245 T ASPECTS OF

THE BIOLOGY OF THE RED BISHOP

EUPLECTES ORIX

AND OTHER EUPLECTES SPECIES

5R by

100 Adrian John Fergus Knott Craig.

Submitted in partial fulfilment of
the requirements for the degree of
Doctor of Philosophy
in the Department of Zoology,
University of Natal, Pietermaritzburg.

November, 1977.

CONTENTS

	Page
ABSTRACT	1
ACKNOWLEDGEMENTS	2
INTRODUCTION	3
THE STUDY AREAS	6
CHAPTER ONE: The population structure of the Red Bishop and related species	
Introduction	9
Methods	10
Results	11
The catch size at Cedara	14
Wing-length	16
Sex ratio	28
Dominance and sex hormones	40
Mortality rates and survival	42
Discussion	
Seasonal movements	46
Sexual dimorphism	49
The sex ratio	51
The role of social dominance	58
Survival and mortality	60
Summary	64
CHAPTER TWO: The annual cycle of the Red Bishop and related species	
Introduction	65
Methods	66
Results	
Testis development, nuptial plumage and bill colour in the Red Bishop	68
Pre-nuptial moult	69
The gonad cycle	72
The post-nuptial moult	75
Weights	87
Feeding	97

	Page
Discussion	
The pre-nuptial moult	101
The gonad cycle	104
The post-nuptial moult	104
Weights	110
Feeding	114
Summary	115
CHAPTER THREE: Breeding in the Red Bishop	
Introduction	117
Methods	117
Results	
Breeding and rainfall	121
Nest-building	128
Nest sites	129
Nesting by immature males	136
Egg-laying and the nesting period	138
Clutch size	140
Breeding success	142
Parasitism by the Didric Cuckoo	147
Predation	149
Breeding success of individual males	152
Discussion	
The breeding season	159
Proximate factors	161
1. Photoperiod	161
2. Temperature	164
3. Rainfall	165
4. Food	168
Clutch size	170
1. Genetic determination	171
2. Geographical variation	171
3. Age of the female	174
4. Population density	174
5. Food supply	175
6. Variations during the breeding season	176
7. Second clutches	177

Page

Breeding success 178
Predation 185
1. The identity of the predators 187
2. Behaviour towards predators 188
3. Nest site and predation 189
Breeding success of individual males 191
Summary 192

CHAPTER FOUR: The evolution of polygyny in the genus Euplectes

Introduction 194
Methods 195
Results
Territorial behaviour 197
Courtship and mate selection 201
Vocalizations of male Euplectes in captivity 208
Vocalizations of E. orix 209
Nesting 212
Feeding and roosting flocks 215
Discussion
A general theory of polygyny 217
Sexual selection 224
The role of the territory 226
The behaviour of the male 229
The colony and the flock 234
Conclusion
The evolution of the Euplectes species 237

SUMMARY 242

REFERENCES 244

ABSTRACT

The breeding biology and the annual cycle of the Red Bishop Euplectes orix was studied over a two year period in Natal. Some comparative data were also gathered for the related species the Red-shouldered Widow E. axillaris and the Red-collared Widow E. ardens, and additional data from a ringer in Rhodesia have been analysed. The breeding season of these polygynous ploceids coincides with the summer rainy season, and the amount of breeding activity in the Red Bishop appeared to be correlated with the amount of rain during the previous year. Breeding success at the colony studied was low; predation was the major cause of nest failure. In all three species the entire population, including the juveniles, undergoes a complete moult at the end of the breeding season. There is some evidence that the birds may make local movements during the winter dry season.

These species are sexually dimorphic, the males being larger than the females. The population sex ratio was significantly biased in favour of males in the Red Bishop and the Red-shouldered Widow but not in the Red-collared Widow. However, about half the male birds are subadults which do not breed, so that there is an excess of females in the breeding population. Adult males undergo a partial moult at the start of the breeding season and acquire a distinctive nuptial plumage. This is shed again at the post-nuptial moult, and in eclipse plumage they resemble the females. There is a similar pattern of weight change in all three species, with peaks early in the breeding season and again during the moult. The lowest annual weights are recorded during the dry season. The mortality rate of the Red Bishop is not high for a small passerine.

The findings of this study are compared with the available information on other members of the genus, and discussed in relation to the evolution of polygyny in the Euplectes species.

ACKNOWLEDGEMENTS

I am indebted to Mr. J. Masson for allowing me free access to all parts of his farm "Malton", to observe, erect hides, and ring birds; to Dr. P. Hildyard, Regional Director of the Department of Agricultural Technical Services, who gave me permission to ring birds on the grounds of the Cedara College of Agriculture; and to Mr. W.N. MacGillivray, who allowed me to ring and capture birds at "Gartmore Farm".

Professor Gordon Maclean ably supervised my field work in Natal, and offered constructive criticism on the various drafts of the thesis. During my stay in West Germany, Professor Klaus Immelmann and his colleagues at the Department of Ethology of the University of Bielefeld also gave me every assistance. Mr. A.J. Manson of Salisbury, Rhodesia generously placed six years' ringing data at my disposal. Mr. R.K. Brooke, Dr. L.G. Underhill and Mr. G. Wilson have also provided unpublished data, and Mr. W. Reynolds and Mr. F. Essenwein provided rainfall figures. Mr. D. Campbell supervised the construction of the aviary, Mr. J. Mendelsohn assisted with the ringing, Prof. K. Gordon-Gray identified grass specimens, Mr. A. Channing prepared some of the sonograms, and Mr. K. Willan set out rodent traps. I am most grateful to all those mentioned for their help, advice and encouragement, and especially to my wife Cheryl, who shared many hours at the desk and in the field.

The year which I spent in West Germany was financed by the Deutscher Akademischer Austauschdienst, and the South African Council for Scientific and Industrial Research granted me a post-M.Sc. bursary for the three years spent at the University of Natal. Additional running expenses were met by a University of Natal Research Fund grant to Professor G.L. Maclean. The National Unit for Bird-ringing Administration provided free rings at the start of the project. I gratefully acknowledge the financial support of these organisations.

INTRODUCTION

The weavers (Ploceidae) are a typically African family, and all but five species of the sub-family Ploceinae are confined to Africa and the adjacent islands. The genus Euplectes occurs in grassland areas throughout Africa south of the Sahara.

This genus was formerly divided into the Euplectes species with a low tail/wing ratio, the Coluispasser species with a high tail/wing ratio, and one or more monotypic genera. Delacour & Edmond-Blanc (1933) first proposed that all the species should be included in a single genus Euplectes, retaining Coliuspasser as a sub-genus. This arrangement was later followed by Moreau (1960), and has become generally accepted since the work of Hall & Moreau (1970). Their nomenclature will be followed for all the African passerines mentioned in this study.

All Euplectes species build a woven, domed nest with a lateral entrance, and the males moult into a colourful nuptial plumage during the breeding season, while at other times of the year they resemble the brown-streaked females. The nuptial plumage is either plain black, or black with areas of red or yellow feathers. This is reflected in the English names of the different species: those with roughly equal areas of black and red or yellow plumage are known as "bishops" or "bishop birds", while the predominantly black species are called "widows" or "widowbirds".

Although they are familiar to many people through their striking plumage and displays, the biology of these species has been little studied. Crook's (1964) review of the behaviour of the Ploceinae provides a framework for further studies. The genus Quelea is considered to be closely related to Euplectes (Delacour & Edmond-Blanc 1933; Moreau 1960; Crook 1964), and the economic importance of the Red-billed Quelea Quelea quelea has resulted in an extensive literature on its biology. Since this species is monogamous whereas the Euplectes species are polygynous, comparative data are of particular interest, and may explain why only Quelea poses a major threat to agriculture.

