Table 4: Estimates of the primary moult parameters of individual primary feathers for adult widow birds in South Africa

Primary	Mean starting date	Standard error (days)	Standard deviation (days)	Standard error (days)	Duration (days)	Standard error (days)	Mean completing date	Standard error (days)
(a) Yellow Bishop, Western Cape grids 3318 and 3418, n = 777								
1	11 Dec	2.2	19.7	1.4	14.4	2.1	25 Dec	1.9
2	12 Dec	2.1	19.5	1.3	17.3	2.2	29 Dec	1.9
3	18 Dec	2.1	19.4	1.3	18.7	2.2	6 Jan	1.8
4	24 Dec	2.4	25.2	1.5	24.3	2.5	17 Jan	2.0
5	4 Jan	1.9	19.0	1.3	21.4	2.1	25 Jan	1.7
6	19 Jan	1.9	21.2	1.4	20.9	2.1	8 Feb	1.8
7	30 Jan	1.9	22.2	1.4	21.7	2.2	21 Feb	1.9
8	11 Feb	2.1	25.3	1.5	28.5	2.5	11 Mar	2.2
9	25 Feb	2.2	26.1	1.6	24.5	2.5	22 Mar	2.4
Mean					21.3			
(b) Fan-tailed Widow, KwaZulu-Natal grid 2930, n = 1 002								
1	9 Apr	2.5	24.4	1.7	6.8	1.7	16 Apr	2.6
2	7 Apr	2.4	21.5	1.7	6.4	1.6	14 Apr	2.7
3	11 Apr	2.4	20.8	1.6	8.5	1.9	19 Apr	2.6
4	11 Apr	2.3	19.4	1.4	11.7	2.3	23 Apr	2.7
5	13 Apr	2.2	17.4	1.3	17.2	2.7	30 Apr	2.6
6	24 Apr	2.5	18.2	1.5	9.6	2.4	3 May	2.6
7	29 Apr	2.6	15.1	1.5	11.0	2.5	10 May	2.4
8	3 May	2.5	14.9	1.3	17.8	2.8	21 May	2.2
9	17 May	2.2	10.4	1.2	13.0	2.3	30 May	1.6
Mean					11.3			
(c) White-winged Widow, Gauteng, n = 685								
1	21 Apr	2.7	29.0	2.4	5.0	1.5	26 Apr	2.7
2	20 Apr	2.6	28.2	2.2	8.8	1.9	29 Apr	2.7
3	24 Apr	2.5	25.7	2.1	8.1	1.8	2 May	2.5
4	27 Apr	2.5	25.0	2.1	7.3	1.8	4 May	2.5
5	30 Apr	2.3	22.4	1.8	11.6	2.1	12 May	2.4
6	8 May	2.2	19.9	1.7	7.7	1.8	16 May	2.2
7	16 May	2.2	17.6	1.8	5.2	1.5	21 May	2.1
8	20 May	2.1	17.6	1.9	5.7	1.5	26 May	2.0
9	23 May	2.5	23.2	2.0	13.0	2.3	5 Jun	2.5
Mean					8.1			
(d) Red-collared Widow, Gauteng, n = 667								
1	6 Apr	3.1	39.9	2.9	16.0	2.4	22 Apr	2.9
2	6 Apr	3.0	38.6	2.7	17.9	2.5	24 Apr	2.9
3	10 Apr	2.9	37.0	2.6	17.5	2.5	27 Apr	2.9
4	19 Apr	2.7	34.0	2.4	14.4	2.2	3 May	2.7
5	28 Apr	2.6	31.4	2.3	9.4	1.8	7 May	2.6
6	2 May	2.4	27.3	2.0	12.9	2.1	15 May	2.4
7	10 May	2.2	24.9	2.0	10.7	1.9	21 May	2.3
8	15 May	2.1	21.8	1.8	13.6	2.1	28 May	2.2
9	18 May	1.9	19.4	1.6	17.1	2.2	4 Jun	2.1
Mean					14.4			

mass/log length) were related to flight characteristics and habitat rather than to phylogeny (Dawson 2005). European Starlings *Sturnus vulgaris*, with rounded wings, are able to take off from the ground at a steeper angle of ascent than those species with relatively more pointed wingtips (Swaddle and Lockwood 2003). The mean tail lengths of male and female Long-tailed Widows are 411mm and 62mm, respectively (Hockey *et al*. 2005); males have larger wings than females, to compensate for the aerodynamic costs of a large tail in the male (Balmford *et al.* 1994). This cost may also be a reason for the more rounded shape of the wing in this species, compared to other *Euplectes* species. Whether there is a difference in relative primary feather masses between males and females is worth investigation. The only species in which only the male has a long tail and for which feather mass

