Chapter 1

Introduction

Introduction

The Introduction covers four aspects. Firstly, it sets the background of the family Ploceidae, a large family found in Africa and southern Asia. Secondly, it briefly describes the biogeography and breeding seasonality of the weavers in southern Africa. Thirdly, it provides an introduction to moult and explains the methodology of the statistical analysis for duration and start of primary moult. Lastly, it presents an outline of the thesis chapters.

A. Ploceidae

Lack (1968) considered weaverbirds such a particularly interesting family from the perspective of studying ecological adaptation that he devoted a full chapter of this influential book to them. In spite of this emphasis, many aspects of their life histories remain poorly studied nearly four decades later.

The weaverbirds are in a large family of birds found mostly in Africa, with a few species found in southern Asia and the West Indian Ocean islands (Craig 2004). Following Craig (2004), there are 116 species in 16 genera. These can be placed in three subfamilies which, in broad terms, consist of genera which make stick nests, grass nests and woven nests (Table 1). *Ploceus* is the largest bird genus in Africa (Benson *et al.* 1971). The weaverbird family is a diverse group, illustrated by the following extremes. The pest Red-billed Quelea *Quelea quelea* is considered by some to be the most numerous land-bird in the world, there being an estimated 1 500 million individuals (Elliott 1989). Contrast this with the rarest weaver: the threatened Mauritius Fody *Foudia rubra* with an estimated population of 210–250 birds (BirdLife International 2004). For such a large family the size range is relatively small; the smallest weaver is the Yellow-crowned Bishop *Euplectes afer* (mean wing of West African males 57.5 mm, Fry and Keith 2004) while the largest is the Long-tailed Widow *Euplectes progne* (mean wing of males 138 mm, Fry and Keith 2004). The communal nest of the Sociable Weaver *Philetairus socius* is the largest single structure built by any bird species in the world; it can weigh up to a ton and attain a width of 7 m and a height of 4 m (Tarboton 2001).

The weavers are largely seed-eating birds, in which they resemble sparrows Passeridae, buntings Emberizidae, canaries Fringillidae and waxbills Estrildidae in morphology; but some weaver species are mainly insectivorous (Moreau 1960). The bill is always straight, but varies from slender and sharp-pointed in insectivorous species to thick and conical in specialist granivores (Craig 2004). Granivores husk seeds, and large-billed species can crack seeds such as sunflowers and the kernels of forest fruits. All species seem to take insects opportunistically, and some are virtually omnivorous, and besides grain, include berries, nectar, flowers, arthropods and a few small vertebrates in their diet.

Sexes may be similar, or strongly dissimilar in plumage and size. Where similar, there is no seasonal change in plumage, but in highly dimorphic species males alternate between breeding and non-breeding plumages, the latter resembling that of the female (Moreau 1960). In most dimorphic species the male apparently does not moult into breeding plumage until at least two years old (Craig 2004), e.g. Southern Masked Weaver *Ploceus velatus* (Tarboton 1965). The breeding plumages are mainly red, black and yellow (carotenoids and melanins). The chemical precursors of carotenoids are acquired from the diet and cannot be synthesized by the birds *(Euplectes:* Kritzler 1943). In breeding plumage, the males of some *Euplectes* species have long ornamental tail feathers (Craig and Villet 1998). In some species there is a coloured patch in the flight feathers, or a distinctive epaulet on the wrist joint. There is no coloured pattern on the tail. There is often a seasonal change in bill colour in males. Female and non-breeding male plumage is generally a streaked, brownish 'sparrowy' pattern. Iris colour is often yellow or red or brown, sometimes differing according to sex or age class (Craig 2004).

The wings are short and rounded to long and pointed with 10 primaries (Maclean 1993). The 10th primary is 10–40% of the length of the longest primary (Moreau 1960). The flight of weavers is straight and direct, though many smaller species are highly manoeuvrable. The tail has 12 feathers in all weaver species. The outermost pair are generally the longest; this is also true of the species which have ornamental tail plumes in breeding plumage. On the ground, birds hop or walk while arboreal species are agile and are able hang upside down while probing bark and leaves.

There is a clear link between the feeding ecology and social organization of weavers, ranging from solitary, monogamous insectivores to colonial, polygynous granivores (Crook 1964). Crook (1964) described three main types of pair formation in the Ploceinae. Each of these three types is largely associated with a different habitat and a different type of breeding organization. In the first pair formation type, the male sings and chases the female, and builds a nest either during or after this period. This type occurs mainly in monogamous insectivorous species breeding solitarily in evergreen forest, and both parents help to feed the young. In the second type, the male builds a nest and then displays at it to attract a mate. This type is found mainly in polygynous graminivorous species breeding colonially in trees in savanna or acacia country. Each male defends an extremely small area in the colony, within which he first builds one nest to which he attracts a mate, and then builds another to attract a second mate, so that polygyny is successive. Each female raises her brood unaided. In the third type, the male builds a nest and then seeks to attract a female by aerial display and song-flight, and only after he has done so does he lead her to a nest. This type is found mainly in polygynous granivores breeding in tall annual grasses or reeds, each male defending a small territory within which, like the colonial species, he first builds a nest for one female, and after he has obtained a mate, builds another nest for a second mate, and so on. The nests are dispersed within the male's territory and each female raises her brood unaided.

