

Chapter 9

Annual cycles in southern African weavers: breeding seasonality and moult patterns



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Introduction

With 116 species, the weavers comprise a large family with a wide diversity of life histories, as highlighted by Crook (1964). Lack (1968) acknowledged that Crook's approach to the study of ecological adaptations in weavers formed part of the inspiration for his classic text *Ecological adaptations for breeding in birds*. Of all passerine families, the weavers, along with the blackbirds Icteridae of North and South America, show the greatest diversity in breeding habits (Lack 1968). This diversity is also seen in the diversity of timing and duration of primary moult presented in this thesis. Moult has been studied in several southern African species previously, but only two papers (Oschadleus *et al.* 2000, Craig *et al.* 2001) used a rigorous statistical technique (the Underhill-Zucchini model) that allows precise comparisons between species and geographic areas.

This chapter is an overview of the preceding chapters and summarizes the annual cycle of southern African weavers, in particular the timing of breeding and post-nuptial moult. First, however, the relative wing shapes of southern African weavers are discussed.

Relative feather masses

Weaver wing shapes are fairly uniform in that the primaries increase in size from the innermost and then decrease near the outermost primaries. There is variation on a finer scale as to which primary is the largest, and in the extent of reduction of the 10th primary. In the Ploceidae generally the degree to which the outermost (10th) primary is reduced is subject to much variation. Moreau (1960: 449–451) studied the length of the outer primary in a large number of weavers and found no correlation with taxonomy or habitat.

The primary feathers of the wings were weighed, in order to calculate relative feather masses, for Sociable Weavers *Philetairus socius*, Chestnut Weavers *Ploceus rubiginosus*, Thick-billed Weavers *Amblyospiza albifrons*, Lesser Masked Weavers

Ploceus intermedius, White-winged Widows *Euplectes albonotatus* and Long-tailed Widows *E. progne* (Table 1). In addition, relative feather masses were obtained from the literature for Cape Weavers *Ploceus capensis* (Underhill and Joubert 1995), Southern Masked Weavers *P. velatus* (Oschadleus *et al.* 2000), Village Weavers *P. cucullatus*, Red-billed Queleas *Quelea quelea* and Southern Red Bishops *E. orix* (Craig *et al.* 2001). Primary moult parameters for Lesser Masked Weavers were not included in this thesis because the available sample size was small.

Plotting the individual primary feather mass percentages showed an increase in percentage mass from Primary 1 to Primary 9, although the relative masses of Primaries 8 and 9 are similar (Figure 1). Primary 10 is small in all species, accounting for between 0 and 2% of total primary feather mass (Table 1). All weaver wings analysed showed a rounded wing, across different genera. Thick-billed Weavers, Long-tailed Widows, and to a lesser extent Sociable Weavers, however, had more rounded wings than those of other weavers, with the feather mass of Primary 9 being less than Primary 8 (Figure 1). These three species differ in size and are in different genera.

Within the four *Ploceus* species there was little variation in relative feather masses (Table 1); most of the variation related to the extent of reduction in Primary 10. Craig *et al.* (2001) did not provide masses for Primary 10 in Village Weavers; in this species Primary 10 is vestigial (pers. obs.).

Potential factors influencing wing shape are protection against physical abrasion and aerodynamics (take-off, migration, flight displays). Thus Sociable Weavers may have rounded wings to protect the outer primaries from abrasion on their nests (see Chapter 2). Dawson (2005) suggested that, in a range of European passerines, that the greater relative mass of the outer primaries in some species may reflect a protective role against physical abrasion, or an aerodynamic role in that each of these feathers provides a leading edge to the wing. He found that scaling relationships (log mass vs log length) were related to flight characteristics and habitat, rather than to phylogeny.

In European Starling *Sturnus vulgaris*, take-off parameters vary with wingtip shape; birds with more rounded wingtips tended to take off from the ground at a steeper angle of ascent than those with relatively more pointed wingtips (Swaddle and Lockwood 2003). Given the wide variety of flight activities of the weaverbirds, an inter-species

analysis of wingtip shape with the ploceids is likely to be a rewarding avenue for future research.

Wing shape is related to migration, with long-distance migrants having more pointed wings (Underhill and Joubert 1995). Weavers are not long distance migrants, and the longest movements occur in Red-billed Quelea (Jones 1989). Chestnut Weavers are resident in some areas but show regular movements in others, often correlated with rainfall (Fry and Keith 2004); the longest known movement is 213 km in East Africa (Backhurst 1977) and 284 km in southern Africa (Oschadleus and Brooks 2005). These two species, Chestnut Weaver (males) and Red-billed Quelea, have the most pointed wings of the weaver species for which data are available, with the relative mass of Primary 9 being greater than 14.5% (Table 1).

Long-tailed Widows have larger wings in males than in females to compensate for the aerodynamic costs of a large tail in the male (Balmford *et al.* 1994). This may also be a reason for the more rounded shape of the wing in this species compared to other species. The 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 data for both sexes are available is the Cape Sugarbird *Promerops cafer* (Underhill and Joubert 1995); their data shows considerable differences between the sexes. Male sugarbirds use their wings to produce a snapping sound in display flights, and this may explain part of the difference in relative primary masses between males and females in this species (Skead 1967).

Underhill and Joubert (1995) modelled wing shapes using relative masses of primary feathers, using second order Tchebycheff polynomials in a regression analysis, to describe the shape of a bird's wing with two parameters. The same method was employed here using the first nine primaries of the weavers. The advantage of using Tchebycheff polynomials is that the estimates of the regression coefficients are uncorrelated with each other (Underhill and Joubert 1995). This method produces three regression coefficients, denoted R, S and T. Underhill and Joubert (1995) showed that the coefficient R is of no interest in describing wing shape, and that S and T summarize the manner in which relative primary masses change. A plot of S vs T thus summarizes the nine-dimensional relative feather mass data in a two-dimensional plot; Underhill and Joubert (1995) plotted

S vs $-T$, and this convention is followed here. If a species has both $S=0$ and $T=0$, all nine primaries are of equal mass; if both S and T of a species are near to zero, so that are close to the origin in the plot, the species must have a relatively uniform set of primaries.

Figure 2 provides a plot of S vs $-T$ for the 11 species of weavers for which data are available. The Red-billed Quelea has a relatively large positive value for S and T is nearly zero; Underhill and Joubert (1995) show that this indicates that the feather masses form a geometric progression from the smallest (innermost) to the largest (outermost) primaries. Both male and female Chestnut Weavers have large positive values for S and small negative values for T (Figure 2). This indicates that the rate of increase in mass decreases for the outermost primaries; however in this species the outermost primary is still the heaviest. The Thick-billed Weaver and Long-tailed Widow have a relatively small positive values for S and large negative values for T ; this is characteristic of species for which the outermost primaries are not the largest. Most of the remaining weavers in Figure 2 have intermediate values for both S and T , indicating that that the rate of increase in mass decreases for the outermost primaries, but several of the outermost feathers may be similar in mass. The potential of the approach to describe one aspect of wing shape pioneered by Underhill and Joubert (1995) should be further explored with a larger sample of species.

Breeding in southern Africa weavers

In the eastern parts of southern Africa, especially KwaZulu-Natal, peak summer rainfall is in December; farther north in Zimbabwe, the peak is in January; to the west, in Botswana and Namibia, peak rainfall occurs in late summer, in January and February (Allan *et al.* 1997; see Figure 1 of Chapter 1). The overall pattern is that the time of peak rainfall across the summer rainfall region of southern Africa moves in an anticlockwise direction. Most granivorous birds in the summer rainfall region breed in mid- to late summer, in response to rain which results in a flush in insect abundance to feed their young and also results in seed crops from rains several weeks earlier (Skinner 1995).

The peak breeding was plotted as a median for each species per region, using the data from the BirdLife South Africa Nest Record Card Scheme (NRC) (RP Prÿs-Jones

and I Newton unpublished data). Peak breeding in the Western Cape was in September for the four weaver species that occur there (Appendix 1). Peak breeding for all other regions was more spread out for different species, and occurred mainly in summer with some records in late spring or autumn (Figure 3).