The Red Bishop *Euplectes orix* is probably the best-known species in Southern Africa. Its distribution is shown in Figure 1; there is also an introduced breeding population on the Murray River, 40 km south of Adelaide in Australia. These birds are evidently descended from aviary escapees, and their numbers and range appear to have remained constant since 1929 (H.J. Frith 1976). Allied species occur in West Africa and in the coastal region of East Africa. The Orange Bishop *E. franciscanus* is often treated as a race of the Red Bishop, but I shall follow Hall & Moreau (1970) and treat them as separate species. From previous work in the Cape (Craig 1973, 1974) I was familiar with the behaviour of the Red Bishop, and since it breeds in colonies where the nests are readily found, the breeding biology of this species was studied in detail.

Six other representatives of the genus occur in Natal. The Cape Bishop *E. capensis* is generally restricted to the higher areas, in particular the foothills of the Drakensberg. The Golden Bishop *E. afer* is rare, except in the northern parts of the province. The Long-tailed Widow *E. progne*, the Red-collared Widow *E. ardens*, the White-winged Widow *E. albonotatus* and the Red-shouldered Widow *E. axillaris* were all found in the study areas. Both Red-collared and Red-shouldered Widows were caught regularly during ringing operations, so that data on their moult, weight and sex ratios could be obtained for comparison with the Red Bishop.

The new information presented here, together with that drawn from literature, augments our understanding of the annual cycle in granivorous tropical passerines.

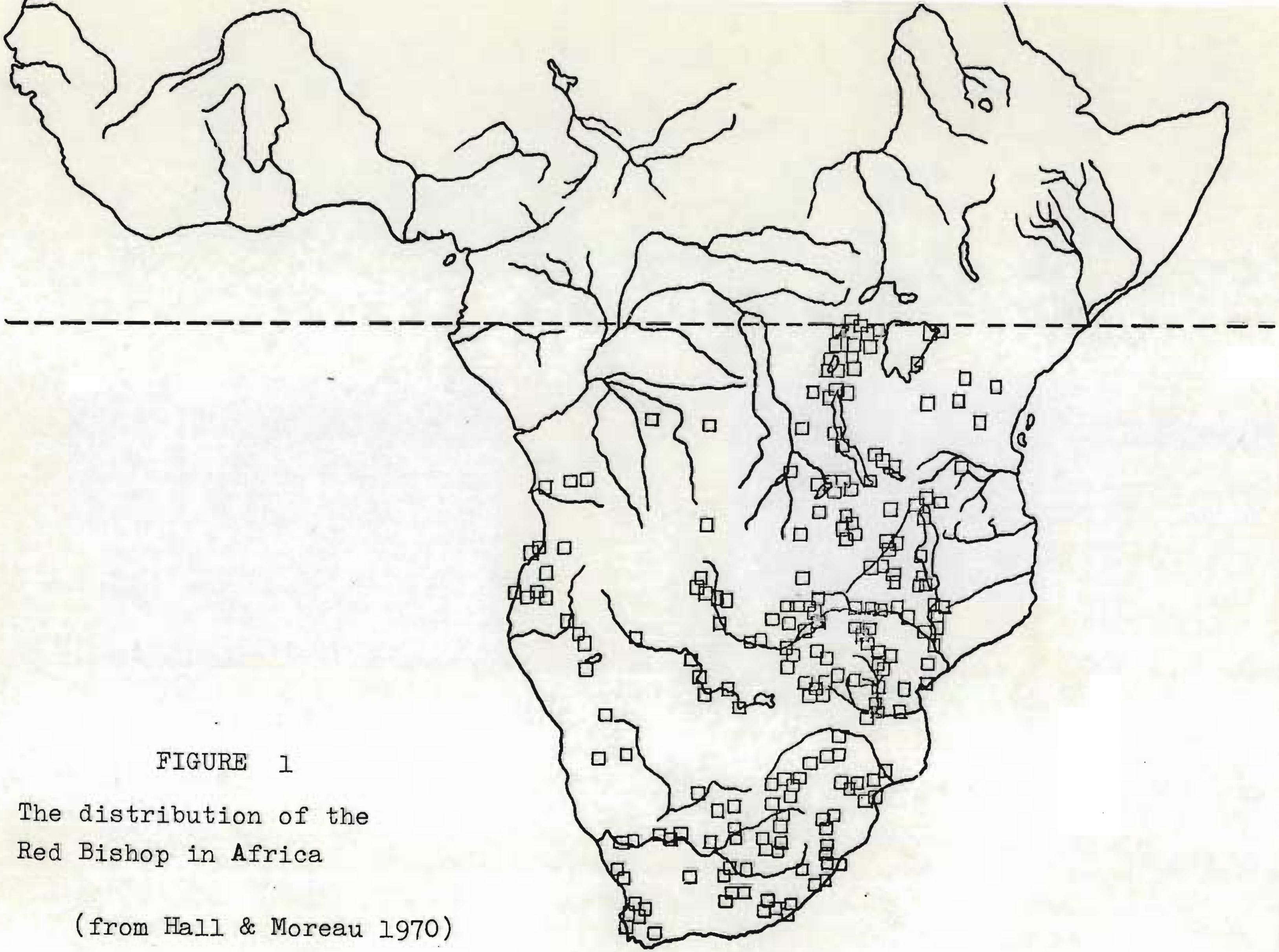


FIGURE 1

The distribution of the
Red Bishop in Africa

(from Hall & Moreau 1970)

THE STUDY AREAS

The main study areas were selected during the summer of 1975, and the field work was continued until August 1977. The farm Malton (29^{o} 30' S 30^{o} 25' E) is 16 km north of Pietermaritzburg, in a belt of dry grassland and thornveld. Figure 2 shows its location. The Red Bishop colony studied was in clumps of reeds (*Phragmites australis*) on the fringes of the dam marked S; this will be referred to as the study colony. The birds also nested along the stream leading to the large dam D, in the bulrushes (*Typha latifolia*) and reeds around the edges of this dam, and downstream of it. However, in these areas it was not possible to keep a regular check on all the nests. In one year many birds also nested in a field of mealies (*Zea mays*), marked Z on Figure 2.

At the study colony the nesting area was restricted and all nests were accessible. There was no human interference, and during the birds' breeding season cattle grazed this field only for short periods. Grass was abundant in summer, and it was only during the dry season that they ate the reeds and sedges.

Unfortunately the study colony was used for roosting only during the breeding season, when I did not wish to disturb the birds by netting there, and the other roosts at Malton were not easily accessible. Consequently most of the ringing was done at a roost in the grounds of the Cedara College of Agriculture (29^{o} 33' S 30^{o} 15' E), 21 km from Pietermaritzburg (Fig. 2). The nesting areas at Cedara were over deep water and soft mud, so that it proved impractical to monitor breeding at this site as well. The various paddocks in the grounds of the college are used for both stock and crops, but the vlei areas are treated as a bird sanctuary, and they are the refuge of a wide variety of animals.

The birds kept in the aviary at the University of Natal were caught on Gartmore Farm (29^{o} 21' S 30^{o} 16' E) in the Karkloof Valley, some 42 km from Pietermaritzburg.