Table 5: Breeding and moult in *Euplectes* species in South Africa. Average incubation and nestling periods are in days (Tarboton 2001). The dates of median and end of egg laying (taken as the 95th percentile) and start of moult are calculated from data in Tables 1 and 3. Localities are abbreviations for South African provinces: WC = Western Cape, KZN = KwaZulu-Natal, Tvl = former Transvaal

Species	Incubation period	Nestling period	Sum	Locality	Median egg laying (month)	Start of moult (month)	Period between start of moult and median egg laying date (months)	End of egg laying (month)	Period between start of moult and end of egg laying (months)
Southern Red Bishop	13	14.5	27.5	WC	9.7	12.4	2.7	11.5	0.9
				EC	12.6	4.9	4.3	2.6	2.3
				Tvl/GP	12.8	3.8	3.0	2.9	0.9
Yellow Bishop	13.5	14.5	28	WC	9.6	12.1	2.5	11.2	0.9
Fan-tailed Bishop	12.5	15.5	28	KZN	12.4	4.1	3.7	2.5	1.6
White-winged Widow	12	12	24	Tvl	1.3	4.6	3.3	2.9	1.7
Red-collared Widow	14	16	30	Tvl	12.6	4.2	3.6	2.6	1.6
Long-tailed Widow	14	15	29	KZN	12.4	3.9	3.5	2.6	1.3
				Tvl	12.9	3.9	3.0	2.8	1.1

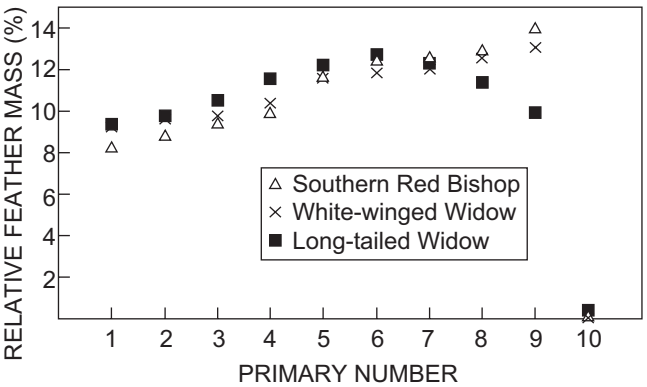

Figure 3: Relative feather masses for three adult *Euplectes* species in South Africa. Open triangles = Southern Red Bishop (from Craig *et al*. 2001); crosses = White-winged Widow; solid squares = Long-tailed Widow

data for both sexes are available is the Cape Sugarbird *Promerops cafer* (Underhill and Joubert 1995); their data show considerable differences between the sexes.

Breeding seasonality in widows and bishops in both the summer and winter rainfall areas is well-defined (Table 1). In the summer rainfall areas, nest construction can only start once grass and reed growth makes nest sites available (Brooke 1966); breeding therefore commences near the middle of summer, when the arthropods on which chicks are fed are also abundant. Primary moult took place soon after breeding activities were completed (Table 5); this late summer to autumn period is the time of the year when the seeds upon which adults feed are most abundant (Skinner 1995). During the period when seed is scarcest — winter and spring — widows and bishops in the summer rainfall region are neither breeding nor moulting. In the winter rainfall area, the arthropod peak occurs in spring, after the end of the cold rainy winter. Breeding of Red Bishops and Yellow Bishops in the Western Cape takes place at this time of the year. Primary moult takes place immediately after breeding is completed, in late summer, so that neither breeding nor moulting occurs during the cold and wet period of the year.