Breeding in the winter rainfall region is towards the end of the wet season, and in the summer rainfall regions at the start of the wet season. In the winter rainfall region breeding does not take place at the start of the wet season, because temperatures are then low and falling, so that vegetation and insects are slow to respond to the rain (Moreau 1950). Breeding is postponed until late in the wet season, when temperatures are increasing (Figure 4a). In contrast, in the summer rainfall region temperatures are rising when the rainy season begins so vegetation and insects appear soon after the rain starts (Moreau 1950), allowing breeding to commence soon after the rains begin (Figure 4b). In arid regions breeding seasonality depends on rainfall which is variable, both in timing and quantity (Tyson 1987). Southern Masked Weavers have been recorded breeding along the Kuseb River when the river flooded even though the rainfall which had generated the flood, and consequent insect flush, was in a distant catchment area (Jensen 1972). Sociable Weavers lay eggs after rainfall with a lag of as little as six days (Maclean 1987). In arid regions, birds breed when there is no rain, e.g. Chestnut Weavers (Komen and Buys 1990), but clutch size is reduced relative to years with higher rainfall (Lepage and Lloyd 2004). Average clutch sizes in Southern Red Bishops were related to the amount of rainfall during the breeding season, with a larger average clutch size in seasons with a higher amount of rainfall (Friedl 2002). Thus rainfall, rather than evapotranspiration, has been regarded as the most important determinant of primary productivity in the arid regions of South Africa (Lepage and Lloyd 2004).

Several studies show that the timing of the breeding season in the Southern Red Bishop is usually related to rainfall. Craig (1982) found that Southern Red Bishop clutches were mostly laid in, or shortly after, the rainy season throughout the summer rainfall region of southern Africa. Craig (1982) also found that a high amount of rainfall preceding the breeding season corresponded to high breeding activity within that season. Friedl (2002) analysed breeding activity in relation to rainfall in a Southern Red Bishop population in the Addo National Park, Eastern Cape. He found that in seasons with poor

rainfall, breeding activity as measured in terms of the total number of nests built and total number of eggs laid during a breeding season was reduced. A detailed study on the temporal pattern of rainfall and breeding activity within breeding seasons showed that peaks in egg-laying usually followed 10 to 20 days after major rainfall events; the total number of eggs laid corresponded to the amount of rainfall in the preceding rainfall peak and showed that poor rainfall preceding breeding delayed the start of the breeding season. This was also recorded by Brooke (1966a) studying Southern Red Bishops in Zimbabwe.

The breeding season of Southern Red Bishops in the Eastern Cape was often characterised by two distinctive breeding peaks with a period in between in which there were only few or even no nests at all that contain nestlings or incubated eggs (Friedl 2002). Between the breeding peaks the general activity level was reduced and the males spent considerably less time on the territory, until good rains initiated the second breeding peak and the males started with nest-building again (Friedl 2002). In contrast to the Eastern Cape, rainfall does not seem to affect the temporal pattern of breeding activity within a season in KwaZulu-Natal (Craig 1982).

The termination of the breeding season is also influenced by rainfall, with breeding seasons of Southern Red Bishops lasting longer in years with good mid-seasonal rain (Friedl 2002). The first indication of the end of the breeding season is the termination of nest-building by the males. Gradually other activities such as territorial displays and courtship behaviour decrease in frequency and the males spend less time on their territories. Soon after they have started the postnuptial moult the first males leave the colony. Some of the territorial males will stay longer, and these are usually males with nests that contain incubated eggs or chicks (Friedl 2004).

Breeding by weavers in the summer rainfall region of southern Africa is usually in summer, but it is often delayed or advanced by unseasonal rainfall (Table 2). Southern Masked Weavers bred early in Namibia after heavy rains (Immelmann and Immelmann 1968). Southern Masked Weavers and White-winged Widows showed breeding behaviour after late rains over wide areas in the northern and central parts of the Kruger National Park (Johnson 1983). Other records of early or late breeding in response to late rains (Table 2) are from the Karoo, Northern Cape, Botswana and Namibia, i.e. semi-arid

regions, where seasonality of rainfall is more variable than in the more mesic eastern parts of southern Africa. Even with the winter rainfall region in the Western Cape, rainfall events cause perturbations in the timing of breeding: Cape Weavers started breeding in June, when temperatures in the region are generally decreasing, after a very wet April (Rowan 1953).

In this thesis, the breeding season was defined as the period of egg-laying. Breeding cycles, i.e. mean incubation plus mean fledging periods, in southern African weavers, last three to five weeks: 22–38 days (Table 3). Breeding cycles are related largely to bird size (Table 3), so larger weavers have a longer breeding cycle. The shortest breeding cycle is that of the Red-billed Quelea, at 21.5 days. Lloyd (2004) found that the incubation periods of some *Eremopterix* sparrow-larks and Red-billed Quelea are at least two days shorter than those reported for any other African species. The shared features of their ecology that might select for very short incubation periods are their high degree of nomadism and typically short windows of opportunity for breeding. The length of a breeding cycle is a key component in determining where moult should be located within this annual cycle (see also Figure 4). In the case of breeding after unseasonal rainfall, there needs to be enough rainfall to sustain a breeding cycle.

Patterns of moult in southern Africa weavers

The major outcome of this thesis has been the application of the moult model of Underhill and Zucchini (1988) to 15 species of ploceids in southern Africa (Table 4). For seven of these species moult parameters are now available for more than one locality, and for the Southern Masked Weaver independent estimates are available for two time periods, so that there are a total of 31 sets of primary moult parameters (Table 4). This excludes the 32 sets of annual estimates of moult parameters in Chapter 8. This approximately doubles the number of available sets of estimates of primary moult parameters (see Table 2 of Chapter 1).

The duration of primary moult in some arid-region weavers, namely White-browed Sparrow-weavers *Plocepasser mahali* and Scaly-feathered Finches *Sporopipes*

squamifrons, the Underhill-Zucchini model is not usable because the moult patterns are irregular (pers. obs.).

There is remarkably little available information relating to the primary moult of weavers from elsewhere in Africa (Chapter 1, Table 2). With two exceptions, papers which allude to primary moult of weavers unfortunately present only the moult scores for a very small sample of captured birds or contain a vague comment about the timing and/or duration of moult.

Two studies deserve further mention. Hanmer (1984) studied Southern Brown-throated Weaver *Ploceus xanthopterus* in Mopeia, Mozambique, and Nchalo, Malawi. The breeding season in Nchalo is from October to April, but actual dates in any year were dependent on rainfall. Males started moult while there were eggs or chicks in the nests, whereas females started moult immediately after the last brood left the nest. Duration of moult was estimated from the change in moult scores of recaptured birds, giving 87 days for adult males and 98 days for adult females.

Brooke (1985) studied the annual cycle in Seychelles Fody *Foudia sechellarum* on Cousin Island. This species is the only weaver known to have a regular pre-nuptial primary moult. Primary moult is concentrated in the months February to May, followed by breeding in the months May to September. Duration of moult was estimated from the change in moult scores of recaptured birds and averaged 101 days in 1978 and 89 days in 1979. The annual cycle consists of moult, which Brooke (1985) estimated to last three months, followed by nesting (minimum 1.5 months), caring for fledged young (up to four months), and a possible lean period (2–3 months).

Within the southern African database (Table 4), the results in this thesis indicate that moult followed soon after breeding in all species other than Sociable Weavers. By species and area, primary moult started between 11 November and 31 May, a range of nearly six months; the earliest dates were all in the Western Cape (Table 4, Appendix 2). The completion date of moult varied between 17 February and 5 November, an even longer range of 10.5 months; moult ended first in the winter rainfall region, then in the mesic part of the summer rainfall region along the east coast, and lastly in the arid regions in the western interior.

The duration of primary moult in southern African weavers also varied widely in different species and different areas, from 1.6–7.2 months (Table 4). Duration was longer at 5.1–6.9 months in the two species restricted to arid and semi-arid regions of northern Namibia, namely Sociable and Chestnut Weavers. Duration is shorter in the eastern summer rainfall region of southern Africa (in particular *Euplectes* species), ranging from 1.6–4.1 months (median 2.8 months). The Red-billed Quelea is found in both the arid west and in the wetter east. Its duration, however, is longer in the mesic east (3.4–4.1 months) than in the dry west (2.5–2.8 months).

In sexually dimorphic species, there seems to be a tendency for male weavers to start moult earlier than females, e.g. Chestnut Weavers (Chapter 3). Elliott (1973) found male Cape Weavers to moult three weeks earlier than females. Hanmer (1984) found that in Southern Brown-throated Weaver, the males started moult while there were eggs or chicks in the nests and females started moult after the last brood left the nest. The sexual difference in onset of moult is partly because the males are polygynous and leave the colonies while the females finish breeding. Craig and Manson (1979), however, found no sexual difference in onset of moult in the polygynous Southern Red Bishops, Red-collared Widows *E. ardens* and Fan-tailed Widows *E. axillaris*. Laycock (1982) found little or no difference between males and females in onset of moult in Thick-billed Weavers. There are not likely to be differences between sexes in start date of moult in monogamous species, such as Spectacled Weaver *P. ocularis*.