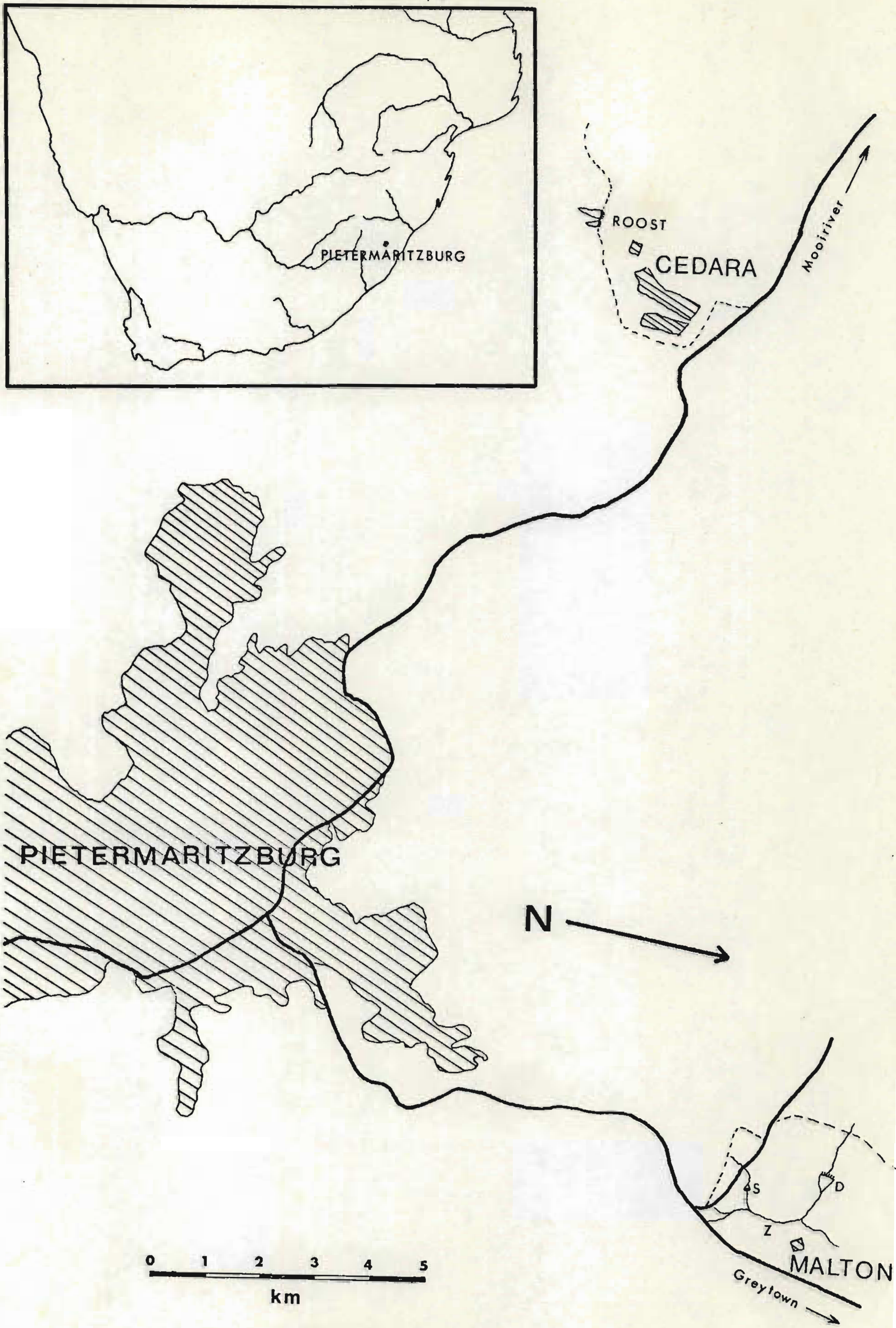


FIGURE 2

The study areas in Natal

Initially some ringing was done on this farm, but this was discontinued because of the additional travelling involved.

While Malton no longer represents an undisturbed natural habitat, little of the total area is planted with crops, and there are still large patches of *Acacia karroo* and *Acacia sieberana* thorntrees. The wildlife has been carefully preserved, and I have to date recorded 184 species of birds on the farm. Mammals seen include Black-backed Jackal, Cape Clawless Otter, Slender Mongoose, Cane Rat, Oribi, Grey Duiker and Reedbuck, and I have found fresh traces of Aardvark and Porcupine. Nile Monitors and Pelomedusid Turtles are common. According to the owners, the Red Bishops have nested at the study colony for many years, and on this farm they obviously coexist with man very successfully.

CHAPTER ONE

The population structure of the Red Bishop and related species

Introduction

A population of any animal species is made up of different age and sex classes, the relative proportions of which vary at different periods. These changes take place through losses from death and emigration, and recruitment by means of immigration and births. No study of the biology of a species can disregard the composition of the population, since this will influence the behaviour and ecology of the animals under observation.

In a field study it is seldom possible to record changes in numbers directly, and these have to be estimated from the composition of samples taken at regular intervals. There is an extensive literature describing mathematical techniques which can be used in such studies (see Seber 1973), but unfortunately the models derived from theory often ignore the realities of the biological situation. However, if similar methods are used, the figures do provide a basis for comparison between different species and areas.

When Lack (1966) reviewed long-term population studies of birds, he included only those studies which had extended over more than four years. Two tropical species were mentioned, the Red-billed Quelea *Quelea quelea* and the White-bearded Manakin *Manacus manacus*. Since then Morel's (1969) detailed study of the Red-billed Firefinch *Lagonosticta senegala* has appeared (though the main points were cited by Lack in 1966), but there is still little information available on tropical passerines.

The *Euplectes* species are of particular interest since they show both sex and age dimorphism. There are few reliable records of the sex ratio in polygynous species, and many erroneous statements have been perpetuated in the literature. The present study covered less than two years, but in addition I have records for the Western Cape, and

A.J. Manson's extensive records for Rhodesia, which cover six years. Rowan (1964) analysed the records of a Transvaal ringing station and estimated the mortality of the Red Bishop Euplectes orix and other ploceids. Some 25 000 Red Bishops have now been ringed in South Africa, and there are enough recoveries of dead birds to justify analysis of these data as well. Some preliminary observations on intraspecific dominance will also be discussed, since this may affect the survival of individuals under natural conditions. These results will be compared with the information available for other passerine species.

Methods

In the present study all birds except those ringed in the nest were caught in mist-nets. Table 1 includes 95 Red Bishop nestlings, but since no measurements were taken and none of these birds were recaptured, they can be disregarded in the present chapter. Male Red-shouldered Widows Euplectes axillaris were ringed with 3-mm aluminium rings as were male Long-tailed Widows E. progne, but for all others 2,5-mm aluminium rings were used. Most of the catching was done at Cedara, where three 12-m mist-nets were set up at the same site on each occasion. The nets were erected in the late afternoon, and taken down after sunset, once all the birds had settled in the roost.

The wing-length of each bird was measured from the carpal joint or wrist to the tip of the longest primary, correct to the nearest mm. Kelm (1970) has discussed the different techniques of wing measurement, and points out that the results obtained by different methods are not comparable. I did not use the method which he considers gives the maximum wing-length, but I ensured that all birds were measured by me personally, and I used the same method consistently: the ruler (fitted with a stop at one end) was slid under the wing, which was held folded against the body, and the primaries were then pressed flat on the ruler.

Birds in non-breeding plumage were sexed primarily on the basis of wing-length, as described below. In the first few weeks after fledging juveniles can be distinguished by their pale gapes and buffy body plumage, but after the first moult I was able to distinguish subadult birds only in the case of male Red-shouldered Widows and male Red-collared Widows E. ardens. All birds with wing-moult were excluded from the wing-length tabulations, as were juveniles. Any birds which could not be sexed or aged with certainty were also omitted from the sex ratio totals.