In addition to the social organization of the Ploceinae, the following types of social organization are found in other weaver subfamilies: communal breeding in a single nest structure in one species, the Sociable Weaver; co-operative breeding in family groups in a few species; and a lek mating system is known for one grassland species, the Jackson's Widowbird *Euplectes jacksoni* (Andersson 1991).

Weaver nests represent one of the most remarkable constructions produced by any animal. In most species the male makes the major contribution to nest construction, and the female adds lining if she accepts a nest. In the 'true' weavers (subfamily Ploceinae) males construct intricately woven nests using thin strips of plant material. Typically, nest-building starts with the construction of a bridge between supports, usually thin twigs. The male then perches on this bridge while weaving the nest bowl (Collias and Collias 1964). The nest entrance is either to the side or faces vertically downwards; in some species it is

extended into a tunnel from 10 cm to more than 1 m long. Nests of buffalo-weavers (Bubalornithinae) and sparrow-weavers (Plocepasserinae) are composed of dry pieces of vegetation, inserted and interlocked into a complex structure without any weaving or knotting (Collias and Collias 1964). Several weaver species strip the leaves of the twigs around their colonies; this makes the colony more visible but it may be a displacement activity (Oschadleus 2000). In the polygynous species, males build a succession of nests to which they attract females by displaying; the females line the nest, lay, incubate, and rear the nestlings with no or little male assistance. Colonies can consist of hundreds of males or single males (Tarboton 2001). In the monogamous species, sexes share parental duties and build a single nest per breeding season (Tarboton 2001).

Clutch size is 2–6, usually 2–3. The egg colour is varied, with the ground colour often bluish, plain, lightly spotted, or heavily patterned (Schönwetter and Meise 1983). In some species the egg colour is fixed while in others there is enormous individual variation in the ground colour and markings of eggs produced by different females. As many as 10 egg groups have been identified for Southern Masked Weavers (Hunter 1961). This may be an evolutionary response to parasitism by cuckoos or to intraspecific nest parasitism *(Ploceus:* Freeman 1988). The Diederik Cuckoo *Chrysococcyx caprius* is a brood parasite of weavers, in particular Baglafecht Weaver *Ploceus baglafecht*, Cape Weaver *P. capensis*, Golden Weaver *P. xanthops*, Lesser Masked Weaver *P. intermedius*, Southern Masked Weaver, Village Weaver *P. cucullatus*, Spectacled Weaver *P. ocularis* (Freeman 1988); also Bocage's Weaver *P. temporalis*, Black-winged Bishop *Euplectes hordeaceus*, Southern Red Bishop *E. orix* and Red-headed Weaver *Anaplectes rubriceps* (Colebrook-Robjent 1984).

Nestlings are naked with small patches of down on the feather tracts. The inside of the mouth is red and there are no mouth markings (Craig 2004). In all the Ploceidae the nestlings are altricial (Tarboton 2001).

The taxonomy of the Ploceidae has been revised several times over the last 100 years, the main revisions being by Chapin (1917) and Moreau (1960). In the past the sparrows have frequently been included as a sub-family of the weavers, but recent authorities have separated the sparrows from the weavers because of the distinct electrophoretic patterns of egg-white proteins (Sibley 1970). Sibley and Monroe (1990),

using a major higher-level re-organization on the basis of DNA-hybridization studies, placed the Ploceinae as a sub-family of the Passeridae (subfamily Ploceinae). Craig (2004), however, retained Ploceidae as a family and this arrangement is followed here. The genus *Ploceus* has 63 species and the whole family is in need of a new phylogeny based on genetic studies.

In southern Africa there are 29 species in eight genera (Table 1): Red-billed Buffalo-weaver, White-browed Sparrow-weaver, Sociable Weaver, Scaly-feathered Finch, Thick-billed Weaver, 12 *Ploceus* species, three *Quelea* species, and nine *Euplectes* species (Maclean 1993). Distributions of these species have been mapped in detail (Harrison *et al.* 1997). Eggs of all, and nests of many, southern African species are illustrated in Tarboton (2001).