The length of the breeding cycle places an upper limit on how far in advance of females the males could start moult. In this thesis, sexual differences in start of moult were noted in Chestnut Weavers, but were not investigated in other species due to lack of adequately sized samples of reliably sexed birds. This is because many weaver species are difficult to age and sex, especially in their non-breeding plumage. There is a need to develop ageing and sexing criteria for weavers, and for the production of a guide analogous to that of Svensson (1992), which in its successive editions has steadily refined the ageing and sexing criteria for passerines in Europe, and is extensively used by ringers.

In the monogamous weavers, both males and females can be expected to start moult at the same time because they share incubation and nesting duties equally. There were enough data to estimate the parameters of moult for only one monogamous *Ploceus*

weaver in this study, the Spectacled Weaver. Monogamous *Ploceus* weavers are solitary and often found in forest habitats, making it a challenge to obtain sample sizes sufficient to undertake analyses of primary moult, e.g. Dark-backed Weaver *P. bicolor*, of which 112 birds have been ringed in southern Africa in the period 1948–2001 (Oschadleus 2002).

Two species, the Southern Masked Weaver (see Chapter 8) and Thick-billed Weaver (see Chapter 7), have undergone range expansions in the last century and the new populations appear to show evolving patterns in the timing of moult. Both species have advanced the timing of breeding and onset of moult relative to the areas from which they presumably originated, clearly an adaptation to local environmental conditions. Several species of ploceids continue to undergo range expansions, and this will provide further opportunities to study adaptations to timing of breeding and primary moult in relation to a new environment. In particular, the species that is likely to present a major opportunity in this direction is the Red-billed Quelea; this species is being mist-netted by ringers in the Western Cape with increasing frequency (Tygerberg Ringing Unit 2003, SAFRING unpubl. data). Given the rate of range expansion and establishment into the KwaZulu-Natal Midlands, and the Eastern Cape, the colonization of the winter rainfall region appears to be inevitable. Although this will be an event of alarming proportions to the extensive cereal-farming regions of the Swartland and Overberg, it will present an opportunity to investigate pace and progress of the patterns of change in the annual cycle of a species confined to the summer rainfall region when confronted with a winter rainfall regime. The opportunity to study these adaptations when the Southern Masked Weaver invaded the Western Cape between the 1940s and 1970s was lost.

Individual primary feather growth rates

The number of primaries growing simultaneously varied between an average of 1.0 and 2.3 feathers (Table 5, Figure 5). Craig and Manson (1979) obtained slightly higher values for individual number of feathers growing in *Euplectes* species in KwaZulu-Natal than in the present study: Southern Red Bishop 1.98, Red-collared Widow 2.57, Fan-tailed Widow males 2.30 and Fan-tailed Widow females 2.63. Laycock (1982) recorded an

average of 1.75 primaries growing simultaneously in Thick-billed Weavers in KwaZulu-Natal. Brooke (1985) measured an average of 2.4 primaries growing simultaneously in Seychelles Fodies. Figure 4 shows the rate of growth of the individual primaries for several weaver species.

The number of growing primaries seems to be related broadly to environment, and not to the overall speed of primary moult. In the species in arid regions 1.0–1.2 feathers grow simultaneously on average. In the eastern parts of southern Africa 1.6–2.3 feathers grow simultaneously. These numbers are biased in that when a bird starts and ends moult less primaries will be growing than during moult of the middle primaries. In the arid areas, the moult of the quelea is much shorter than that of the Chestnut or Sociable Weavers, yet all of them are moulting about one feather at a time. (The growth of one feather of the quelea is more rapid than that of a Chestnut or Sociable Weaver.) A possible reason for growing one primary at a time in arid regions is that it allows birds to suspend moult more easily than if several primaries are growing simultaneously, and to commence breeding if a rainfall event occurs. In mesic regions, birds can moult several primaries simultaneously as food is less likely to be a limiting factor. Thus weavers in mesic areas moult approximately two feathers simultaneously, but the rate of growth of individual primaries can vary to determine the overall length of moult which needs to be fitted into the annual cycle.

Conclusion

The annual cycle of birds is affected by the environment in which they live. Southern Africa is a large region, with a wide variety of climatic factors. This has an effect on bird distributions within the region (e.g. Harrison *et al.* 1997), as well as an effect on life-history parameters (Lepage and Lloyd 2004).

The weavers in the drier parts breed in summer but due to the variability in rainfall, often breed in response to rainfall at any time of year. Primary moult is protracted in species found mainly in arid regions. The weavers in the mesic east have well defined breeding periods, followed by primary moult. No weavers are restricted to the winter rainfall region; the four species that occur breed and moult earlier than

weavers elsewhere in southern Africa. The two weavers that show the most movement within southern Africa, the Red-billed Quelea and Chestnut Weaver, have the most pointed wings of the weavers studied. These two species show some temporal coordination of moult, particularly in the termination of moult being synchronized within each species.

This thesis provides the most comprehensive primary moult data available on an African group of birds, high-lighting general trends across species and climatic regions, as well as illustrating individual species adaptations. Rainfall patterns affect breeding seasonality and timing of moult while aridity affects number of primaries growing simultaneously. Enormous potential resides in the SAFRING database to study moult in southern Africa.

Finally I list a set of key findings:

- Sociable Weaver show variation in average body mass and wing length which is not clearly correlated with region, season or climate, other than a negative correlation of body mass with average annual water deficiency (Chapter 2).
- Body mass of Sociable Weavers near Kimberley showed a long-term decrease of 2.9 g, probably related to the prediction that body mass probably results from a trade-off between the risks of starvation at low mass and predation at high mass (Chapter 2).
- Individual primaries of Sociable Weavers were moulted mainly one at a time, each taking 20–28 days to grow fully. Prolonged duration of moult in this species is probably an adaptation to reduce energy expenditure, and to grow more durable feathers due to abrasion when entering the nest (Chapter 2).
- The lack of clear patterns of geographical variation in biometrics suggests that the contiguous populations of Sociable Weaver should belong to the nominate subspecies (Chapter 2).

- For both male and female Chestnut Weavers from northern Namibia wing length declined during and after the breeding season due to extensive feather wear (Chapter 3).
- Adult male Chestnut Weavers started primary moult three weeks earlier than females and moult lasted 17 days (9%) longer (Chapter 3).
- The onset and duration of primary moult in Red-billed Quelea in southern Africa varied substantially by region but completion of primary moult was well synchronized, ending in August in all sub-regions (Chapter 4).
- Rate of production of feather mass in Red-billed Quelea was remarkably uniform in different regions; moult speed was adjusted by the number of primaries growing concurrently – fewer feathers grew simultaneously when moult was faster. Counter-intuitively, a shorter duration of moult (i.e. fast moult) was achieved by growing fewer feathers concurrently but growing them faster (Chapter 4).
- The peak breeding seasons of Cape and Southern Masked Weavers coincided throughout South Africa, in all areas studied, except in the Western Cape where breeding by Southern Masked Weavers was delayed by a month relative to that of Cape Weavers. In these two weavers, and in the Red Bishop, primary moult started in the month within which the last eggs were laid (Chapter 5).
- The Southern Masked Weaver expanded its range into the south-western part of the Western Cape, and here it has advanced its peak breeding and moult onset by one month relative to other areas, but is still one month behind that of the Cape Weaver (Chapter 5).

- The number of primaries growing simultaneously in six species of widow-birds in South Africa was similar in these species (Chapter 6).
- The breeding seasonality of several *Ploceus* species is similar in the Eastern Cape and former Transvaal regions, both also being summer rainfall areas, but there was greater variability than in KwaZulu-Natal (Chapter 7).
- The Thick-billed Weaver had a similar durations of primary moult in Gauteng and KwaZulu-Natal of 71 and 73 days respectively, but the start date was five weeks earlier in Gauteng, an area to which the species has expanded in recent decades, for reasons which are not clear (Chapter 7).
- Annual variation in the starting dates of primary moult in Cape Weavers and Southern Red Bishops over 11 years in the Western Cape was correlated to variability in timing of the end of the wet winter season in different years; no similar pattern was detected for Southern Masked Weavers (Chapter 8).
- The onset of primary moult in the Southern Masked Weaver in the Western Cape shifted earlier; the species expanded its range into this new environmental in the middle of the 20th century, and it is proposed that the species is still adjusting the timing of its breeding and moult cycles (Chapters 5, 8).
- The weavers in the drier parts breed in summer but due to the variability in rainfall, often breed in response to rainfall at any time of year. Primary moult is protracted in species found mainly in arid regions. The weavers in the mesic east have well defined breeding periods, followed by primary moult. No weavers are restricted only to the winter rainfall region; the four species that occur breed and moult earlier than weavers elsewhere in southern Africa (Chapter 9).
- The annual cycle of southern African weavers was less variable in the mesic eastern part of southern Africa than in the arid west. The more regular rainfall of

the mesic regions allowed weavers to grow more than one primary simultaneously (1.6–2.3 feathers). In the arid regions weavers grew one primary at a time (1.0–1.2). Thus the number of growing primaries seems to be related broadly to environment, and not to the overall speed of primary moult (Chapter 9).