In some preliminary experiments on the hormonal basis of dominance, a group of one adult male, one subadult male and ten female Orange Bishops Euplectes franciscanus were observed in an indoor aviary at the Universität Bielefeld, West Germany. They were kept under a daily cycle of 14-h light : 10-h dark, and individual birds were monitored for a period of one hour at the same time each day. Two low-ranking birds were treated with 1 mg of testosterone propionate, injected subcutaneously just anterior to the right leg. Initially two doses were given on successive days, and thereafter six further doses at two-day intervals. At the University of Natal a group of 14 male Red Bishops was kept in an outdoor aviary, and observations were made at irregular intervals. Three of these birds were surgically castrated, and the effects on their behaviour recorded.

Results

The total number of Euplectes ringed during the study is shown in Table 1. For comparison, the number of Le Vaillant's Cisticolas Cisticola tinniens, a common reed-bed inhabitant, is included. The recapture rate for the Euplectes species is very low, and few birds were recaptured more than once, whereas almost half the Le Vaillant's Cisticolas were recaptured at some stage, and some individuals were caught five times at the same site. The distribution of the recaptures during the year shows that the Red Bishop and Red-shouldered Widow were recaptured

TABLE 1

The numbers of birds ringed and recaptured during the study

Species	No. ringed	No. of recaps.	Birds recaptured	% recaps.
E. albonotatus	32	0	0	0
E. ardens	488	44	40	8,2
E. axillaris	880	130	115	13,1
E. capensis	1	0	0	0
E. orix	1522	113	101	6,6
E. progne	4	0	0	0
Total Euplectes	2927	287	256	8,7
Cisticola tinniens	37	30	14	37,8

TABLE 2

The numbers of birds last recaptured after particular time intervals

Species	Months elapsed since ringing		
	6	12	18
♂ ardens	2	6	0
♀ ardens	6	1	1
♂ axillaris	11	17	0
♀ axillaris	10	6	0
♂ orix	22	6	1
♀ orix	5	4	1

TABLE 3

The number of recaptures in different months

Month	No. of recaptures of each species		
	orix	axillaris	ardens
January	7	18	3
February	16	23	4
March	15	16	8
April	8	8	15
May	9	7	7
June	10	5	1
July	6	2	2
August	4	2	2
September	1	2	0
October	8	8	1
November	16	12	0
December	13	27	1
Total	113	130	44

most often during the breeding season, and the Red-collared Widow chiefly at the end of the breeding season (Table 3). Few birds were caught at long intervals after ringing (Table 2), but this was to be expected in a study of limited duration.

The catch size at Cedara

Since the catching procedures were standardized, it was possible to compare the catches of each species at Cedara in different months of the year (Table 4). Young (1961) has described a simple method of testing whether catches are random or not, based on the theory of runs. This test was applied to the data in Table 4, and showed that only the catches of Red Bishops were random. The numbers of Red-shouldered and Red-collared Widows vary through the year in a significantly non-random manner.

This implies either that the population size at the Cedara roost varies in the course of the year, or that catching efficiency varies seasonally. In winter the reeds die back and the nets are much more exposed, so that the birds may see them in time to avoid them. However, visual counts also suggested that fewer birds used the roost in winter than in summer, and the regular occurrence of species such as the White-winged Widow E. albonotatus, which was not present at Cedara in summer, does imply that seasonal movements of the birds occurred. The recapture pattern shown in Table 3 confirms my impression that many birds reappear at the start of the next breeding season, after several months' absence. In both the Red Bishop and the Red-shouldered Widow, males caught during the winter were recaptured in subadult plumage during the following breeding season. Perhaps the winter roosting population contains a high proportion of juveniles, while the adult birds tend to move away, only returning the next spring. However, the present data are too fragmentary to establish this.

Seber (1973) describes a number of methods which can be used to obtain population estimates from capture-recapture data. None of these can be used in the present instance.

TABLE 4

The number of <u>Euplectes</u> caught at the Cedara roost in different months

Month	No. of catches	No. of orix	No. of axillaris	No. of ardens	Total
10/75	6	72	99	28	199
11/75	3	31	72	33	136
12/75	2	32	34	37	103
02/76	3	83	14	5	102
03/76	1	26	11	2	39
04/76	1	41	12	6	59
05/76	4	71	43	13	127
06/76	4	85	15	23	123
07/76	2	57	6	6	69
08/76	4	76	32	33	141
09/76	4	22	29	12	63
10/76	3	38	111	20	169
11/76	2	38	63	9	110
12/76	2	96	95	10	201
01/77	3	58	79	48	185
02/77	4	115	93	52	260
03/77	2	69	91	52	212
04/77	3	27	14	88	129
05/77	4	40	15	24	79
06/77	4	21	20	18	59
07/77	3	12	4	1	17
Total	64	1110	952	520	2582

Note: the monthly totals include recaptures of birds ringed in previous months.

The "Lincoln index" and related formulae make the initial assumption that one is dealing with a closed population, where neither death nor emigration occurs during the sampling period - this is unlikely to be true for any natural population. The Jolly-Seber method and its modifications accepts the occurrence of deaths, births and population exchange. However, this method assumes that emigration is permanent - it does not allow for the possibility that some animals may be absent for a period and then return, as seems to happen in the present case. Sampling must also be random, which was not true for two of the three species at Cedara. Finally Seber recommends that the subsequent samples should contain a minimum of ten recaptures for reasonably accurate estimates - this only happened twice in more than 60 catches. Consequently I regard the calculation of population size from the data available as a worthless exercise.

Figure 3 represents the variations in catching success graphically. It appears that several thousand birds use the Cedara roost during the course of the year, and the number of roosting birds is smaller in winter. This may be due to seasonal movements, the extent of which is not yet known.

Wing-length

The sexual dimorphism of the Euplectes species is clearly reflected by the wing-lengths of the birds, and this is the most convenient method of sexing the birds rapidly in the hand. In the case of the Red-shouldered, Red-collared, White-winged and Long-tailed Widows the adult males are identifiable at all seasons, since they retain the black primaries. Adult male Red Bishops can only be distinguished from subadult birds during the breeding season, when they are in nuptial plumage.

For all species the histograms of wing-length show two clear peaks, and in some there is a third smaller peak. However, there is an appreciable degree of overlap between the different components of the population. Harding (1949) has described a method using probability