B. Biogeography and breeding of the southern African weavers

The annual cycles of birds are affected by the environments in which they live. Southern Africa is a large region, with an exceptional variety of climatic factors. Within southern Africa there are strong climatic gradients from east to west, with rainfall (Figure 1) being the key factor (Allan *et al.* 1997). This has an effect on bird distributions within the subregion (e.g. Harrison *et al.* 1997), as well as an effect on life-history parameters (Lepage and Lloyd 2004).

In southern Africa there are three main regions with different rainfall patterns: the winter rainfall region of the Western Cape, with a typical Mediterranean climate, the south coast region with rain throughout the year, and the summer rainfall region over the remainder of South Africa (Allan *et al.* 1997, Figure 1). Within the summer rainfall region, especially along the latitudinal band between 24˚S and 30˚S, there is a striking rainfall gradient from the mesic subtropical coastal forest on the east coast to desert on the west coast. A more subtle variation is in the timing of the onset and peak of the summer rains; this is earliest in the southeastern section of the summer-rainfall region in KwaZulu-Natal and latest in the northwest, in northern Namibia (Figure 1). It is also noteworthy that the winter-rainfall region of the Western Cape lies on the same latitudinal band (32˚–34˚S) as the summer-rainfall region of the Eastern Cape; this makes

it possible to study the effect of seasonality of rainfall on the annual cycle of bird species (including the timing of moult) independent of the effect of day-length.

The western parts of southern Africa have a lower and less predictable rainfall than in the eastern parts. Lepage and Lloyd (2004) found clutch size in 106 bird species to be smaller in the more arid regions because this favours a bet-hedging strategy. Lepage and Lloyd (2004) suggested that birds in arid regions breed irrespective of rainfall, but increase clutch size when rain does fall, to maximize breeding success in an unpredictable environment.

There is a large variation in vegetation zones within southern Africa. The Western Cape largely contains the fynbos biome, while Gauteng and KwaZulu-Natal have mainly savanna and grassland biomes. The Eastern Cape has a mixture of biomes. Allan *et al.* (1997) provided a good introduction to the vegetation zones of southern Africa in relation to its avifauna.

The southern African weavers fall into three broad distributional groups (Table 1): five species in Arid and semi-arid west, dry woodland; 10 species found mainly in the mesic eastern parts of southern Africa, although their biogeographic preferences are broader in some species outside of this region; 10 species are found throughout the region or have intermediate distributions covering mesic and semi-arid habitats. The remaining four species have restricted ranges in Zimbabwe or Mozambique.

Breeding seasonality data were obtained from the BirdLife South Africa Nest Record Card Scheme (RP Prŷs-Jones and I Newton unpublished data). They estimated the month of laying of the first egg for each nest record and then summarised breeding seasonality for all birds in South Africa by presenting monthly totals of clutches laid per species per region. 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 in Chapters 5-7. Possible biases are that the Nest Record Cards may not cover the entire breeding season in all regions; the Nest Record Card records were not collected in the same years as the moult data; the sample size may be low for some species in some regions. The sample sizes for the species and regions with moult data, however, are large and collected randomly (by different observers in different years), giving confidence in the results obtained.

C. Moult and the analysis of moult

Feathers

Feathers are unique to birds. Feathers are used for flight, thermoregulation, camouflage and display. Flight and body feathers wear out and need to be regularly replaced in a predictable way and usually on an annual time-scale (Stresemann and Stresemann 1966). This is termed 'moult' and is necessary to ensure future survival because old feathers are constantly abraded due to behavioural activities, exposure to sunshine and other environmental stresses (Jenni and Winkler 1994). Small passerine birds moult all their flight feathers at least once a year (Jenni and Winkler 1994); there is a small number of passerines that moult twice a year (e.g. Willow Warbler *Phylloscopus trochilus*, Underhill *et al.* 1992; Black-chested Prinia *Prinia flavicans*, Herremans 1999); a list of seven species is given by Prŷs-Jones (1991). The most common pattern, found in adult breeders of most sedentary species in temperate and arctic regions as well as most migratory species, is that moult occurs soon after termination of breeding (post-nuptial moult); this is a moult of all body and all flight feathers. A proportion of migrants, especially long distance migrants, delay moult until after their southwards migration (Jenni and Winkler 1994). There is usually also a moult of the body feathers before breeding (pre-nuptial moult). Even among European passerines, living under relatively uniform environmental conditions, there are diverse strategies for the coping with the problem of fitting primary moult into the annual cycle (Jenni and Winkler 1994).

Moult and the annual cycle of birds

Moult is energetically demanding, both in terms of energy and nutrients (Murphy 1996) and time (Langston and Rohwer 1996). Thus timing of moult plays an important part in the annual cycle of a bird to reduce conflict with other energetically costly events, such as breeding and, in many species, migration (Murphy and King 1992). Thus moult in passerines usually follows soon after breeding (Payne 1972) so it can be completed before migration and/or the unfavourable conditions (e.g. less food supply) of mid winter.