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Table 1: Mean relative masses of each primary feather of selected species of weavers in southern Africa (see text and Underhill and Joubert 1995 for further detail); the heaviest feather for each species is underlined

Primary	1	2	3	4	5	6	7	8	9	10	Source
Sociable Weaver	8.5	9.1	10.0	10.9	11.6	12.6	12.4	<u>12.7</u>	12.2	0.0	Chapter 2
Chestnut Weaver female	8.0	8.4	8.8	9.8	11.4	12.4	12.9	13.4	<u>13.6</u>	1.3	Chapter 3
Chestnut Weaver male	7.7	8.1	8.6	9.5	10.8	12.4	13.1	14.1	<u>14.5</u>	1.4	Chapter 3
Thick-billed Weaver	9.5	10.2	10.3	10.9	11.9	<u>12.3</u>	11.8	11.0	10.1	1.9	Chapter 7
Village Weaver	8.6	9.0	9.6	10.3	11.5	12.5	12.6	<u>13.1</u>	12.8	0.0	Craig <i>et al.</i> 2001
Cape Weaver	8.4	8.9	9.7	10.3	11.4	12.3	12.5	<u>12.8</u>	12.4	1.3	Underhill and Joubert 1995
Southern Masked Weaver	8.7	9.0	9.5	10.5	11.6	12.1	<u>12.3</u>	12.3	12.1	2.0	Oschadleus <i>et al.</i> 2000
Lesser Masked Weaver	8.9	9.7	9.6	10.6	11.5	11.7	12.0	12.1	<u>12.6</u>	1.4	Chapter 9
Red-billed Quelea	8.0	8.9	9.1	9.9	11.3	12.1	12.3	13.6	<u>14.9</u>	0.0	Craig <i>et al.</i> 2001
Red Bishop	8.3	8.8	9.4	9.9	11.7	12.4	12.6	12.9	<u>14.0</u>	0.0	Craig <i>et al.</i> 2001
White-winged Widow	9.3	9.6	9.8	10.4	11.6	11.8	12.0	12.5	<u>13.0</u>	0.0	Chapter 6
Long-tailed Widow	9.3	9.8	10.5	11.5	12.2	<u>12.7</u>	12.3	11.4	9.9	0.4	Chapter 6

Table 2: Unseasonal breeding in southern African weavers; published records of weavers breeding earlier or later than usual due to early or late rainfall events in southern Africa. Locality abbreviations for South African provinces and regions: N Cape = Northern Cape, KNP = Kruger National Park, W Cape = Western Cape

Area	Early or late rain	Rainfall	Breeding notes	Reference
Scaly-feathered Finch				
N Cape	late	heavy rain in April	nest building next day	Winterbottom (1967)
N Cape		first good rain shower	eggs laid 8 and 35–46 days after rain	Maclean (1971)
Sociable Weaver				
N Cape	none	drought	many colonies abandoned	Brooke (1987)
Southern Masked Weaver				
Namibia	early	heavy rain on 29 September	eggs & chicks 17–23 Oct 1965	Immelmann and Immelmann (1968)
Karoo	late	heavy rain Jan–Mar	eggs in March	Martin <i>et al.</i> (1986)
N Cape		first good rain shower	eggs laid 14 and 15 days after rain	Maclean (1971)
KNP	late	heavy rain on 19 March	displaying on 26 March	Johnson (1983)
N Cape	late	heavy rain 18–23 May	eggs & chicks at end of May	Winterbottom and Rowan (1962)
Karoo	late	Feb/Mar rain	eggs & chicks in May	Martin and Martin (1970)
Chestnut Weaver				
Namibia	late	Dec–Feb rains	eggs laid in large colonies	Braine and Braine (1971)
Cape Weaver				
W Cape	early	very wet April	breeding started 4 weeks early: nests in June; eggs in July	Rowan (1953)
Karoo	late	Feb/Mar rain	building in May	Martin and Martin (1970)
Lesser Masked Weaver				
Botswana	late	good, late rains	nests built in vast colonies	Cole (1958)
Southern Red Bishop				
Karoo	late	heavy rain Jan–March	chicks in April	Martin <i>et al.</i> (1985, 1986)
former Transvaal	late	long, severe winter	nest building in November, rather than in October	Haagner (1901)
Red-collared Widow				
Mozambique	prolonged	prolonged good rains	breeding continued during dry season	Brooke (1966b)
White-winged Widow				
KNP	late	heavy rain on 19 March	mating & displaying on 23 March	Johnson (1983)

Table 3: Clutch sizes, incubation and fledging periods, and sizes of weavers in southern Africa (data from Fry and Keith 2004)

Species	Mean clutch size	Incubation period (days)	Fledging period (days)	Incubation + Fledging (days)	Mass of female (g)	Wing of female (mm)	Tarsus of female (mm)
Red-billed Buffalo-weaver <i>Bubalornis niger</i>	3.5	11	21.5	32.5	81.3	115.0	29.5
White-browed Sparrow-weaver <i>Plocepasser mahali</i>	2	15	20	35	46.3	101.5	26.2
Sociable Weaver <i>Philetairus socius</i>	3.5	13.5	22	35.5	27.3	70.7	17.0
Scaly-feathered Finch <i>Sporopipes squamifrons</i>	4	11	16	27	12.4	56.0	15.0
Thick-billed Weaver <i>Amblyospiza albifrons</i>	3	15	20.5	35.5	40.0	85.8	22.0
Dark-backed Weaver <i>Ploceus bicolor</i>	3	16	22	38	32.0	83.5	27.0
Olive-headed Weaver <i>Ploceus olivaceiceps</i>	2.5	–	–	–	19.6	77.8	18.5
Spectacled Weaver <i>Ploceus ocularis</i>	3	13.5	17	30.5	28.2	73.3	24.5
Village Weaver <i>Ploceus cucullatus</i>	2.5	12.2	19	31.2	38.1	81.4	20.5
Chestnut Weaver <i>Ploceus rubiginosus</i>	3.5	12.5	14.5	27	28.0	79.0	22.0
Cape Weaver <i>Ploceus capensis</i>	2.5	13.5	17	30.5	40.4	84.5	22.5
Southern Masked Weaver <i>Ploceus velatus</i>	2.5	13	16.5	29.5	25.7	80.3	21.0
Lesser Masked Weaver <i>Ploceus intermedius</i>	2.5	12.5	15.5	28	21.9	69.0	20.0
Golden Weaver <i>Ploceus xanthops</i>	2	14	20.5	34.5	39.0	83.6	24.0
Yellow Weaver <i>Ploceus subaureus</i>	2.5	–	20.5	–	26.4	77.1	21.1
Southern Brown-throated Weaver <i>Ploceus xanthopterus</i>	2.5	15.5	16.5	32	19.1	64.6	20.0
Red-headed Weaver <i>Anaplectes melanotis</i>	2.5	12	17	29	22.0	77.6	19.0
Red-billed Quelea <i>Quelea quelea</i>	3	11	10.5	21.5	19.0	65.0	18.0
Red-headed Quelea <i>Quelea erythrops</i>	2	13	13	26	21.1	60.0	17.0
Southern Red Bishop <i>Euplectes orix</i>	3	12.5	13	25.5	20.7	66.3	21.5
Black-winged Bishop <i>Euplectes hordeaceus</i>	3	12.5	12	24.5	19.0	66.5	20.0
Yellow-crowned Bishop <i>Euplectes afer</i>	3.5	13	17	30	15.3	61.8	17.3
Yellow Bishop <i>Euplectes capensis</i>	3	14.5	18	32.5	30.4	71.6	23.0
Fan-tailed Widow <i>Euplectes axillaries</i>	3	12.5	15.5	28	22.0	71.1	23.5
White-winged Widow <i>Euplectes albonotatus</i>	3	13	12.5	25.5	18.9	66.2	18.0
Yellow-mantled Widow <i>Euplectes macrourus</i>	2.5	13	15	28	19.7	68.3	19.5
Red-collared Widow <i>Euplectes ardens</i>	3	13.5	15.5	29	19.1	66.8	20.5
Long-tailed Widow <i>Euplectes progne</i>	3	13	17	30	32.0	93.0	23.3

Table 4: Estimates of the primary moult parameters of southern African weavers using the maximum likelihood method of Underhill and Zucchini (1987); this summary contains the results for all species analysed in this thesis (except those of Chapter 8), and also results from * Oschadleus *et al.* (2000) and # Craig *et al.* (2001)

