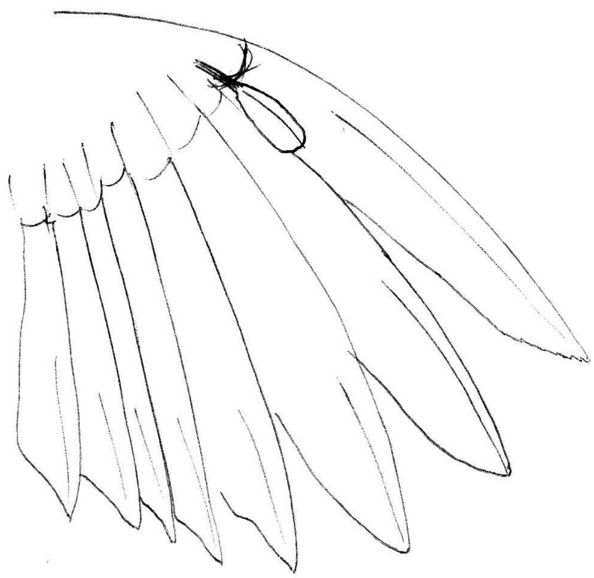
Chapter 8

Annual variation in primary moult parameters in Cape Weavers, Southern Masked Weavers and Southern Red Bishops in the Western Cape, South Africa



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Abstract

Duration of primary moult was similar in Cape Weavers and Southern Red Bishops (96 days) and slightly shorter in Southern Masked Weavers (75 days) over 11 years in the Western Cape. Mean start date of moult averaged over 11 years was earliest in Cape Weavers (12 November), intermediate in Southern Red Bishops (5 December) and latest in Southern Masked Weaver (14 January). The difference between earliest and latest starting dates for different years was greatest for Southern Red Bishops (35 days), intermediate in Cape Weavers (31 days) and least for Southern Masked Weavers (21 days). This variation in start dates was due to variability in timing of rainfall in different years. End of moult followed after breeding which was correlated with the end of the rainy season. In a model of dry periods following the rainy season and peak breeding, Cape Weavers started primary moult an average of 29.2 days after the first dry period in October. Similarly Southern Red Bishops started moult 58.8 days after the first dry period in October. Southern Red Bishops seemed to continue breeding for longer than Cape Weavers after the first dry period after October. A possible reason for this ability to breed for longer may be that Southern Red Bishop chicks were less dependent on insects than were Cape Weaver chicks. The Southern Masked Weaver, however, showed the onset of moult as late January in earlier years, and then stabilized around 6 January. Thus onset of moult in different years in the Southern Masked Weaver appears to have advanced over time. Timing of breeding in this species is predicted to advance in the future, and this could mean an advance in timing of moult.

Introduction

Annual variation in moult parameters has been poorly documented, especially in the southern hemisphere. There are several published studies in the northern hemisphere (Cassin's Auklet *Ptychoramphus aleuticus,* Emslie *et al.* 1990; Curlew Sandpiper

Calidris ferruginea, Figuerola and Bertolero 1995; Dunnock *Prunella modularis,* Ginn 1975; Reed Bunting *Emberiza schoeniclus,* Sondell 2000; Pied Flycatcher *Ficedula hypoleuca,* Siikamaki *et al.* 1994; Bullfinch *Pyrrhula pyrrhula,* Newton 1966, 1999; Lesser Redpoll *Carduelis flammea,* Evans 1966; Mountain White-crowned Sparrow *Zonotrichia leucophrys* Morton and Morton 1990).

The Southern Masked Weaver *Ploceus velatus,* Cape Weaver *P. capensis* and Southern Red Bishop *Euplectes orix* are three common ploceids in the Western Cape, South Africa. They are polygynous, colonial, seed-eating weavers. Cape and Southern Masked Weavers breed mainly in trees or reeds; Southern Red Bishops breed chiefly in reeds (Fry and Keith 2004). The Southern Masked Weaver is a relatively new arrival in the Western Cape, having expanded its range into this region since the 1940s (Oschadleus *et al.* 2000 and references therein; see also Chapter 5).

In the Western Cape the Cape Weaver breeds from August to November, the Southern Red Bishop from August to early December (Craig *et al.* 2001), and the Southern Masked Weaver from September to November (Oschadleus *et al.* 2000; Chapter 5).

In the Western Cape adult wing-moult is known to be from October to March in Cape Weavers, November to April in Southern Red Bishops, and January to March in Southern Masked Weavers (Oschadleus *et al.* 2000, Craig *et al.* 2001; Chapter 5). In these species moult of the primaries is ascendant, with the feathers renewed from innermost to outermost. This paper investigates inter-year variation in the timing of primary moult for these three species over an 11-year period in the Western Cape.