The rate at which new feather mass is accrued is a physiologically and energetically important factor. Dawson *et al.* (2000) demonstrated that for some European passerine species total mass of new primary feathers increases at a constant rate throughout most of the duration of moult and hypothesized that this was a universal feature of moulting birds. The rate of increase in total mass is constant because the number of feathers being grown concurrently decreases as moult progresses toward the outer primaries (Dawson and Newton 2004). For if breeding is delayed, the start of moult is delayed resulting in more rapid moult of poorer quality, less massive feathers (Dawson *et al.* 2000). This is an adaptive mechanism mediated by decreasing day lengths that allows late-breeding birds to complete moult in time. Delaying breeding and moult in Blue Tits *Parus caeruleus* experimentally, resulted in higher thermoregulatory costs in the following winter and reduced survival and breeding success in the following season (Nilsson and Svensson 1996). Birds breeding late tend to start moult later than non-breeders and birds completing breeding early; late breeders then tend to moult more quickly (Morton and Morton 1990).

The annual cycle seems to rely on an endogenous rhythm organizing annual events like breeding, moult and migration (Gwinner 1996). This circannual clock is species- or population-specific and seems to be synchronized by environmental cues such as photoperiod. Moult strategies are not readily related to a few environmental factors in general (Salewski *et al.* 2004) and our understanding about these ecological factors is limited (see Jenni and Winkler 1994).

The quantitative description of primary moult

The key parameters of moult in a population are the average starting date and the duration. These parameters need to be studied in the context of the timing of the other major events in the annual cycle: breeding and, in some species, migration (Underhill 2003). For moult studies in many species, it is appropriate initially to focus on the moult of the primary wing feathers, because the main annual moult duration of many other feather tracts takes place within the period of moult of the primaries (Underhill 2003).

Collecting moult data in the field is most frequently undertaken by allocating individual primaries with a score from 0 to 5, where 0 = old feather, 1 = missing or

feather in pin, 2 = one-third grown, 3 = two-thirds grown, 4 = four-fifths grown, 5 = new feather (Ginn and Melville 1983). The primaries are numbered 1 (innermost) to 10 (outermost). In weavers, the 10th primary is reduced; sometimes it is still easily visible, e.g. Chestnut Weavers *Ploceus rubiginosus*, while in many *Euplectes* species it is minute. Traditionally, these individual feather scores are added to give the 'moult score' for a bird on a particular day, as proposed by Ashmole (1962) and developed by Newton (1966). For example, the string of digits 5542000000 indicates that the innermost two feathers are new, the third is four-fifths grown, the fifth is one-third grown, and the remainder are still old; the moult score is 16. For species with 10 primary feathers, moult score therefore increases to 50 when moult is complete. The standard scoring method is convenient for assessing the stage of moult. However, it has the weakness that equal weight is given to each primary feather although the actual lengths and masses of primary feathers may differ considerably. Because the outer primaries are generally larger than the inner ones, moult score does not increase linearly through time but exaggerates moult rate during the early part of moult and underestimates it later. This nonlinearity presents problems when moult-score data are used to estimate timing and duration of moult. Analyses of moult-score data using standard linear regression methods are inappropriate (Summers *et al.* 1983, Underhill and Zucchini 1988).

Prater (1981) noted that the lack of standardization of methods for the analysis of moult made it difficult to make comparisons between moult studies. There is a danger that apparent differences in duration of moult between species or across latitudes are statistical artifacts rather than genuine effects. Prater (1981) also noted the lack of satisfactory methods for estimating the parameters of moult, especially duration of moult. The development of rigorous methods to estimate the parameters of moult was undertaken by Underhill and Zucchini (1988) and Underhill *et al.* (1990). This method relies on a moult index that increases linearly in time; the best available approximation to this to date is to use 'percentage feather mass grown' as a moult index (e.g. Dawson *et al.* 2000), and this requires a knowledge of the masses of individual primary feathers (Summers *et al.* 1980).

To determine the masses of primary feathers, individual feathers from wings of weaver specimens were oven-dried at 60°C for 24 hours and then weighed on a balance

(Ohaus GA200D, precision 0.0001g) (compare Underhill and Summers 1993). Underhill and Joubert (1995) have shown that small samples are adequate to determine the relative masses of primary feathers for a species, because there is little intra-specific variation in this characteristic. The Underhill-Zucchini moult model developed by Underhill and Zucchini (1988) was applied to the data sets. Three types of moult data can be analysed:

1. birds classified only as not yet moulted, in moult and completed moult

2. as for type 1, but the moult indices are available for all birds in moult

3. only available data are the moult indices for the birds in moult

In this study all the data were considered to be of 'type 2' of the five types described by Underhill and Zucchini (1988) and Underhill *et al*. (1990), 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 moult index recommended by Summers (1976) and Summers *et al.* (1980, 1983), designed to reduce the bias introduced by the fact that the individual feathers are of different masses. The moult index used was percentage feather mass grown (PFMG), calculated according to the method of Underhill and Summers (1993). This transformation has been demonstrated to increase sufficiently linearly with time to reduce, and in some cases, to eliminate, bias in moult parameter estimation (Summers 1980; Summers *et al.* 1980, 1983). Because it is based on feather mass, the Underhill-Zucchini method with PFMG index is of greater physiological and energetic relevance than the standard method based on moult score.