Euplectes bishops and widows are largely grassland birds and thus have fairly similar distributions; the core of their ranges, as indicated by the areas of high reporting rates, is concentrated in the areas where grassland occurs (Figure 1). The Yellow Bishop, however, is found more in fynbos and montane habitats, while the Red-collared Widow is often found in savanna with scattered trees and bushes, and the White-winged Widow often occurs in rank weeds. Duration of primary moult is similar for all species in the summer rainfall regions (two months or less), but the Yellow Bishop in the Western Cape winter rainfall region takes nearly 3.5 months to complete moult. Seeds are probably scarcer in the fynbos habitats of the Yellow Bishop than in the grassveld occupied by the other *Euplectes* species; it is therefore not unexpected that the duration of moult of the Yellow Bishop is c. 65% longer than the average of the species in summer rainfall areas (Table 3). Onset of moult (late March or April) is similar in the summer rainfall species. Yellow Bishops start moult in December in the winter rainfall region, as do Southern Masked Weavers and Southern Red Bishops (Oschadleus *et al.* 2000, Bonnevie *et al.* 2004). The duration of primary moult in the Southern Red Bishop in three different parts of South Africa varied from 72–89 days (Table 3). It would be beneficial to obtain moult records for the Yellow Bishop from other parts of their range, to understand how the timing and duration of moult is adjusted in different environmental regions.

Craig and Manson (1979) made preliminary estimates of the parameters of primary moult from a small sample of recaptures and from the numbers of simultaneously growing primaries in KwaZulu-Natal and Zimbabwe. They estimated duration of moult to be 110 days in Southern Red Bishops, 100 days in male Fan-tailed Widows, and 80 days for Red-collared Widows and female Fan-tailed Widows. These durations are longer than the 47–61 days estimated in the present study for widows in the summer rainfall region.

Adult Yellow Bishops needed 2–4 weeks to grow individual primaries, while the other species moulted individual primaries more quickly. The estimated durations of moult of the indi-