Species	Group (Locality, race, years)	Mean start date	Standard error (days)	Standard deviation (days)	Standard error (days)	Duration (days)	Standard error (days)	Mean end date	Standard error (days)	n
Sociable Weaver	<i>eremnus</i> (SA)	31 Dec	6.1	38.0	2.2	168.9	8.1	17 Jun	3.7	481
	<i>geminus</i>	28 Jan	5.9	67.5	5.0	215.8	13.8	31 Aug	12.0	231
	<i>socius</i>	26 Jan	4.1	37.7	1.9	151.7	7.2	26 Jun	3.8	838
Spectacled Weaver	KwaZulu-Natal	3 Feb	3.4	21	1.3	114.1	4.3	28 May	2.3	388
Cape Weaver	Western Cape, 1998–2003, grid 3318	11 Nov	1.4	24.2	0.6	98.1	2.0	17 Feb	1.3	3226
	KwaZulu-Natal, 1998–2003, grid 2930	2 Feb	4.1	31.5	2.7	124.2	9.5	6 Jun	7.4	238
	Eastern Cape #	9 Jan	4	25.2	2.1	106	7	25 Apr	4.7	316
Yellow Weaver	KwaZulu-Natal	27 Feb	2.6	19.7	1.4	65.8	3.9	4 May	2.8	653
Southern Masked Weaver	Western Cape, 1986–1995 *	9 Jan	7.5	24.0	2.1	73.8	13.2	24 Mar	6.5	2318
	Western Cape, 1998–2003, grid 3318	27 Dec	2.4	33.2	1.2	84.4	3.3	22 Mar	2.2	1411
	North-west Province, 1983–1995 *	15 Feb	2.7	22.7	1.6	80.4	3.9	7 May	2.5	1547
	Gauteng, 1998–2003	11 Feb	0.9	18.8	0.6	75.9	1.7	28 Apr	1.3	2556
	Eastern Cape #	22 Mar	3	24.8	1.9	67	5	28 May	3.6	391
Village Weaver	KwaZulu-Natal, grid 2930	12 Feb	2.4	28.5	1.1	96.1	3.4	19 May	2.1	1215
	Eastern Cape #	17 Feb	5	40.1	2.4	109	6	5 Jun	3.7	436
Chestnut Weaver	male	9 Apr	2.9	39.5	1.2	205.8	3.8	1 Nov	1.8	975
	female	30 Apr	3.2	37.5	1.5	189.4	4.8	5 Nov	2.9	552
Red-billed Quelea	Namibia, 1999–2004	21 May	4.3	37.4	1.9	74.6	4.8	3 Aug	2.7	1163
	Botswana, 1999–2004	31 May	3.6	35.1	1.8	82.5	4.5	21 Aug	2.6	543
	Gauteng, 1999–2004	23 Apr	2.6	32.7	1.2	100.9	3.6	2 Aug	2.4	1105
	Eastern Cape #	6 Apr	2	36.5	0.8	124	3	8 Aug	1.4	3077
Southern Red Bishop	Western Cape, 1998–2003, grid 3318	13 Dec	1.1	25.3	0.6	88.6	1.7	12 Mar	1.2	3154
	Gauteng, 1998–2003	23 Mar	1.5	35.1	1.1	71.9	2.5	3 Jun	2.3	4808
	Eastern Cape #	28 Apr	4	47.3	2.9	89	7	26 Jul	6.1	622
Yellow Bishop	Western Cape, grids 3318 & 3418	4 Dec	2.0	23.3	1.0	103.4	3.0	17 Mar	1.8	777
Fan-tailed Widow	KwaZulu-Natal, grid 2930	2 Apr	1.9	18.1	0.9	50.5	2.8	23 May	2	1002

Table 4 continued

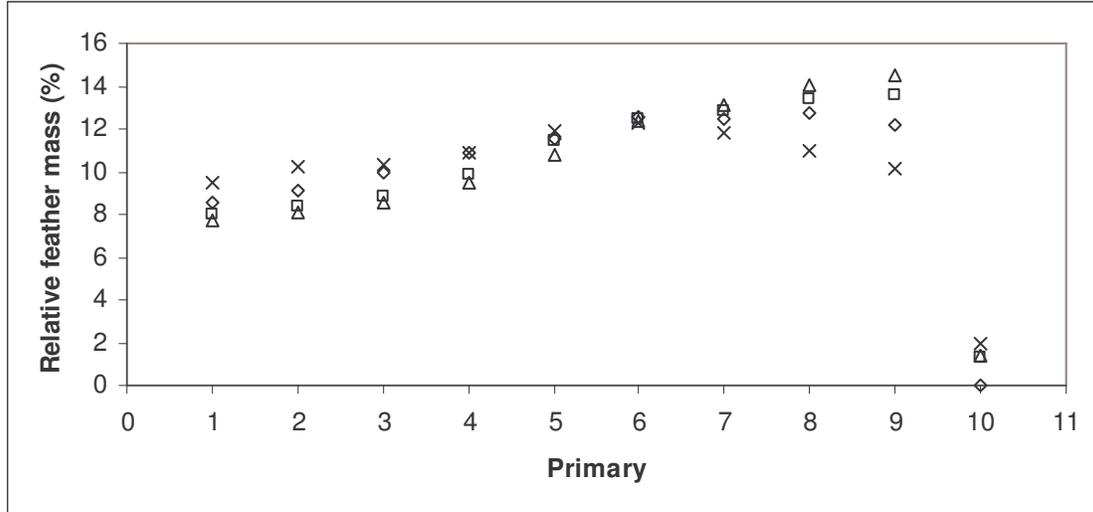
Species	Group (Locality, race, years)	Mean start date	Standard error (days)	Standard deviation (days)	Standard error (days)	Duration (days)	Standard error (days)	Mean end date	Standard error (days)	n
White-winged Widow	Gauteng	18 Apr	2.5	26.3	1.6	46.5	3.3	3 Jun	2.6	685
Red-collared Widow	Gauteng	5 Apr	2.5	30.8	1.6	59.9	3.5	3 Jun	2.6	667
Long-tailed Widow	Eastern South Africa	26 Mar	4.8	20.6	2.9	60.7	8.7	25 May	7.1	279
Thick-billed Weaver	Gauteng	20 Feb	4.3	23.8	2.6	71.2	6.8	2 May	5.4	179
	KwaZulu-Natal	26 Mar	3.9	22.9	2.2	73.3	6.4	8 Jun	5.2	462

Table 5: Growth rates of individual primary feathers in southern African weavers
 Localities are abbreviations for countries or for South African provinces: NA=Namibia, BW=Botswana, WC=Western Cape, EC=Eastern Cape, NC=Northern Cape, KZN=KwaZulu-Natal, FS=Free State, GP=Gauteng

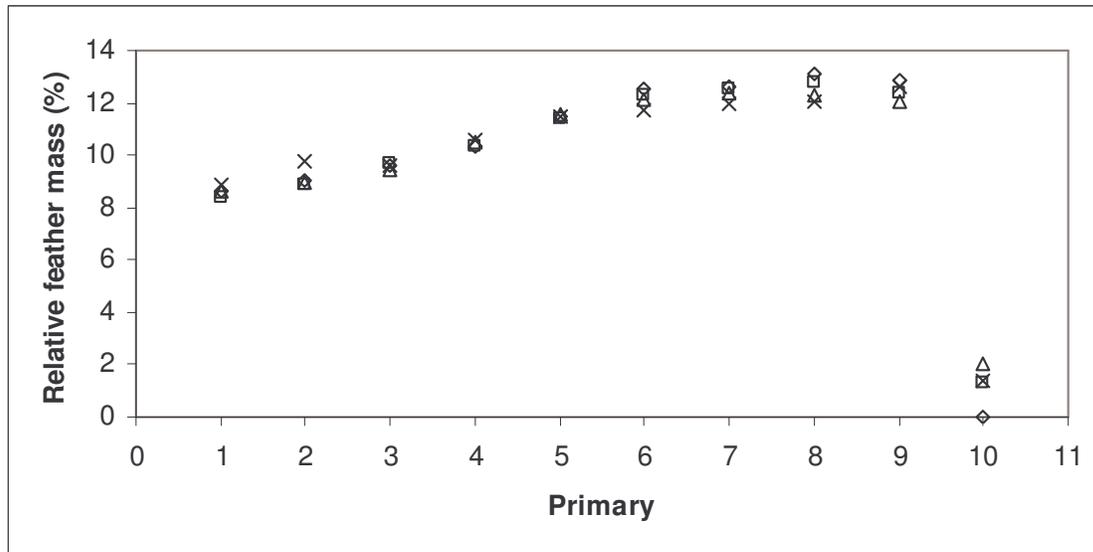
Species	Area	Growing primaries		Individual mean rate (days)	Wing-moult duration (days)
		Range	Mean		
Sociable Weaver	NA+NC	1-4	1.2	24.1	
Spectacled Weaver	KZN	1-4	1.7		114.1
Cape Weaver	KZN	1-4	1.9		124.2
Cape Weaver	WC	1-4	1.9		98.1
Yellow Weaver	KZN	1-3	1.7		65.8
Southern Masked Weaver	GP	1-4	1.9		75.9
Southern Masked Weaver	WC	1-4	1.9		84.4
Village Weaver	KZN	1-4	1.6		96.1
Chestnut Weaver	NA	1-2	1.1	15.3	205.8
Red-billed Quelea	NA	1-2	1.0	9.8	74.6
Red-billed Quelea	BW	1-3	1.1	14.0	82.5
Red-billed Quelea	GP	1-4	1.7	28.4	100.9
Red-billed Quelea	EC	1-4	1.7	23.9	124
Red Bishop	GP	1-5	1.7		71.9
Red Bishop	WC	1-4	1.7		88.6
Cape Bishop	WC	1-4	1.8	21.3	103.4
Fan-tailed Widow	KZN	1-3	1.9	11.3	50.5
White-winged Widow	GP	1-4	1.7	8.0	46.5
Red-collared Widow	GP	1-5	2.1	14.4	59.9
Long-tailed Widow	all	1-4	2.3		60.7
Thick-billed Weaver	KZN	1-3	1.8		73.3
Thick-billed Weaver	GP	1-3	1.9		71.2