An analysis of the moult of Willow Warblers *Phylloscopus trochilus* was the first to apply the statistically rigorous Underhill-Zucchini moult model to make comparisons on a large scale across various moult localities (Underhill *et al.* 1992). This has been followed up by Serra (1998) undertaking a similar study for Grey Plovers. A problem with the use of the Underhill-Zucchini method has been the lack of availability of the associated computer software. The programme developed by W. Zucchini needs skilled intervention to ensure that it converges to the correct result, and a user-friendly version has not yet been produced by the originators of the method (Underhill 2003). In spite of

this shortcoming, many analyses have been published using the Underhill-Zucchini model (Table 2).

Studies of primary moult using the Underhill-Zucchini method focused mainly on the primary feathers as a single unit. Serra (2002) investigated the parameters of moult of individual primary feathers of Grey Plovers *Pluvialis squatarola*. Serra's detailed analysis of the data for this species showed interesting differences between the strategies used by populations moulting under differing climatic conditions. A problem with this type of feather-by-feather analysis is a need for large sample sizes, preferably in excess of 1000 birds in moult. In addition, these samples need to be well spread throughout the moult period; otherwise it is not possible to make satisfactory estimates of the moult parameters for each primary. Because the feathers are being dealt with individually, there is no need to make the transformations recommended when the entire primary moult tract is analyzed (Summers 1980; Summers *et al.* 1980, 1983). Moult scores between 0 and 5 of individual feathers were converted to the values 0, 0.125, 0.375, 0.625, 0.875 and 1, respectively, to form a moult index lying between 0 and 1, as required by the Underhill-Zucchini model. Using the Underhill-Zucchini model to estimate the parameters of moult for individual primary feathers, has also been applied to selected species of waders (Underhill 2003).

Brandao (1998) (see also Underhill *et al.* in press) extended the Underhill-Zucchini (1988) moult model further 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) common to all groups. The motivation for this approach is that it is the starting dates that are likely to be the most variable; exceptionally large volumes of data are needed for each group to be able to estimate both starting dates and duration reliably (Brandao 1998). She also developed rigorous statistical testing procedures, using the likelihood ratio test, of the null hypothesis that the starting date for each group was the same. These extensions effectively enable analyses to be performed with a single "grouping" variable, analogous to one-way analysis of variance. This method was used to analyse inter-annual variation in moult in several species, differences between timing of moult of male and female Chestnut Weavers, and differences in moult parameters in two

different provinces of South Africa. Brandao's (1998) models also need the development of user-friendly versions.

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 synchronized 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. There were not enough recapture records within a moult season to estimate moult parameters from recaptures. The moult records are plotted as relative feather mass versus date for different individuals, including a small number of recaptured individuals.

Possible biases in the moult data are that some birds may move after breeding or before the end of moult; some individual birds may be less easily trapped than others (e.g. females versus males, or late breeders that start moult slightly later than the rest of the population). Other than Red-billed Quelea, weavers are not migrants, particularly in the areas studied. The possible bias of movements in the Red-billed Quelea is addressed in Chapter 4. Most weavers are trapped by ringers at dawn at roosting or breeding sites, and thus trap-shyness is not considered to have any great effect on the data. Birds with arrested moult were omitted from analyses – this involved relatively small numbers of birds, and arrested moult was recognized as adjacent old and new feathers with no growing feathers. If one primary had completed growth before the next fell out, there would still be a feather sheath requiring the feather to be scored as 4 rather than 5 (new); this would prevent confusing arrested moult with slow moult. Weavers were captured by ringers through the year, minimizing biases of early and late moulters having different

rates of moult; i.e. in this thesis the data presented includes all birds and presents population averages. Another potential source of error is in not analyzing secondary moult together with primary moult. Usually the secondary feathers start moulting when Primary 6 is moulted, thus the end of primary moult may be influenced by the energy needed to simultaneously start moult of the secondary feathers. For this thesis, secondary moult data were not available but are considered to have a similar effect on all species, reducing the error in the comparative studies presented here.

There is remarkably little available information relating to the primary moult of weavers from elsewhere in Africa (Table 3). 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.