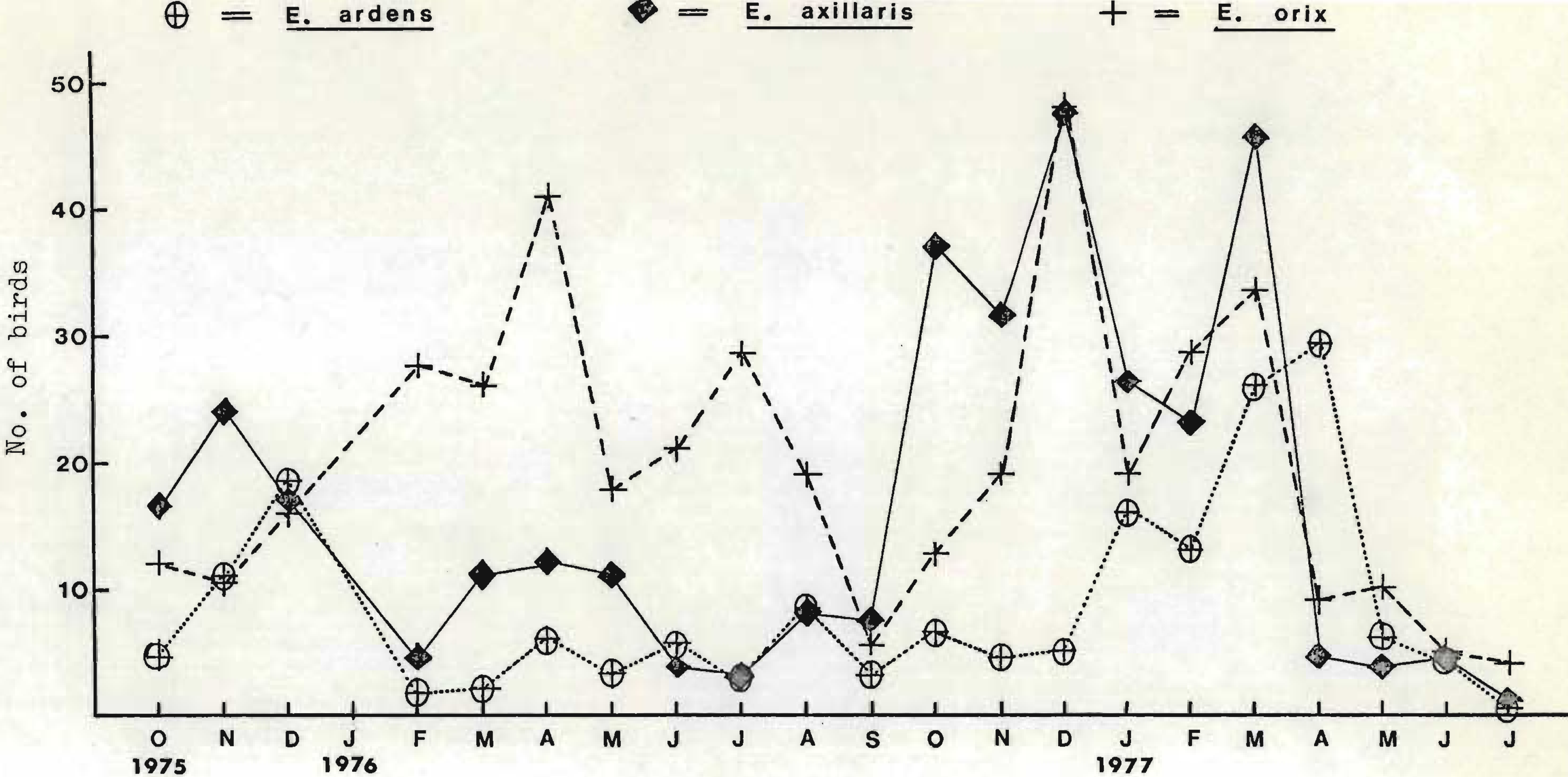


FIGURE 3

Mean numbers of Euplectes caught per night at Cedara in different months paper, by means of which such distributions can be separated into their components, an estimate obtained of the mean and standard deviation of each portion of the population, and the proportions in which they are mixed calculated. This method has been applied in each case. The estimates of wing-length for the sexes of the different species can be compared with the values obtained by other methods (see below), and it appears to be a most valuable technique.

Figure 4 shows the distribution of wing-lengths of the Red-shouldered Widows caught in Natal. There are three separate groups, representing females, subadult males and adult males. These data are plotted on probability paper in Figure 5. The three portions of the curve are then resolved into the three straight lines a, b and c, from which the mean wing-lengths and their standard deviations can be estimated. The percentages at the points of inflection of the curve, 1 and 2, enable one to estimate the relative numbers of the three groups: 197 adult males, 190 subadult males, and 316 females. From the shaded area of Figure 4, there were in fact 208 adult males in the sample, which is very close to the calculated figure. The expected numbers of birds with each wing-length can be calculated from the lines a, b and c, and then compared with the observed numbers by means of the chi-squared test; there is no significant difference between the observed and calculated values (χ^2 = 22,36 d.f. = 16 $p > 0,10$).

The wing-lengths of Natal and Rhodesian Red-collared Widows are shown in Figure 6. Here too, plotting the data on probability paper shows that there are three groups in the samples, and the predicted distributions do not differ significantly from the observed distributions (for the Natal data χ^2 = 8,73 d.f. = 6 $p > 0,10$; for the Rhodesian data χ^2 = 9,23 d.f. = 7 $p > 0,20$).

A large number of White-winged Widows were also ringed in Rhodesia, and their wing-lengths are shown in Figure 7, together with those of a small sample of Cape Bishops *E. capensis*. The sample size for the latter is too small to warrant any further calculations, but there is also an