Methods

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 were extracted from the SAFRING database for Cape Weavers, Southern Red Bishops and Southern Masked Weavers in the one-degree area, 33°–34°S 18°–19°E, for the 11 years from 1 September 1993 to 1 September 2004 (Figure 1). The sites with the most ringing data were Goedeontmoeting farm (33°41'S 18°36'E), Rocklands farm (33°43'S 18°45'E), Protea Hills (33°51'S 18°37'E), and gardens in Durbanville, a suburban area (33°51'S 18°38'E). The closest weather station to these sites is at Altydgedacht (33°50'S 18°38'E) and daily rainfall data were obtained from this station for the period 1993 to 2003.

The relative mass of each primary (as described in Underhill and Summers 1993) was obtained from published sources: Cape Weaver (Underhill and Joubert 1995), Southern Masked Weaver (Oschadleus *et al.* 2000) and Southern Red Bishop (Craig *et al.* 2001). For the first two species 10 primaries were used even though the 10th primary is small; for Southern Red Bishops nine primaries were weighed because the 10th is less than 0.001 g (pers. obs). The Underhill-Zucchini moult model (Underhill and Zucchini 1988), developed to estimate start and duration of primary moult, was applied to the data sets. 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 available for sampling throughout the moult period. 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 from the moult score for the individual feathers according to the method of Underhill and Summers (1993).

Brandao (1998) (see also Underhill *et al.* in press) extended the Underhill-Zucchini (1988) moult model to estimate starting dates for groups of birds (e.g. males and females, or annual groups), holding the other two parameters (duration and standard deviation) the same for all groups. This method was applied to estimate starting dates for three weaver species over 11 years.

The starting date of moult was related to variables derived from the daily rainfall data. In the Western Cape, breeding occurs in the mid to latter part of the winter period during which the bulk of the region's rainfall occurs. However, the timing of this rainfall is variable between years. Because moult occurs after the end of the breeding season, I sought to explore a relationship between the end of the rainy season each year and the timing of moult. If such a relationship existed, it would also indicate that the end of the breeding season is related to the end of the rainy season.

The daily rainfall data were used to set up a daily index of wetness, based on the principle of exponential decay, to simulate the effect of cumulative rainfall.

Putting r_i as the rainfall (mm) on day i, the index of wetness W_i (which has units mm) for day i was computed as

$$W_i = 0.8\ W_{i-1} + r_i$$

Thus the effect of rainfall steadily decays through time. The index of wetness was started each year on 1 January, eliminating any possibility of start up effects in the rainfall index in October and November, the months for which the index was used. A simple strategy was proposed for the cessation of breeding for Cape Weavers and Southern Red Bishops: remain in breeding condition until the beginning of October; cease breeding (and prepare to moult) when conditions become dry. This strategy was operationalised by determining, for each year, the first day after 1 October on which the index of wetness dropped below 2 mm and using this as an explanatory variable to predict the estimated date of start of moult in a regression model. Other explanatory variables based on the rainfall were also considered: the total rainfall during the period 1 May to 30 September, and the date on which the cumulative rainfall for this period reached its median for the year.

Results

Over the 11-year study period 10468 weavers of the three species were captured within the grid 33°S 18°E (Figure 1), providing a large data set to study annual variation in moult parameters. Birds were captured throughout the moult season; this enabled the moult parameters to be estimated reliably. Moult parameters were calculated for the overall time period 1993–2003 (Table 1) and for each of these 11 individual years (Table 2).

For all years combined, the duration of primary moult was similar for Cape Weavers and Southern Red Bishops (96 days) and slightly shorter in Southern Masked Weavers (75 days). Mean start date of moult was earliest in Cape Weavers (12 November), intermediate in Southern Red Bishops (5 December) and latest in Southern Masked Weaver (14 January).

To calculate annual variation in start date of moult, the Brandao extension to the Underhill-Zucchini moult model was used. Over the 11 years, the estimated mean starting date of Cape Weaver primary moult lay between 27 October and 27

November, Southern Red Bishops between 27 November and 1 January, and Southern Masked Weavers between 4 and 25 January (Table 2, Figure 2). There were insufficient data for the algorithm to converge for Southern Masked Weavers in 1997. The difference between earliest and latest starting dates for different years was greatest for Southern Red Bishops (35 days), intermediate in Cape Weavers (31 days) and least for Southern Masked Weavers (21 days) (Table 1).