Figure 1: Relative primary masses for southern African weavers

(a) Sociable Weaver, diamonds; Chestnut Weaver female, squares; Chestnut Weaver male, triangles, Thick-billed Weaver, crosses



(b) Village Weaver, diamonds; Cape Weaver, squares; Southern Masked Weaver, triangles; Lesser Masked Weaver, crosses



(c) Red-billed Quelea, diamonds; Red Bishop, squares; White-winged Widow, triangles; Long-tailed Widow, crosses

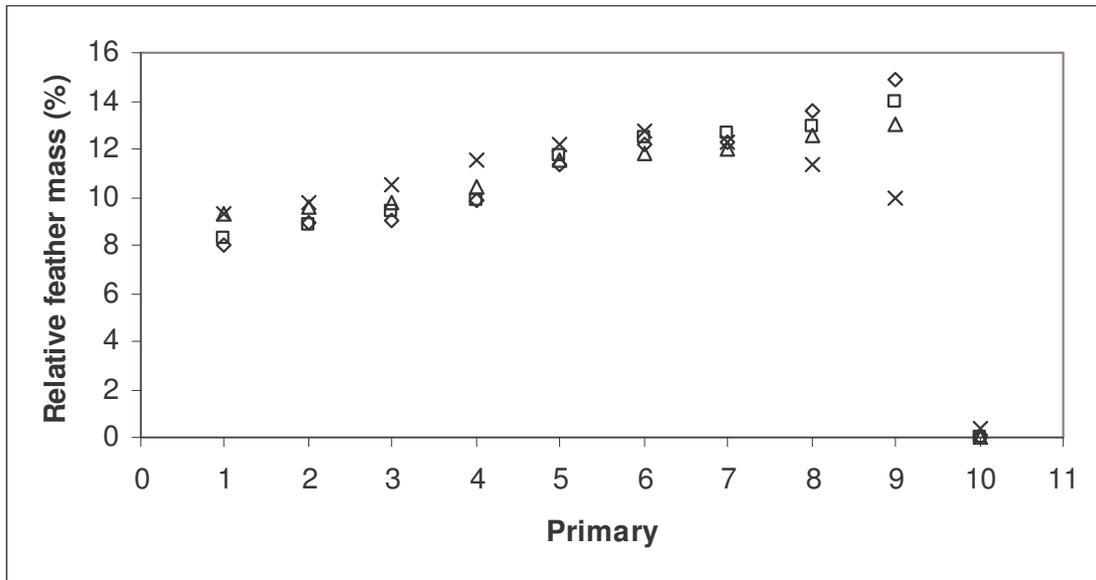


Figure 2: Plot of S against -T for southern African weavers
1=Sociable Weaver, 2=Thick-billed Weaver, 3=Chestnut Weaver male, 4=Chestnut Weaver female, 5=Village Weaver, 6=Cape Weaver, 7=Southern Masked Weaver, 8=Lesser Masked Weaver, 9=Red-billed Quelea, 10=Red Bishop, 11=White-winged Widow, 12=Long-tailed Widow

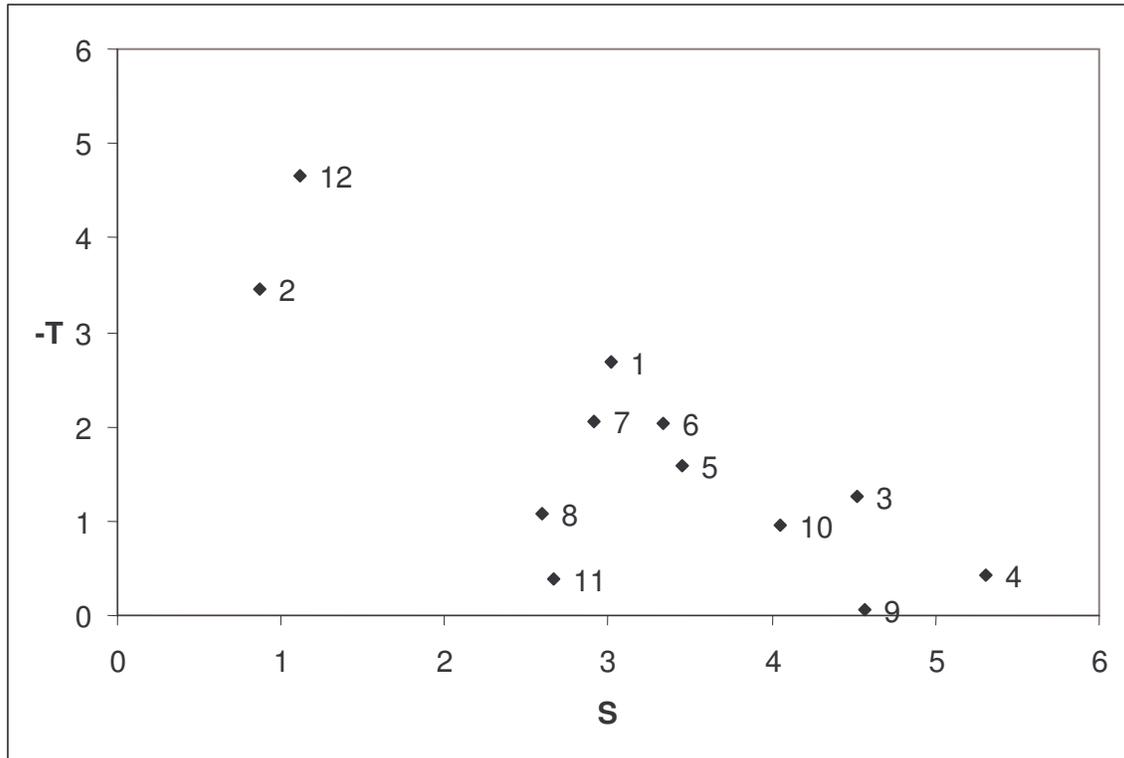


Figure 3: Median months of egg-laying for southern African weavers (from Prÿs-Jones and Newton unpublished data, Zimbabwe data from Irwin 1981). For Thick-billed Weaver in the former Transvaal my own records from Gauteng have been added. For Southern Masked Weavers additional breeding records from northern KwaZulu-Natal are included. For each region the median month of egg-laying per species is shown; symbols indicate genus: open squares are *Ploceus* species, open diamonds are *Euplectes* species, crosses are other species (data in Appendix 1); species with <10 records in an area are omitted