D. A 'roadmap' of the thesis

Background and objectives

The data used in this thesis are from the SAFRING database, data being submitted by many ringers, including my own data. When I was appointed as SAFRING's bird ringing coordinator in 1998, I encouraged ringers to submit ringing data electronically instead of on paper schedules. I also encouraged ringers to submit mass, wing length and primary moult instead of just mass, in addition to the usual data (ring number, species, date, locality, etc). It has been encouraging to see ringers enthusiastically embrace the new changes, although it has taken a lot of work to train ringers in the recording of moult protocols, and for ringers to learn how to use computers, etc. From July 2004 onwards all ringing data have been computerized. Old ringing records are being computerized, although the paper schedules do not include moult data. This has provided a large database ready for analysis, for instance of historical changes of bird distribution, biometric analyses, and particularly of moult analyses. Moult is poorly studied in African birds (Craig 1983) and due to my interest in weaverbirds, I wanted to analyse moult of the weavers. These analyses will be fed back to the ringers to aid them in understanding

and appreciating birds in the hand even more. Thus this thesis is a tribute to the ringers of southern Africa.

Structure of thesis

In addition to this Introduction and the Conclusion, this thesis consists of seven chapters that have been prepared as papers for publication – Chapter 2 has been published (Oschadleus 2004), Chapter 3 is in press and Chapter 4 has been submitted for publication. The format used for each chapter is similar to that used by the journal of African ornithology, Ostrich.

Chapter 2 describes the biometrics and primary moult of the Sociable Weaver, a southern African endemic. Chapter 3 describes the biometrics and primary moult of another species inhabiting a semi-arid region, the Chestnut Weaver *Ploceus rubiginosus* in Namibia. Chapter 4 shows how primary moult duration and timing in Red-billed Quelea *Quelea quelea* varies in different parts of southern Africa so that completion of moult occurs at roughly the same time. Chapter 5 explores the geographic variation in breeding seasonality and primary moult parameters in Cape Weavers, Southern Masked Weavers and Southern Red Bishops in South Africa. Chapter 6 shows that breeding seasonality and primary moult parameters are similar in the *Euplectes* species in the summer rainfall region of South Africa. Chapter 7 describes breeding seasonality and primary moult parameters of Village Weaver *P. cucullatus*, Yellow Weaver *P. subaureus*, Spectacled Weaver *P. ocularis* and Thick-billed Weaver *Amblyospiza albifrons* in KwaZulu-Natal and also in Gauteng for the latter species. Chapter 8 investigates annual variation in start date of moult in Cape Weavers, Southern Red Bishops and Southern Masked Weavers in the Western Cape. Chapter 9 gives an overview of timing and seasonality of breeding and of primary moult in southern African weavers.

This is the first thesis to tackle both an intra- and inter-species study of patterns of primary moult using the Underhill-Zucchini method (Table 2). The only intra-species studies are those on the Willow Warbler (Underhill *et al.* 1992) and on the Grey Plover (Serra 2002). The only inter-species study is on a few wader species (Underhill 2003). The only published moult studies for weavers using the Underhill-Zucchini method are

for Southern Masked Weavers (Oschadleus *et al.* 2000) and five weaver species in the Eastern Cape (Craig *et al.* 2001).

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Table 1: Weaver genera of the world, and a list of the southern African weaver species
Mating system: M = monogamous, P = polygynous, c = co-operative breeder (from Tarboton 2001)
Region: A = arid and semi-arid west, dry woodland; M = mesic east; T = throughout or intermediate; R = restricted range
Moult studied: y = species included in this thesis, n = moult not studied in this thesis

Subfamily	Genus	No. of species	Southern African species	Mating system	Region	Moult studied
Bubalornithinae – buffalo weavers; stick nests						
	Bubalornis	2	Red-billed Buffalo-weaver *Bubalornis niger*	P	A	n
	Dinemellia	1				
Plocepasserinae – sparrow or social weavers; grass nests						
	Plocepasser	4	White-browed Sparrow-weaver *Plocepasser mahali*	M, c	A	n
	Histurgops	1				
	Sporopipes	2	Scaly-feathered Finch *Sporopipes squamifrons*	M	A	n
	Pseudonigrita	2				
	Philetairus	1	Sociable Weaver *Philetairus socius*	M, c	A	y
Ploceinae – true weavers; woven nests						
	Malimbus	10				
	Anaplectes	1	Red-headed Weaver *Anaplectes melanotis*	M or P	T	n
	Ploceus	63	Lesser Masked Weaver *Ploceus intermedius*	P	T	n
			Spectacled Weaver *Ploceus ocularis*	M	M	y
			Cape Weaver *Ploceus capensis*	P	T	y
			Yellow Weaver *Ploceus subaureus*	P	M	y
			Golden Weaver *Ploceus xanthops*	M or P	T	n
			Southern Brown-throated Weaver *Ploceus xanthopterus*	P	T	n
			Southern Masked Weaver *Ploceus velatus*	P	T	y
			Village Weaver *Ploceus cucullatus*	P	M	y
			Chestnut Weaver *Ploceus rubiginosus*	P	A	y
			Dark-backed Weaver *Ploceus bicolor*	M	M	n
			Olive-headed Weaver *Ploceus olivaceiceps*	(M)	R	n
	Pachypantes	1				