A striking aspect of the results was the parallelism between mean starting dates of primary moult of Cape Weavers and Southern Red Bishops in Figure 2; both showed similar pattern of starting dates for moult over 11 years (Figure 2). Cape Weavers started moult on average 28 days (s.d. 5 days) earlier than Southern Red Bishops; this lag was the least in 2003 (22 days) and greatest in 1993 (36 days). Plotting the onset of moult for these two species gives a correlation of 0.66 (Figure 3). For the Southern Masked Weaver, the onset of moult was relatively late from 1993 to 1995, and stabilized around 6 January for the period 1998 to 2003 (Figure 2).

Cape Weavers started primary moult an average of 30 days (s.d. 6 days, range 21–41) after the first dry period after the start of October, defined as the first day after 1 October on which the wetness index was below 2 mm. For Southern Red Bishops, the average delay was 59 days (s.d. 5 days). The regression model to predict the starting date of moult of Cape Weavers (y, days after 1 October) from the date on which the wetness index fell below 2 mm (t, days after 1 October) was $y=33.5 + 0.73t$ ($r^2 = 0.61$, d.f.=8, $P=0.008$). Similarly, the analogous regression model for Southern Red Bishops was $y=61.0 + 0.82t$ ($r^2 = 0.74$, d.f.=8, $P=0.001$).

This model is illustrated for three representative years (Figure 4). There was little rainfall in September 1993, probably resulting in little breeding (Figure 4a); both Cape Weavers and Southern Red Bishops started moult early (on 27 October and 2 December, respectively, Table 2). 1996 was a year with rain through the winter and spring without a dry period (Figure 4b), resulting in a late start to moult (27 November and 1 January, respectively). In 1998 there was little rain in September and October, resulting in an early start in moult (4 November and 8 December, respectively); the relatively large amount of rainfall at the start of November (Figure 4c) was too late for the continuation of breeding and failed to delay the onset of moult.

Other explanatory variables were considered, e.g. total rainfall during the period 1 May to 30 September, but were found to be uncorrelated with the date of start of moult in both Cape Weavers and Southern Red Bishops. Similarly, there was no significant relationship between any of the rainfall variables and the onset of moult of Southern Masked Weavers ($p>0.6$).

Discussion

Averaged across all years, the duration of primary moult was shorter in Southern Masked Weavers than in the other two species (75 days vs 96 days). Primary moult started latest in Southern Masked Weavers, thus the duration is probably reduced to enable moult to end before mid winter. The duration of moult was 96 days in Cape Weavers (Table 1), starting on average on 12 November. Elliott (1973 p. 73) estimated the duration of moult to be 107 days from October to March; Craig *et al.* (2001) estimated moult duration to be 86 days, both in the Western Cape. Southern Red Bishop moult lasted 96 days, and started on average on 5 December. Craig *et al.* (2001) estimated moult to be 110 days, from November to April in the Western Cape. Southern Masked Weaver moult lasted 75 days, and started on average on 14 January. Oschadleus *et al.* (2000) estimated moult to be 74 days, starting on average on 9 January in the Western Cape.

There were differences of three to five weeks between the earliest and latest starting dates of moult for the three species. For Cape Weavers and Southern Red Bishops this wide variation in starting dates appeared to be due to variability in timing of rainfall at the end of the winter wet season in the study area. End of moult followed after breeding which was correlated with the end of the rainy season. The occurrence of rainfall is a key variable in triggering the onset of breeding in weavers in southern Africa (e.g. Martin and Martin 1970, Maclean 1973, Skinner 1995, Friedl 2002). The results here demonstrate that, in the winter rainfall region, the end of the wet season is a cue to terminate breeding and start primary moult.

The onset of moult between years in the Southern Masked Weaver was not related to the wetness index. For the first three years (1993–1995), the average data of commencement was mid-January; for the final six years (1998–2003), moult, on average commenced in the first week of January. The onset of moult therefore appeared to have advanced by about one week. It is possible that this relatively new arrival in the winter rainfall area of the Western Cape is slowly adjusting its breeding seasonality to earlier in the spring, closer to the timing of breeding for most passerines in the region (see also Chapter 5).

Moult onset in different years probably depends more on the end of breeding season than the start or success thereof, because moult follows soon after breeding (Chapters 5–7). This is in accord with Elliott's (1973) study of breeding and moult in Cape Weavers in the Western Cape. He found that the last eggs were laid between 9 November and 25 November in four successive seasons (Elliott 1973, Table 4.3). Although he did not analyse moult rigorously, moult started within a two-week time span over four seasons (Elliott 1973, p. 64 and Table 5.7).

Southern Red Bishops in the Western Cape started moult two months after the first dry period in October. Friedl (2002) analysed breeding activity in relation to rainfall in a Southern Red Bishop population in the Addo National Park, Eastern Cape. Within breeding seasons he showed that peaks in egg-laying usually followed 10 to 20 days after large rainfall events. He found that breeding seasons lasted longer in years with good mid-seasonal rain (Friedl 2002). Thus, for Southern Red Bishops, both the start and termination of the breeding season seem to be influenced by rainfall. Breeding is often related to unseasonal rainfall, e.g. Rowan (1953).