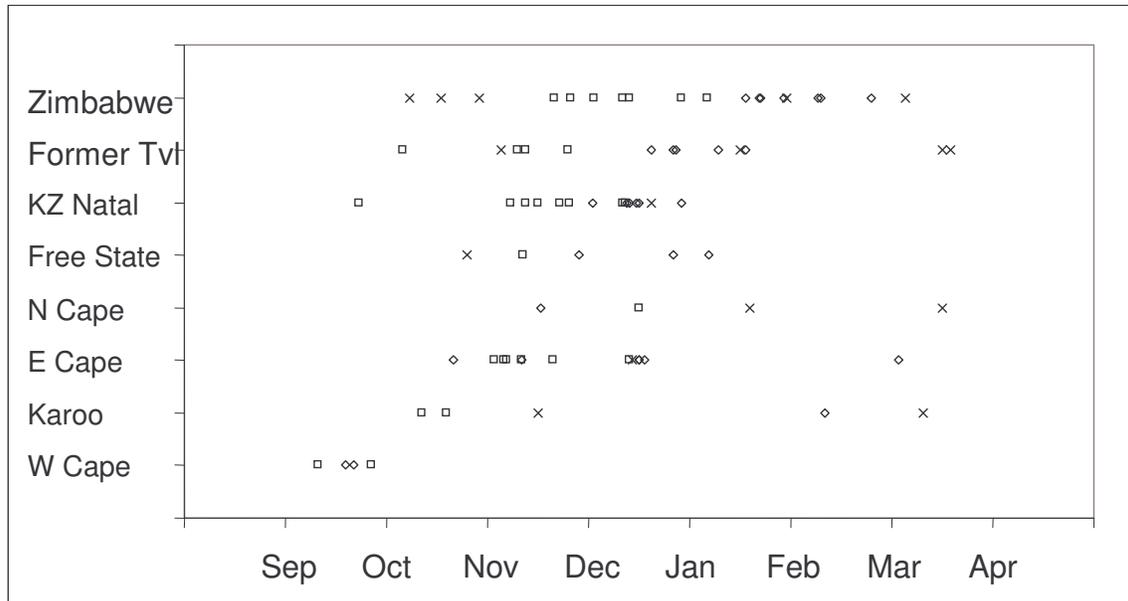
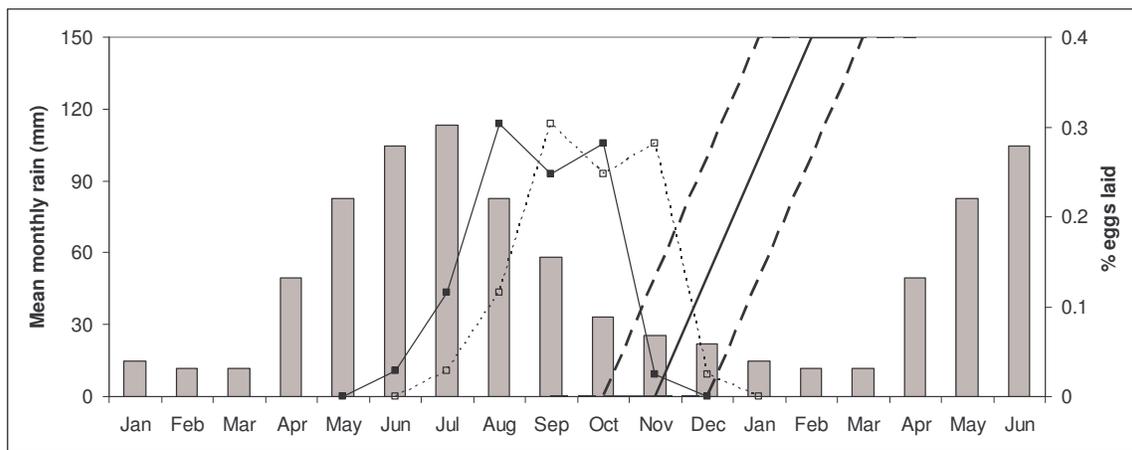


Figure 4: Diagrammatic representation of the annual cycle of southern African weavers. Grey bars show mean monthly rainfall; the solid line joining solid squares shows the percentage of eggs laid per month (from the Nest Record Cards summary by Prŷs-Jones and Newton unpublished data); the dotted line joining open squares shows when the breeding cycle finishes (egg laying date plus incubation plus fledging periods); the solid diagonal line joins the estimated mean start and end dates of moult, while the diagonal dotted lines show the approximate 95% confidence intervals of moult scores on any given date

(a) Cape Weaver annual cycle in a winter rainfall region (rainfall is mean monthly rainfall for 1993–2003 at Altydgedacht rainfall station)



(b) Cape Weaver annual cycle in a summer rainfall region (mean monthly rainfall for Johannesburg, Gauteng)

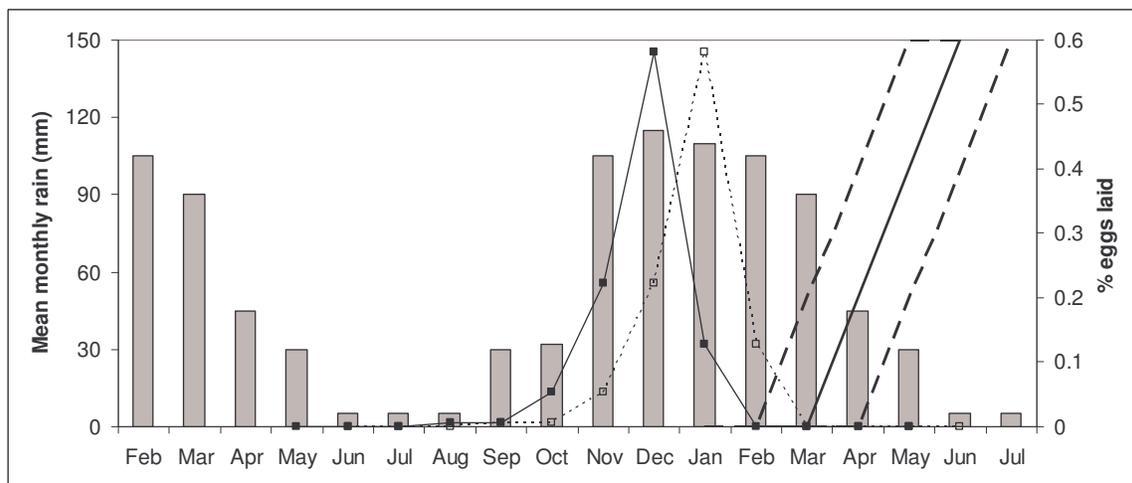
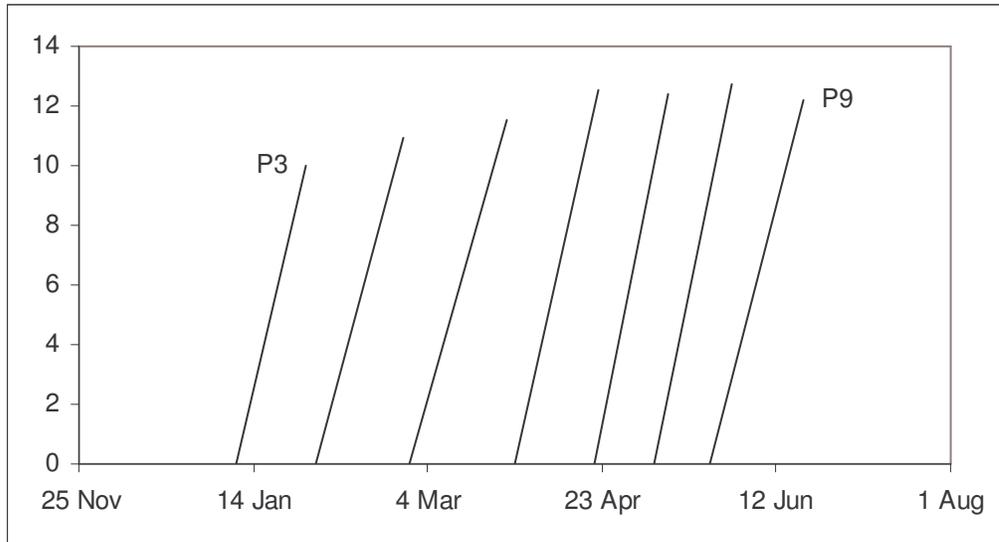
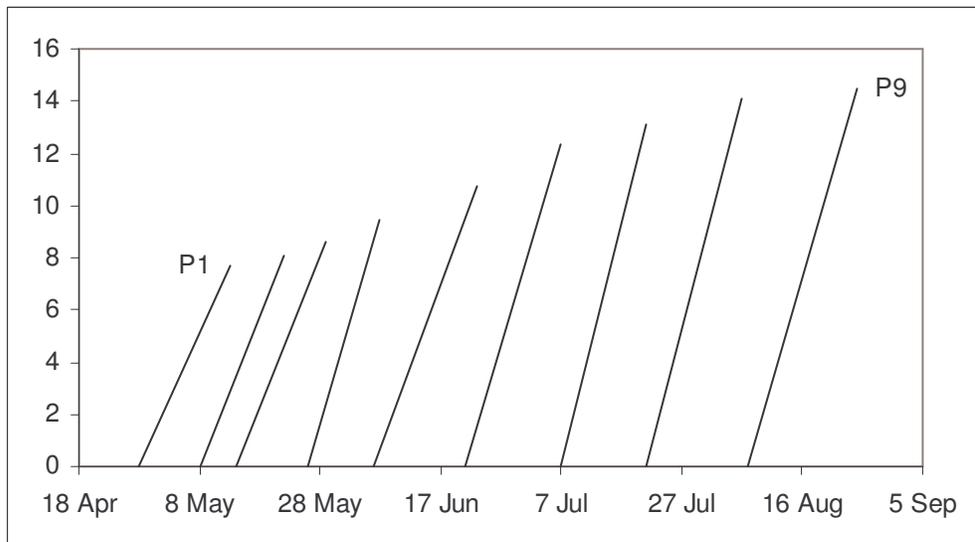