Table 1 continued

Subfamily	Genus	No. of species	Southern African species	Mating system	Region	Moult studied
	Amblyospiza	1	Thick-billed Weaver *Amblyospiza albifrons*	M or P	M	y
	Quelea	3	Cardinal Quelea *Quelea cardinalis* *	P	R	n
			Red-headed Quelea *Quelea erythrops*	M	M	n
			Red-billed Quelea *Quelea quelea*	M	T	y
	Brachycope	1				
	Euplectes	17	Yellow-crowned Bishop *Euplectes afer*	P	T	n
			Black-winged Bishop *Euplectes hordeaceus*	P	R	n
			Southern Red Bishop *Euplectes orix*	P	T	y
			Yellow Bishop *Euplectes capensis*	P	T	y
			Fan-tailed Widow *Euplectes axillaris*	P	M	y
			Yellow-mantled Widow *Euplectes macrourus*	P	R	n
			White-winged Widow *Euplectes albonotatus*	P	M	y
			Red-collared Widow *Euplectes ardens*	P	M	y
			Long-tailed Widow *Euplectes progne*	P	M	y
	Foudia	6				

* vagrant (1 confirmed record)

Table 2: Species with published studies using the maximum likelihood method of Underhill-Zucchini (1988) method to analyse primary moult

Species	Reference
Sooty Shearwater *Puffinus griseus*	Cooper *et al.* (1991)
Ruddy Turnstone *Arenaria interpres*	Summers *et al.* (1989), Underhill (2003)
Grey Plover *Pluvialis squatarola*	Serra (1998, 2002 and papers listed therein), Underhill (2003)
Sanderling *Calidris alba*	Underhill and Zucchini (1988), Underhill (2003)
Knot *Calidris canutus*	Underhill (2003)
Sanderling *Calidris alba*	Underhill (2003)
Redshank *Tringa totanus*	Underhill *et al*. (1990)
Bristle-thighed Curlew *Numenius tahitiensis*	Marks (1993)
Rock Pigeon *Columba guinea*	Underhill and Underhill (1997)
Cape Turtle Dove *Streptopelia capicola*	Underhill *et al.* (1999)
Lesser Honeyguide *Indicator minor*	Underhill *et al.* (1995)
Alpine Chough *Pyrrhocorax graculus*	Winkler *et al.* (1988)
Chough *Pyrrhocorax pyrrhocorax*	Winkler *et al.* (1988)
Black-chested Prinia *Prinia flavicans*	Herremans (1999)
Willow Warbler *Phylloscopus trochilus*	Underhill *et al.* (1992)
Common Starling *Sturnus vulgaris*	Cooper and Underhill (1991), Rothery *et al.* (2001)
Sociable Weaver *Philetairus socius*	Oschadleus (2004), chapter 2 of this thesis
Southern Masked Weaver *Ploceus velatus*	Oschadleus *et al.* (2000), Craig *et al.* (2001)
Cape Weaver *Ploceus capensis*	Craig *et al.* (2001)
Village Weaver *Ploceus cucullatus*	Craig *et al.* (2001)
Red-billed Quelea *Quelea quelea*	Craig *et al.* (2001)
Southern Red Bishop *Euplectes orix*	Craig *et al.* (2001)
Greenfinch *Carduelis chloris*	Newton and Rothery (2005)
Bullfinch *Pyrrhula pyrrhula*	Newton and Rothery (2000)

Table 3: Studies of moult in African weavers which did not use the method of Underhill and Zucchini (1987)
GR = Game Reserve, NP = National Park