From the present study, Southern Red Bishops seem to continue breeding for longer than Cape Weavers after the first dry period after October. A possible reason for this ability to breed for longer may be that Southern Red Bishop chicks are less dependent on insects than are Cape Weaver chicks; female Southern Red Bishops feed chicks both insects and seeds, while Cape Weavers feed mainly insects to their chicks (Fry and Keith 2004).

Both regression models relating the starting date of primary moult for Cape Weavers and Southern Red Bishops had slope coefficients which were less than one (0.73 and 0.82, respectively). This suggests that the period between the end of the wet period (considered here as a proxy for the end of the breeding season) and the onset of moult is shorter when the end of the breeding season is late than when it is early. As expected, it might be predicted that an extended breeding season would result in a short delay in the onset of moult. However, this result is based on relatively small sample size (n=10), and should be investigated further.

Annual variation in moult parameters has been studied in two non-passerines and seven passerines. In a six-year study, annual moult variation was related to male body mass in Cassin's Auklets (Emslie *et al.* 1990); timing of breeding and breeding success varied annually but were not correlated with start of moult. Figuerola and Bertolero (1995) found variation in timing of moult in Curlew Sandpipers in a three-year study at a migration stop-over site; they suggested that start of moult was related to breeding success; females with a high breeding success probably delay start of wing-moult until they reach their wintering grounds. Start of moult was probably related to the end of breeding activity in any year in Dunnocks (Ginn 1975). A few Dunnocks caught in moult in different years showed no significant correlation between timing of moult in the same individual in different years. In a two-year study start of moult was related to the breeding effort in Pied Flycatchers, Siikamaki *et al.* (1994) suggested a trade-off between moult and current breeding; females with large clutches incurred an energetic cost and thus delayed start of moult. Sondell (2000) investigated timing and duration of moult in relation to weather in Reed Buntings in central Sweden for the period 1973–1995. The temperature in summer had a significant influence on the onset of moult and less effect on the duration of moult. Evans (1966) studied timing of breeding, moult and migration in Lesser Redpolls over three years and concluded that primary moult started when the last brood reached independence. Usually moult was completed by the time migration began. Morton and Morton (1990) studied moult in Mountain White-crowned Sparrows over eight years. Moult consistently started earlier and was longer in males than in females. Mean start of moult varied inter-annually by 17 days, and mean duration varied by 2.5 days in males and 4.0 days in females. Start of moult in Bullfinches varied annually in relation to end of breeding in a five-year study (Newton 1966, 1999). Start of moult varied by up to six days in three three-year periods in Cape White-eyes *Zosterops pallidus* in the Western Cape (Hulley 2004); he did not relate these inter-annual variations to any environmental factors.

Annual variations in primary moult parameters depend on the physiological state of the birds, and this could be measured in factors that affect the birds' energetic state like food availability, end of the breeding season, and breeding success. Dawson (2004) showed that Common Starlings *Sturnus vulgaris* that delay moult, do so with a measurable decrease in feather mass suggesting that late-breeding birds are likely to suffer a decrease in the quality of plumage grown during the subsequent moult.

Recording moult in birds is a time-consuming activity because large numbers of birds need to be sampled over many months. Studying inter-annual variation in moult is thus even more difficult, as is shown by the paucity of such studies. This study covers the longest time period in comparing annual variation in moult parameters in three species in the same area.

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Table 1: Estimates of the primary moult parameters of adult Cape Weavers, Southern Red Bishops and Southern Masked Weavers in the Western Cape, 1993–2003

Species	Mean starting date	Standard error (days)	Standard deviation (days)	Standard error (days)	Duration (days)	Standard error (days)	Mean completion date	Standard error (days)	n
Cape Weaver	12 Nov	1.1	23.1	0.5	95.9	1.6	16 Feb	1.0	3500
Southern Red Bishop	5 Dec	1.1	21.56	0.5	95.5	1.6	11 Mar	1.0	3742
Southern Masked Weaver	14 Jan	1.5	29.1	0.7	75.0	1.9	30 Mar	1.2	3226

Table 2: Estimates of the primary moult parameters of adult Cape Weavers, Southern Red Bishops and Southern Masked Weavers in the Western Cape, 1993–2003, for individual years