Figure 5: Timing of moult of each of the nine primaries of southern African weavers. The x-axis represents the date; the y-axis the percentage primary mass (from Table 1). Each line represents one primary (1 to 9 from left to right, in some species less than 9 primaries – see Tables in chapters). For each line, the starting date is shown on the x-axis; the height to which the line rises shows the percentage primary mass; the end-point of the line is directly above the completion date on the x-axis. Thus the slope of the line gives the rate at which feather material is deposited; steep slopes represent rapid growth

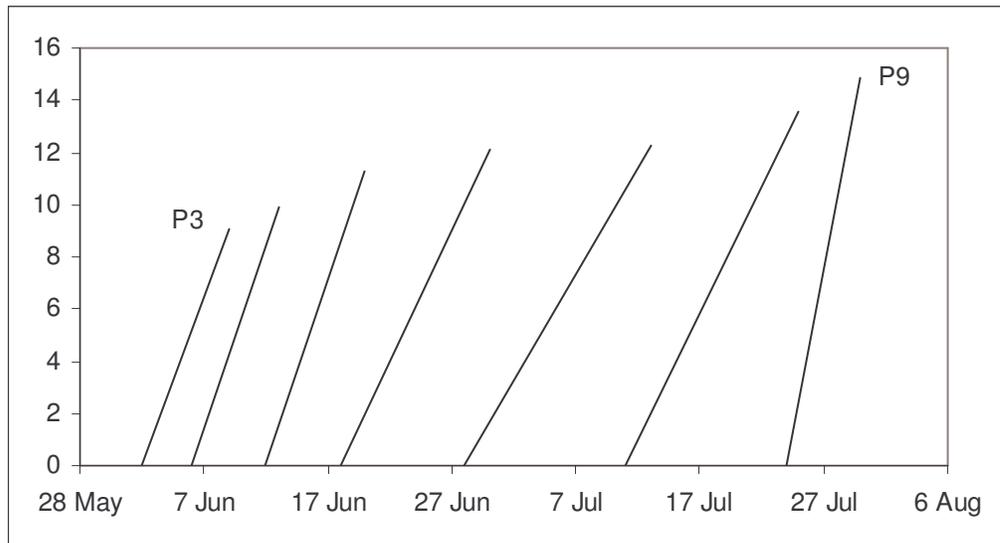
(a) Timing and rate of individual primary feather growth in Sociable Weavers in the Northern Cape



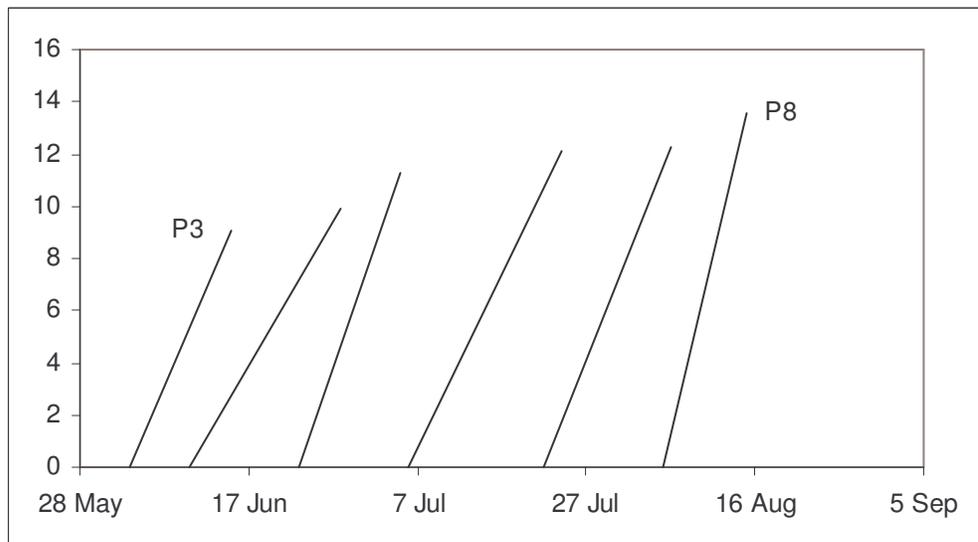
(b) Timing and rate of individual primary feather growth in Chestnut Weaver males in Namibia



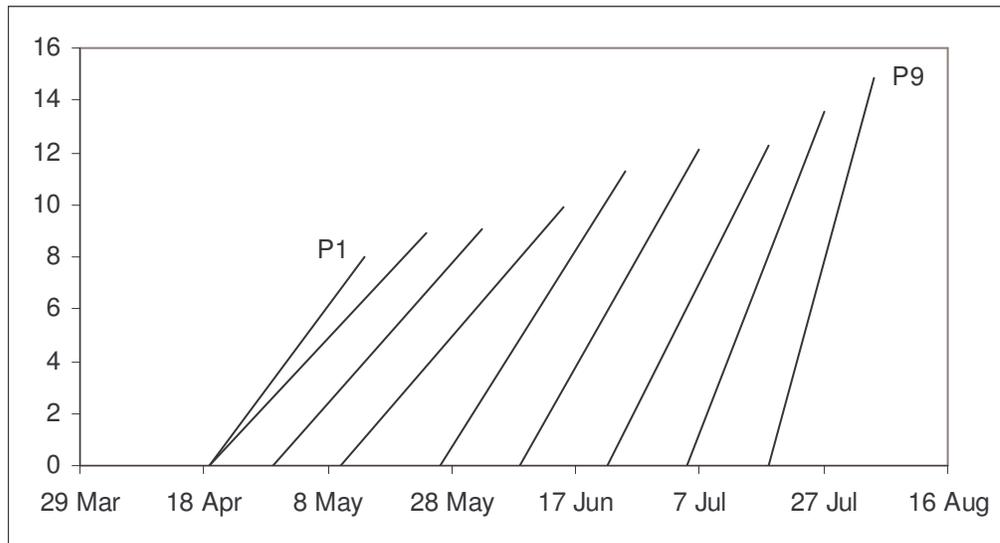
(c) Timing and rate of individual primary feather growth in Red-billed Quelea in Namibia



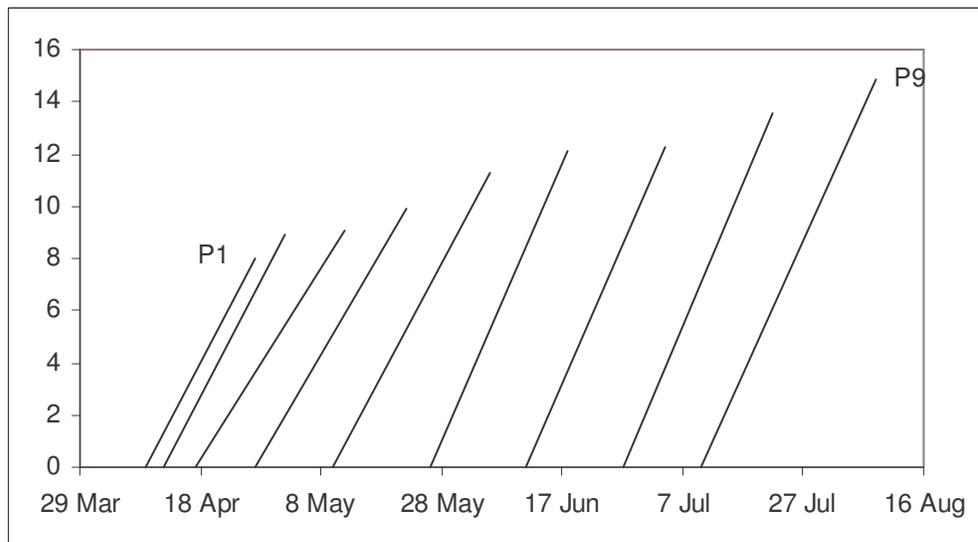
(d) Timing and rate of individual primary feather growth in Red-billed Quelea in Botswana



(e) Timing and rate of individual primary feather growth in Red-billed Quelea in Gauteng



(f) Timing and rate of individual primary feather growth in Red-billed Quelea in the Eastern Cape



(g) Timing and rate of individual primary feather growth in White-winged Widows in Gauteng