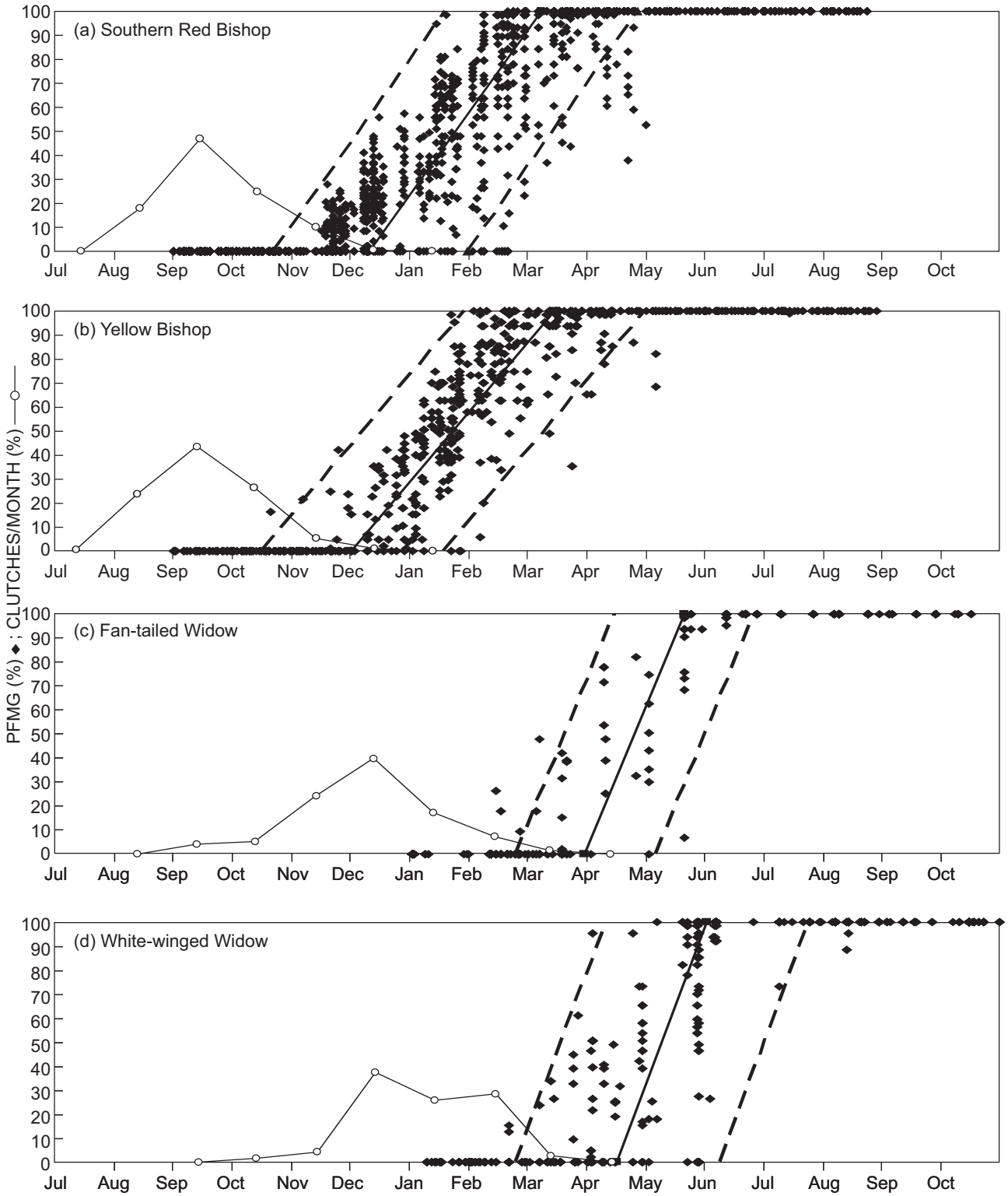

Figure 4: Timing of egg laying and primary moult for adult *Euplectes* species in different parts of South Africa. The open circles on the thin solid line show the proportion of eggs laid per month (from the Nest Record Cards summary by Prŷs-Jones and Newton 1987); the solid diamonds represent PFMG (Percentage Feather Mass Grown) values by date; the solid diagonal line joins the estimated mean start and end dates of moult; the diagonal dotted lines show the approximate 95% confidence intervals of moult scores on any given date. (a) Southern Red Bishop, breeding and moult records in the Western Cape; (b) Timing of breeding and primary moult in Yellow Bishops, Western Cape (grids 3318–3418), using eather masses of White-winged Widow;; (c) Timing of breeding and primary moult in Fan-tailed Widows, grid 2930 (KwaZulu-Natal), using feather masses of White-winged Widow; (d) Timing of breeding and primary moult in White-winged Widows, Gauteng (grids 2527, 2528, 2627, 2628)