Year	Mean starting date	Standard error (days)	Mean completion date	Standard error (days)	n
Cape Weaver, duration 96.3 (1.7) days, s.d. 24.4 (0.5) days					
1993	27 Oct	4.7	31 Jan	6.7	496
1994	15 Nov	2.6	20 Feb	3.6	471
1995	14 Nov	2.9	18 Feb	4.0	427
1996	27 Nov	2.9	3 Mar	4.0	460
1997	15 Nov	4.7	20 Feb	6.4	311
1998	4 Nov	2.9	9 Feb	4.0	514
1999	1 Nov	2.4	5 Feb	3.2	526
2000	17 Nov	2.5	21 Feb	3.5	462
2001	9 Nov	2.4	14 Feb	3.4	552
2002	16 Nov	2.1	20 Feb	3.0	589
2003	13 Nov	2.2	18 Feb	3.2	554
Southern Red Bishop, duration 94.0 (1.5) days, s.d. 20.9 (0.5) days					
1993	2 Dec	3.2	7 Mar	4.6	97
1994	9 Dec	2.2	13 Mar	3.2	182
1995	12 Dec	3.2	16 Mar	4.7	87
1996	1 Jan	4.6	6 Apr	6.6	106
1997	11 Dec	5.3	15 Mar	7.6	126
1998	8 Dec	1.6	12 Mar	2.5	802
1999	27 Nov	1.6	1 Mar	2.5	449
2000	11 Dec	2.5	15 Mar	3.7	416
2001	13 Dec	1.8	17 Mar	2.8	560
2002	10 Dec	1.7	14 Mar	2.7	462
2003	6 Dec	1.9	10 Mar	2.9	455
Southern Masked Weaver, duration 74.7 (1.9) days, s.d. 29.2 (0.7) days					
1993	20 Jan	2.4	5 Apr	3.5	859
1994	18 Jan	1.9	3 Apr	3.0	691
1995	25 Jan	6.2	9 Apr	8.8	91
1996	9 Jan	6.2	25 Mar	8.8	87
1997	*Insufficient data*				
1998	6 Jan	4.6	22 Mar	6.6	255
1999	6 Jan	3.9	21 Mar	5.6	156
2000	9 Jan	4.5	25 Mar	6.5	170
2001	6 Jan	3.5	21 Mar	5.1	290
2002	8 Jan	2.9	24 Mar	4.3	333
2003	4 Jan	3.4	20 Mar	5.0	385

Figure 1: Capture sites for adult Cape Weavers, Southern Red Bishops and Southern Masked Weavers in grid 33°S 18°E in the Western Cape, South Africa, 1993–2003, showing sites from which primary moult data were obtained; Cape Weavers were captured on Dassen and Robben islands as well as on the mainland; the open circle indicates the Altydgedacht rainfall station