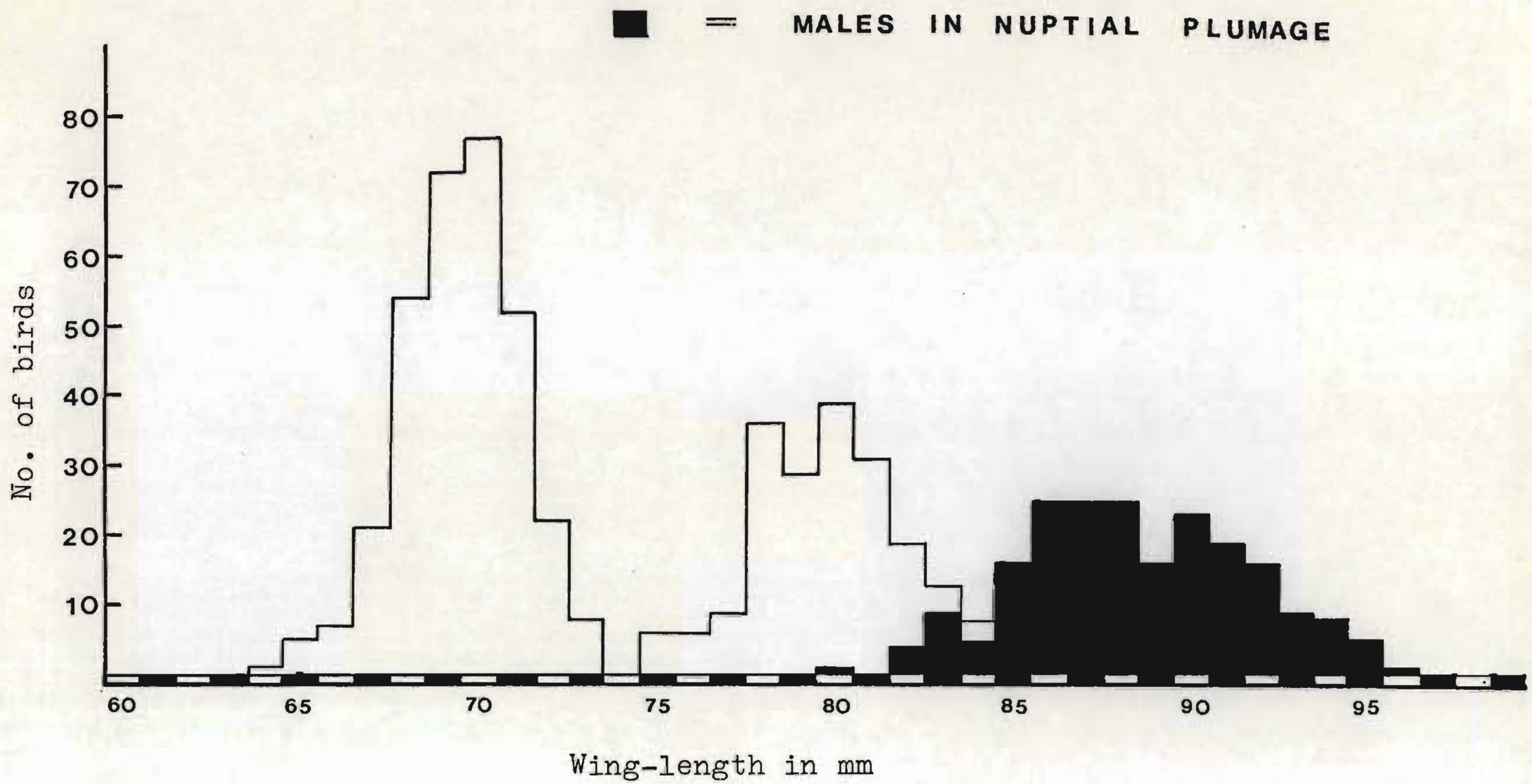


FIGURE 4

Wing-lengths of Natal Red-shouldered Widows

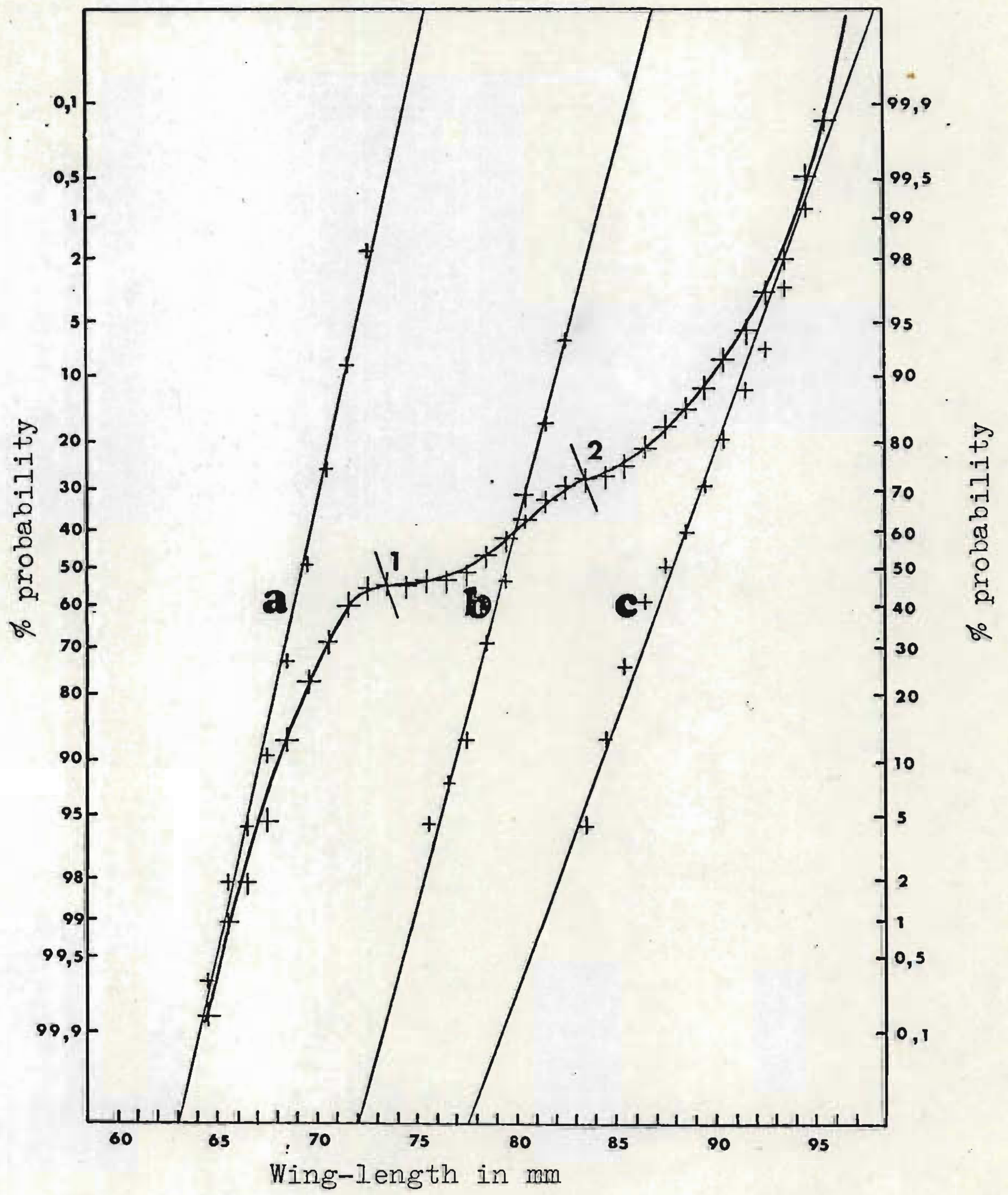


FIGURE 5

Wing-lengths of Natal Red-shouldered Widows plotted on probability paper

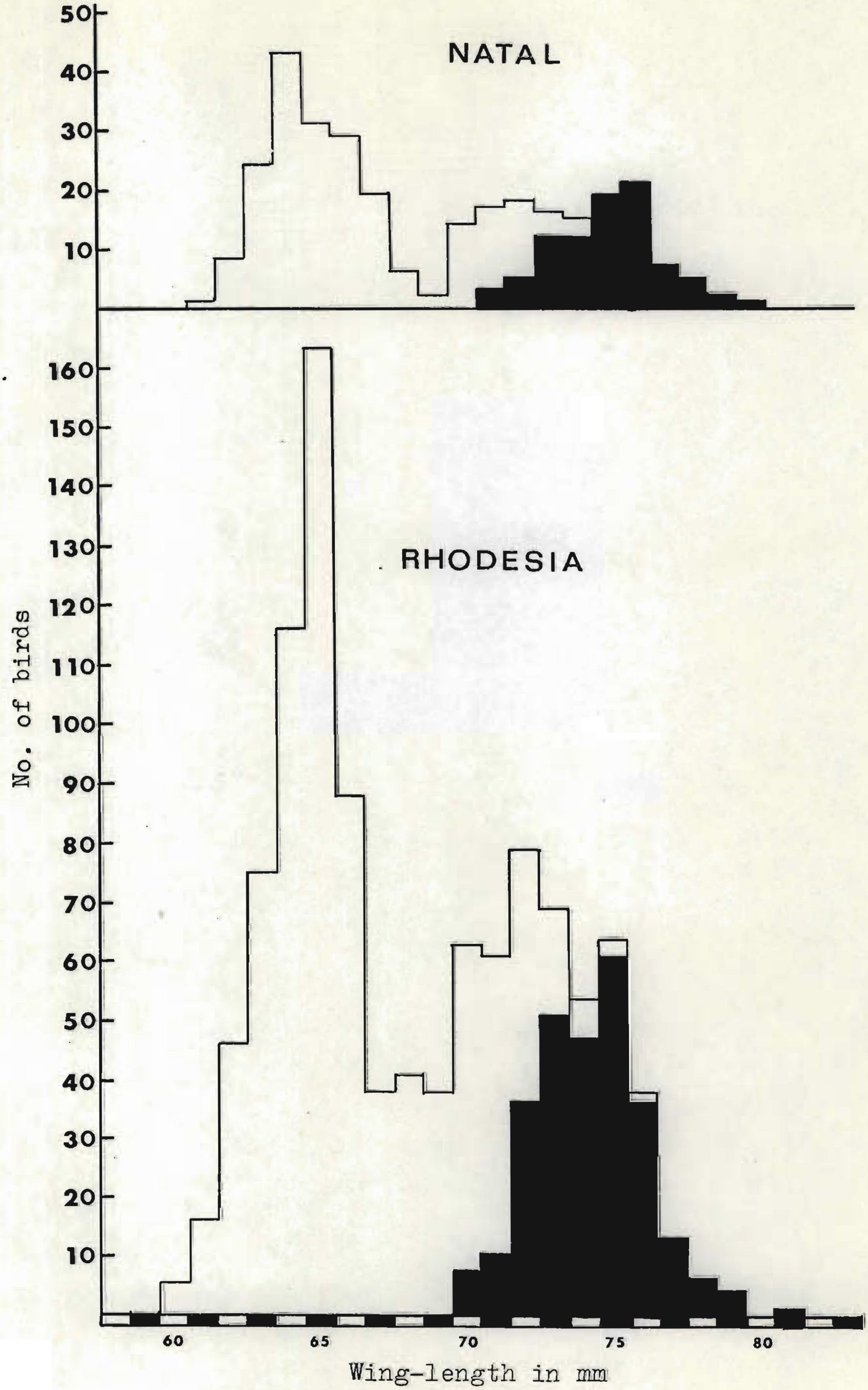


FIGURE 6

Wing-lengths of Natal and Rhodesian Red-collared Wid

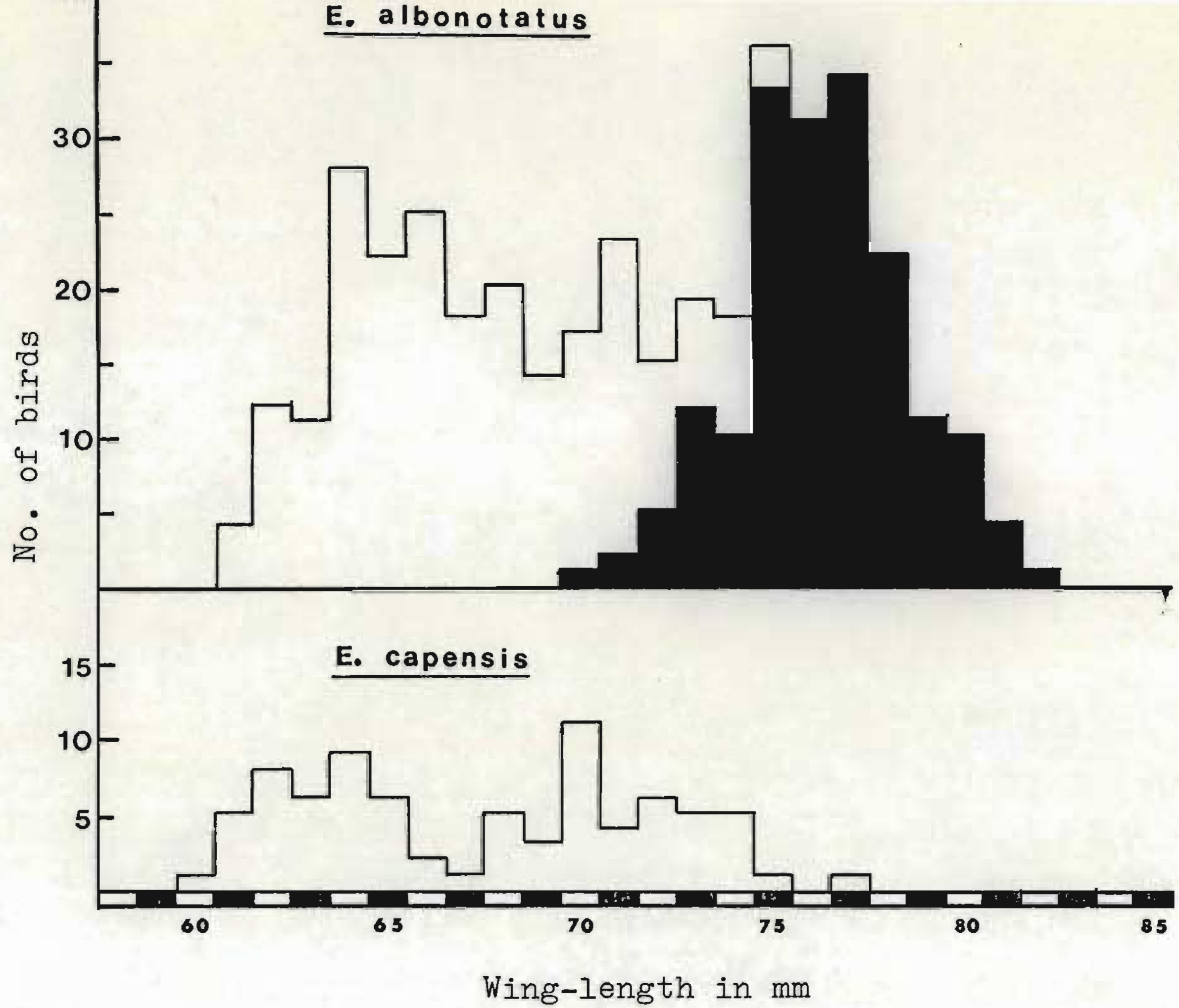


FIGURE 7

Wing-lengths of two Euplectes species in Rhodesia apparent separation into two groups. The data for the White-winged Widow can be separated into three groups on probability paper, and there is no significant difference from the observed distribution (χ^2 = 13,78 d.f. = 8 p > 0,05).

The Red Bishop data for Natal, the Western Cape and Rhodesia show only two peaks on the histograms (Figs 8 & 9), and a single inflection point when plotted on probability paper (Fig. 10). In all three cases the distribution of wing-lengths predicted from probability paper does not differ from the observed distribution (for Natal χ^2 = 8,91 d.f. = 8 p > 0,25; for the Cape χ^2 = 10,5 d.f. = 8 p > 0,20; for Rhodesia χ^2 = 9,73 d.f. = 9 p > 0,20).

Table 5 summarizes the wing-length data for the different species in the three regions. The mean wing-lengths of adult male Red-collared, Red-shouldered and White-winged Widows can be calculated directly from the numbers of birds with black primary feathers, and these figures are in close agreement with the values obtained by the probability paper method. The mean wing-length of female Red Bishops sexed by dissection in the Cape is also very close to the mean read off from probability paper. However, in the case of the male Red Bishops the means obtained from probability paper are significantly lower than those calculated from the wing-lengths of males in nuptial plumage (for the Cape t = 2,4 d.f. = 360 p > 0,02; for Natal t = 5,8 d.f. = 888 p < 0,001; for Rhodesia t = 13 d.f. = 1412 p < 0,001). Since the accuracy of the probability paper method has been confirmed in the other instances, this suggests that the subadult males of the Red Bishop do have smaller wings on average than the adult males, but the differences are not sufficiently marked for them to form a separate category as in the other three species.

Red Bishops from the Western Cape are considerably larger than those from Natal (Table 5). This species seems to follow Bergmann's rule, with the largest birds to be found in the extreme south of its range, and the smallest in the equatorial populations (Delacour & Edmond-Blanc 1933).