Species	Area, country	Reference	Comments
Red-billed Buffalo Weaver *Bubalornis niger*	Maun, Botswana	Payne (1969)	Overlap in breeding and moult
White-browed Sparrow-weaver *Plocepasser mahali*	North-western Botswana	Jones (1978)	Duration estimated at 183 days (10 birds); five incubating females were moulting
Chestnut-crowned Sparrow-weaver *Plocepasser superciliosus*	Mole GR, Ghana	Fry (1971)	General notes on breeding and moult
Speckle-fronted Weaver *Sporopipes frontalis*	Mole GR, Ghana	Fry (1971)	General notes on breeding and moult
Scaly-feathered Finch *Sporopipes squamifrons*	Marble Hall, South Africa	Payne (1969)	Overlap in breeding and moult
	Ruretse, Botswana	Tyler (2001)	Moult duration 200–350 days (25 retraps)
Red-headed Malimbe *Malimbus rubricollis*	Kakamega Forest, Kenya	Mann (1985)	Moult score plots (two data points)
Black-billed Weaver *Ploceus melanogaster*	Kakamega Forest, Kenya	Mann (1985)	Moult score plots (four data points)
Black-headed Weaver *Ploceus melanocephalus*	Lake Kanyaboli, Kenya	Britton (1978)	Moult score plots
Black-necked Weaver *Ploceus nigricollis*	Mombasa, Kenya	Britton and Britton (1986)	Moult 5–6 months but varies in individuals
Dark-backed Weaver *Ploceus bicolor*	Somalia	Wood (1989)	Moult in August, none in September
	Pugu Hills, Tanzania	Mlingwa (2000)	Table of some breeding and moult records
Golden Palm Weaver *Ploceus bojeri*	Mombasa, Kenya	Britton and Britton (1986)	Moult 5–6 months but varies in individuals
Heuglin's Masked Weaver *Ploceus heuglini*	Mole GR, Ghana	Fry (1971)	General notes on breeding and moult
Jackson's Golden-backed Weaver *Ploceus jacksoni*	Lake Kanyaboli, Kenya	Britton (1978)	Moult score plots
Lesser Masked Weaver *Ploceus intermedius*	Pugu Hills, Tanzania	Mlingwa (2000)	Table of some breeding and moult records
Northern Brown-throated Weaver *Ploceus castanops*	Lake Kanyaboli, Kenya	Britton (1978)	Moult score plots
Slender-billed Weaver *Ploceus pelzelni*	Mole GR, Ghana	Fry (1971)	General notes on breeding and moult
	Lake Kanyaboli, Kenya	Britton (1978)	Moult score plots
Southern Brown-throated Weaver *Ploceus xanthopterus*	Mopeia, Moambique and Nchalo, Malawi	Hanmer (1984)	Detailed moult study
Spectacled Weaver *Ploceus ocularis*	Mombasa, Kenya	Britton and Britton (1986)	Moult 5–6 months but varies in individuals
	Pugu Hills, Tanzania	Mlingwa (2000)	Table of some breeding and moult records
Vieillot's Black Weaver *Ploceus nigerrimus*	Liberia	Chapman (1995)	This species shows non-seasonal breeding and wet-season moult

Table 2 continued

Species	Area, country	Reference	Comments
Village Weaver *Ploceus cucullatus*	Mole GR, Ghana	Fry (1971)	General notes on breeding and moult
	Lake Kanyaboli, Kenya	Britton (1978)	Moult score plots
	Pugu Hills, Tanzania	Mlingwa (2000)	Table of some breeding and moult records
Thick-billed Weaver *Amblyospiza albifrons*	Pugu Hills, Tanzania	Mlingwa (2000)	Table of some breeding and moult records
	Pietermaritzburg, South Africa	Laycock (1982)	Primary moult duration 4 months
Red-billed Quelea *Quelea quelea*	Tsavo East NP, Kenya	Thompson (1988)	Start moult before breeding completed
Yellow Bishop *Euplectes capensis*	Mt Cameroon, Cameroon	Eyckerman and Cuvelier (1982)	Regression calaculated for 9 birds
Fan-tailed Widow *Euplectes axillaris*	Lake Kanyaboli, Kenya	Britton (1978)	Moult score plots
Yellow-mantled Widow *Euplectes macrourus*	Mole GR, Ghana	Fry (1971)	General notes on breeding and moult
	Kakamega Forest, Kenya	Savalli (1993)	Egg-laying May–September, moult September–November
Zanzibar Red Bishop *Euplectes nigroventris*	Mombasa, Kenya	Britton and Britton (1986)	Moult 5–6 months but varies in individuals
Northern Red Bishop *Euplectes franciscanus*	Mole GR, Ghana	Fry (1971)	General notes on breeding and moult
	Mole NP, Ghana	Davidson (1978)	Prenuptial body moult
Yellow-crowned Bishop *Euplectes afer*	Mole NP, Ghana	Davidson (1978)	Prenuptial body moult
Aldabran Fody *Foudia aldabrana*	Aldabra	Frith (1976)	Post-nuptial moult, April–June
Mauritius Fody *Foudia rubra*	Mauritius	Safford (1997)	Post-nuptial moult, March–April
Seychelles Fody *Foudia sechellarum*	Cousin Island, Seychelles	Brooke (1985)	Breeding follows primary moult

Figure 1: Histograms of mean annual monthly rainfall (mm) for 2° x 2° grid cells in southern Africa (from Allan *et al.* 1997). The plotted data refer to one weather station within the grid cell or are interpolated from neighbouring grid cells, especially in central Botswana.