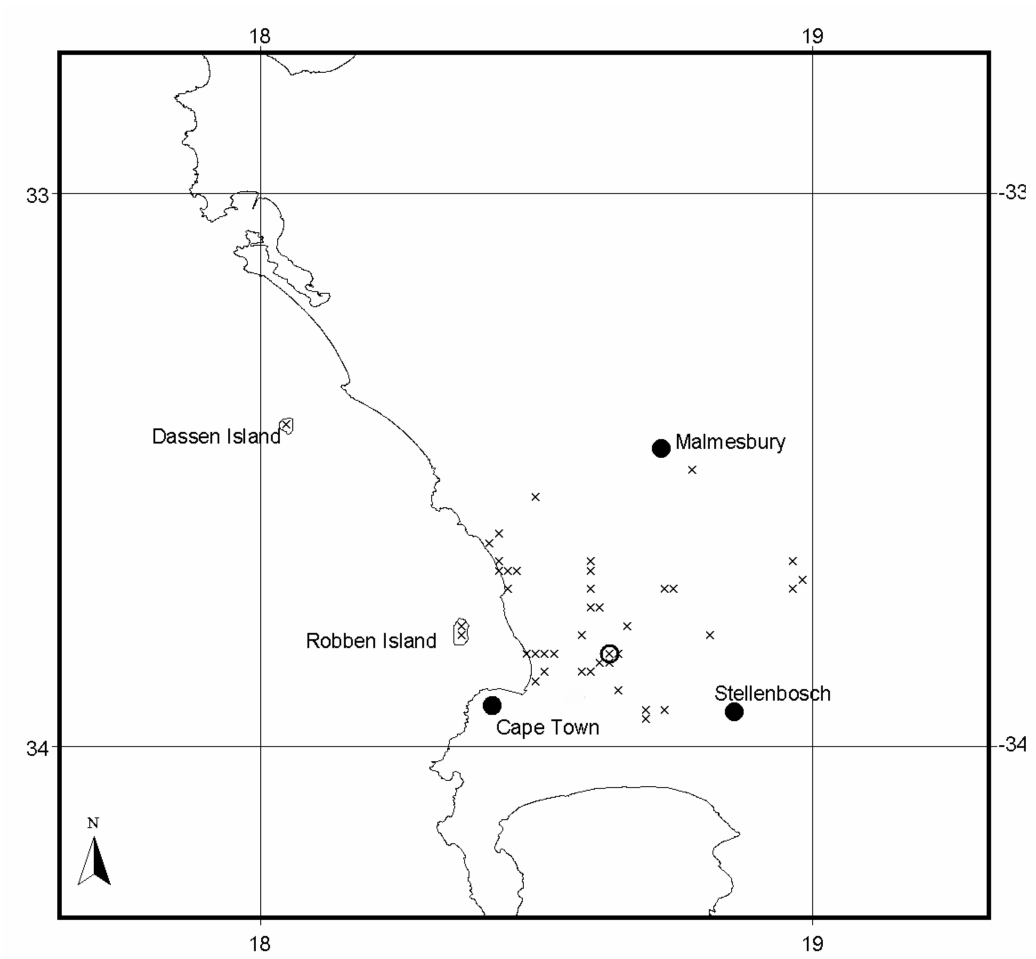


Figure 2: Estimated mean starting dates of primary moult for adult Cape Weavers (open squares), Southern Red Bishops (solid squares) and Southern Masked Weavers (solid triangles) in the Western Cape, South Africa, 1993–2003

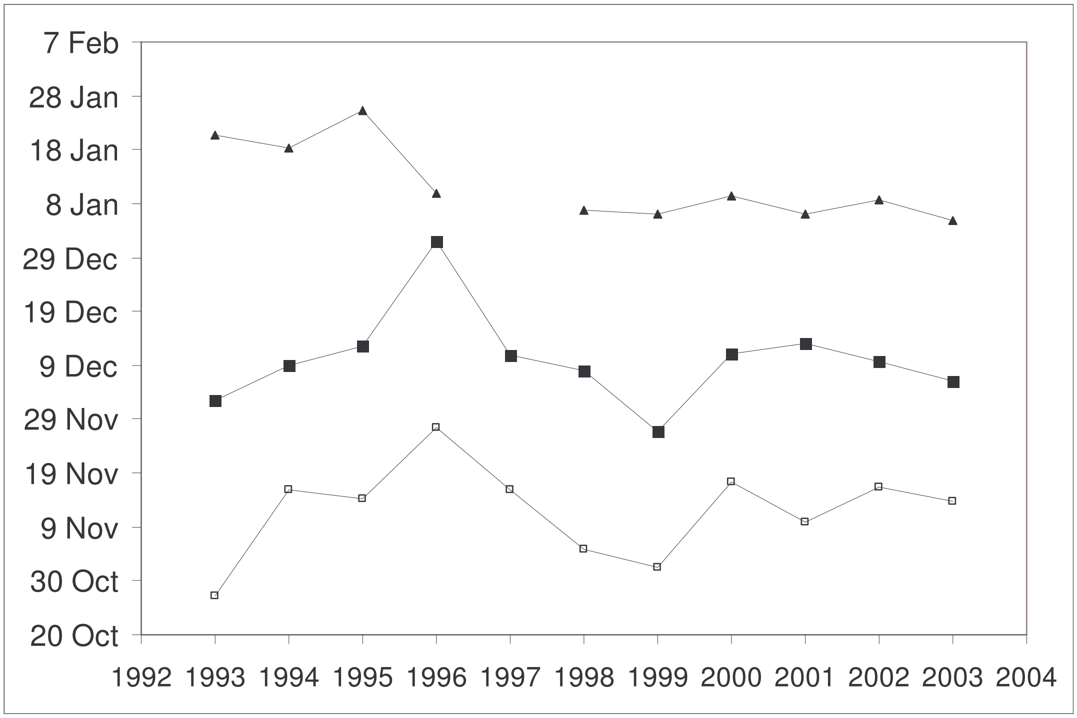


Figure 3: Relationship between the estimated starting date of primary moult in different years in Cape Weavers and Southern Red Bishops in the Western Cape, 1993–2003. The cluster of five points represents the years 1994, 1995, 1997, 2000 and 2002. The regression line is y = 35.7 + 0.82x, where x (days after 1 October) is the predicted day on which Cape Weavers commence moult and y (days after 1 October) is the predicted day on which Southern Red Bishops commence moult ($r^2 = 0.66$, P=0.001)