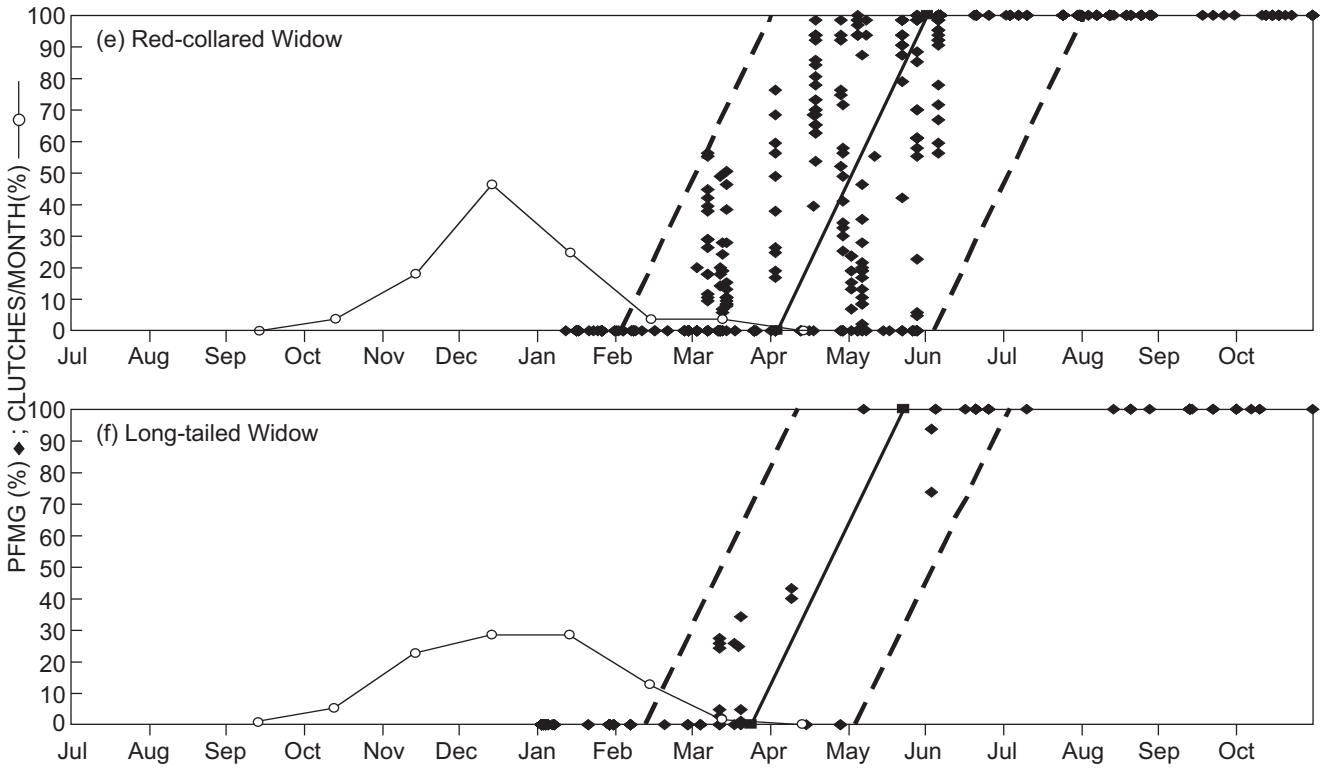

Figure 4 cont.: Timing of egg laying and primary moult for adult *Euplectes* species in different parts of South Africa. The open circles on the thin solid line show the proportion of eggs laid per month (from the Nest Record Cards summary by Prŷs-Jones and Newton 1987); the solid diamonds represent PFMG (Percentage Feather Mass Grown) values by date; the solid diagonal line joins the estimated mean start and end dates of moult; the diagonal dotted lines show the approximate 95% confidence intervals of moult scores on any given date. (e) Timing of breeding and primary moult in Red-collared Widows, Gauteng (grids 2527, 2528, 2627, 2628), using feather masses of White-winged Widow; (f) Timing of breeding and primary moult in Long-tailed Widows, all records

vidual primaries showed considerable variation; this variation is more likely to be attributable to sampling variation than to biological processes. The numbers of birds in moult for each primary feather were mostly small. The average of the individual primary durations for a species is, however, likely to provide a useful characteristic of the species.

The estimated overall duration of primary moult (Table 4) was similar to the interval between the estimated starting date of moult of the first primary to the estimated completion date of moult of the ninth (outermost) primary (Table 3). The estimated starting date of primary moult of Red-collared Widows, for instance, in the overall analysis was 5 April (Table 3) and the estimated starting date for the first primary was 6 April (Table 4 — d); the overall moult ended on 3 June and the moult of the ninth primary was completed on 4 June. Also, the number of primaries growing simultaneously was similar in the different species, indicating relatively uniform growth rates in the different species. Yellow Bishops achieve a long moult duration by growing individual primaries at a slower rate than do other *Euplectes* species, and not by growing fewer primaries simultaneously, as do Sociable Weavers (Oschadleus 2004).

The delay between the end of breeding and start of primary moult varied from 0.9–1.7 months. This delay was greatest in the Yellow Bishop, the species with the longest moult duration. It is not known how the different displays of the male widows (Emlen 1957) affect the birds' energetics, and hence how this affects the time needed to build up energy reserves before moult can commence.

It would be useful to obtain more information on the relative primary masses of all *Euplectes* species to confirm the results in this study. The South African *Euplectes* species for which primary moult parameters remain unknown is the Yellow-crowned Bishop *E. afer*. More moult records for the Yellow Bishop are needed in different environmental regions of South Africa.

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