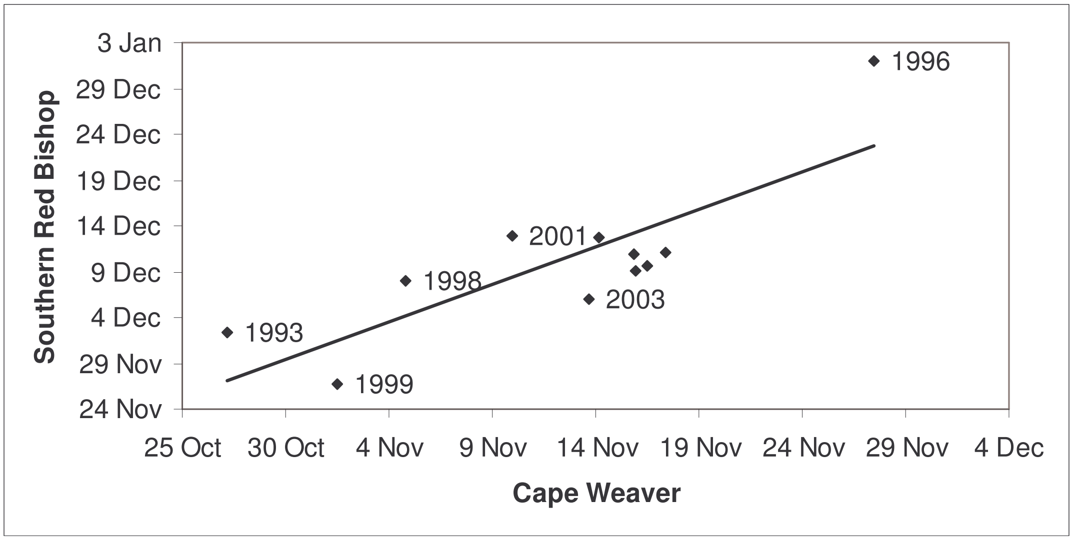
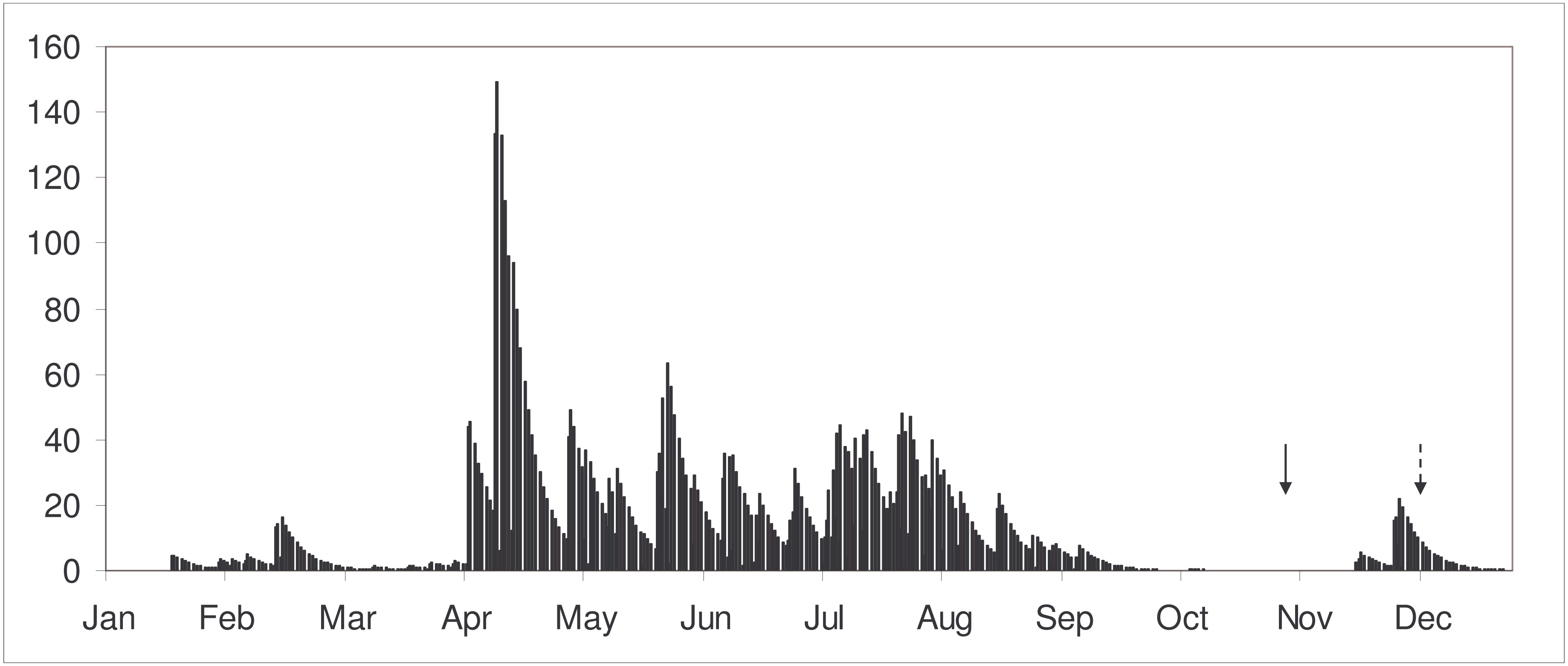
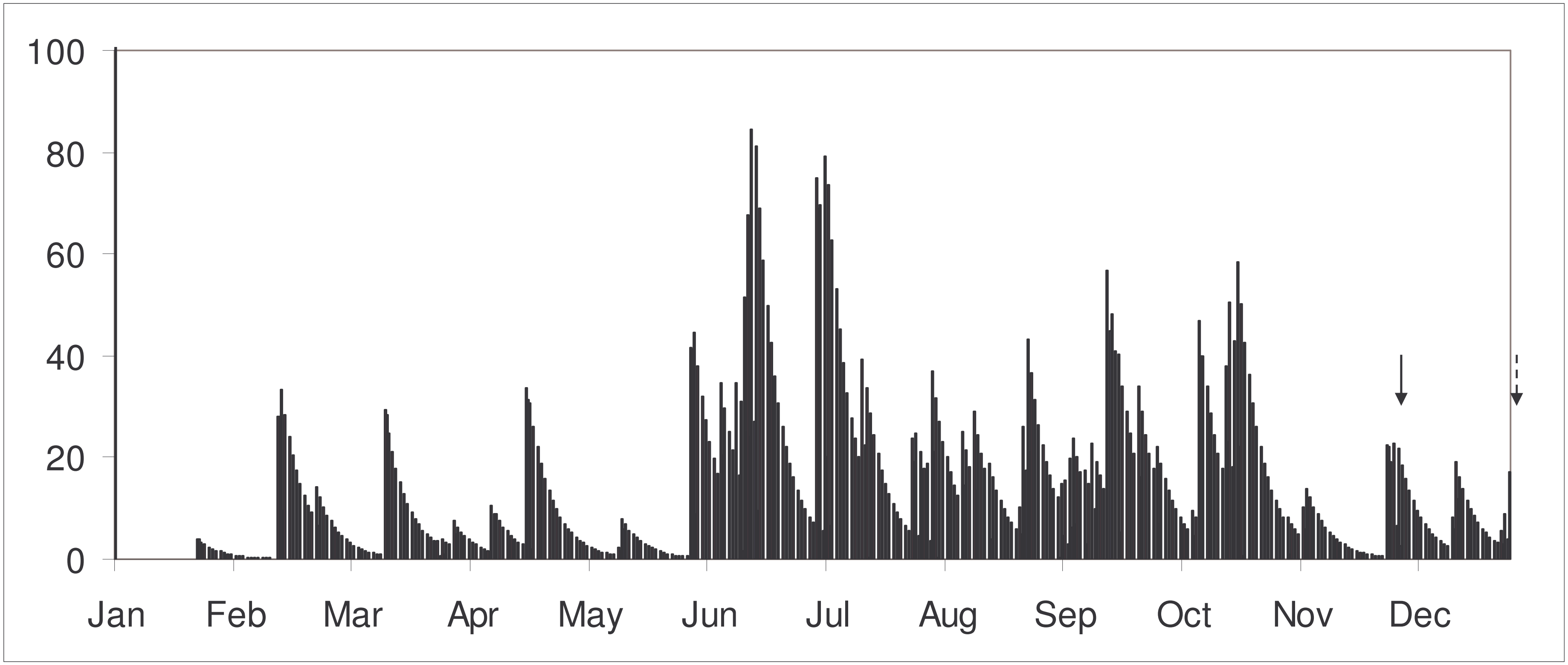


Figure 4: Daily wetness index (for description, see text) for selected years at Altydgedacht rainfall station in the Western Cape, South Africa

(a) 1993, an early wet winter but dry October. Mean date of start of primary moult for Cape Weavers was 27 October (solid arrow), 26 days after 1 October, and for Southern Red Bishops (broken arrow) was 2 December, 62 days after 1 October



(b) 1996, a wet winter and wet spring. Mean date of start of primary moult for Cape Weavers (solid arrow) was 27 November, 57 days after 1 October, and for Southern Red Bishops (broken arrow) was 1 January, 92 days after 1 October



(c) 1998, a wet winter, relatively low spring rainfall, new rains in November. Mean date of start of primary moult for Cape Weavers (solid arrow) was 4 November, 34 days after 1 October, and for Southern Red Bishops (broken arrow) was 8 December, 68 days after 1 October