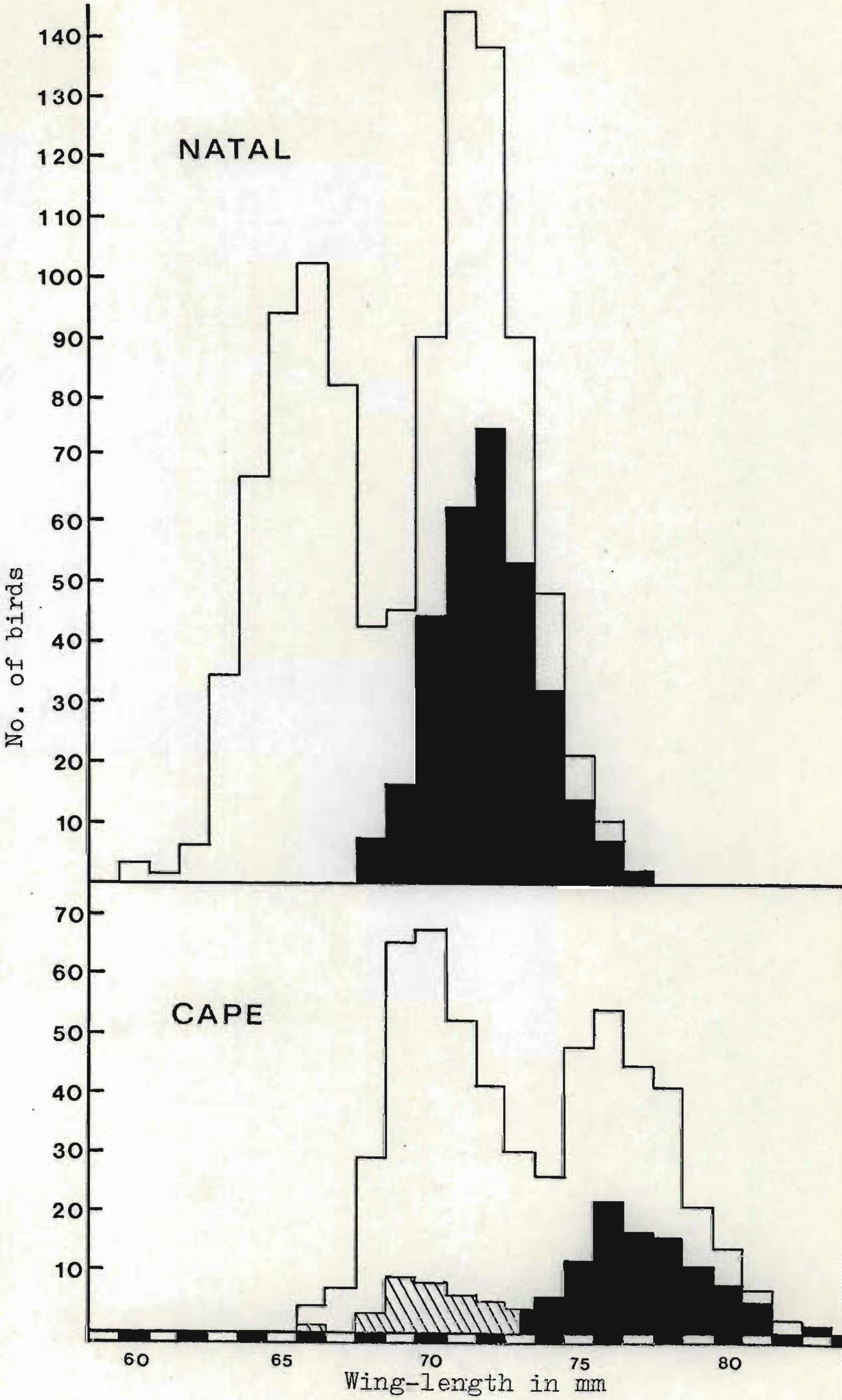


FIGURE 8

Wing-lengths of Natal and Cape Red Bishops

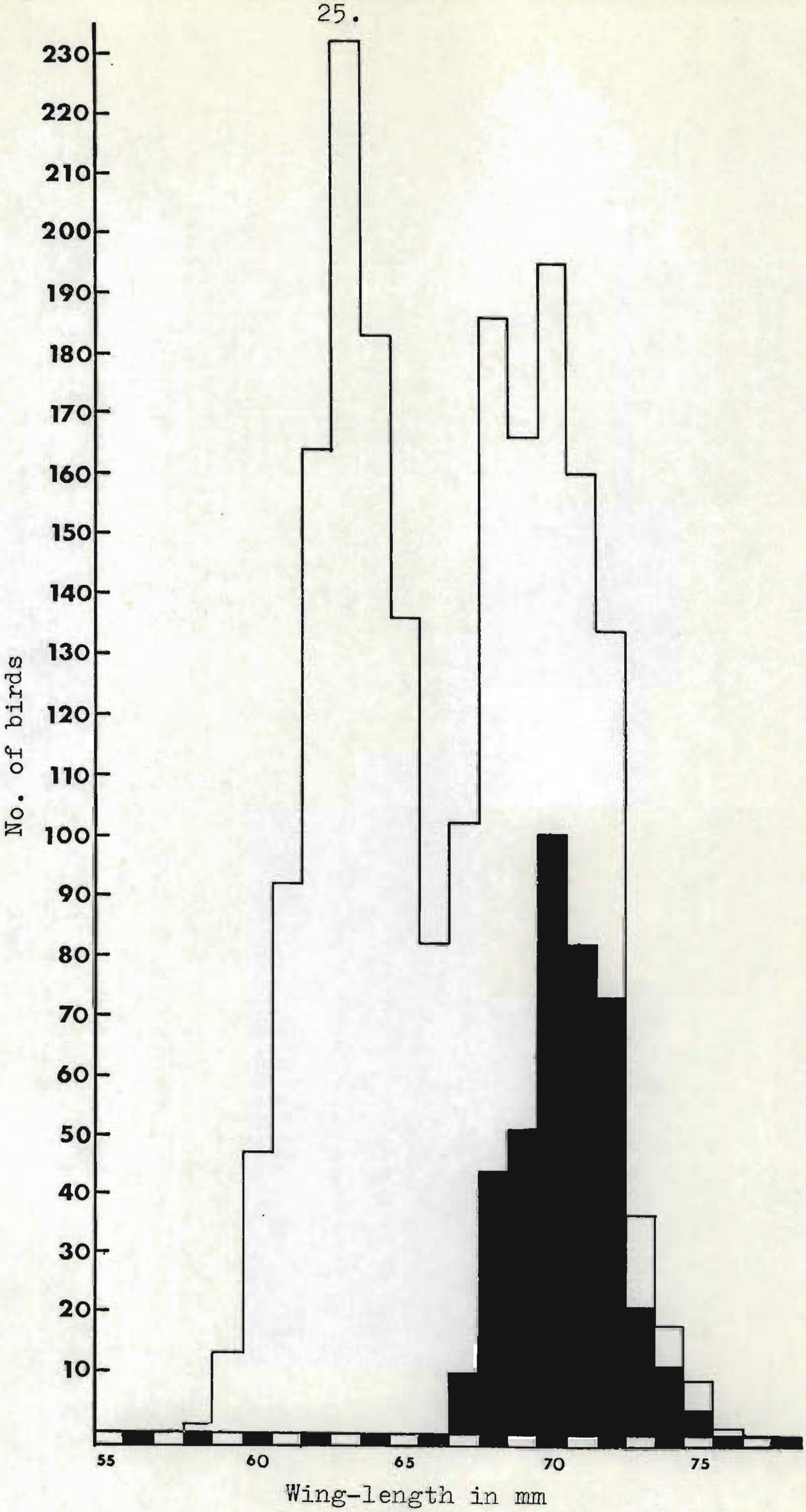


FIGURE 9

Wing-lengths of Rhodesian Red Bishops

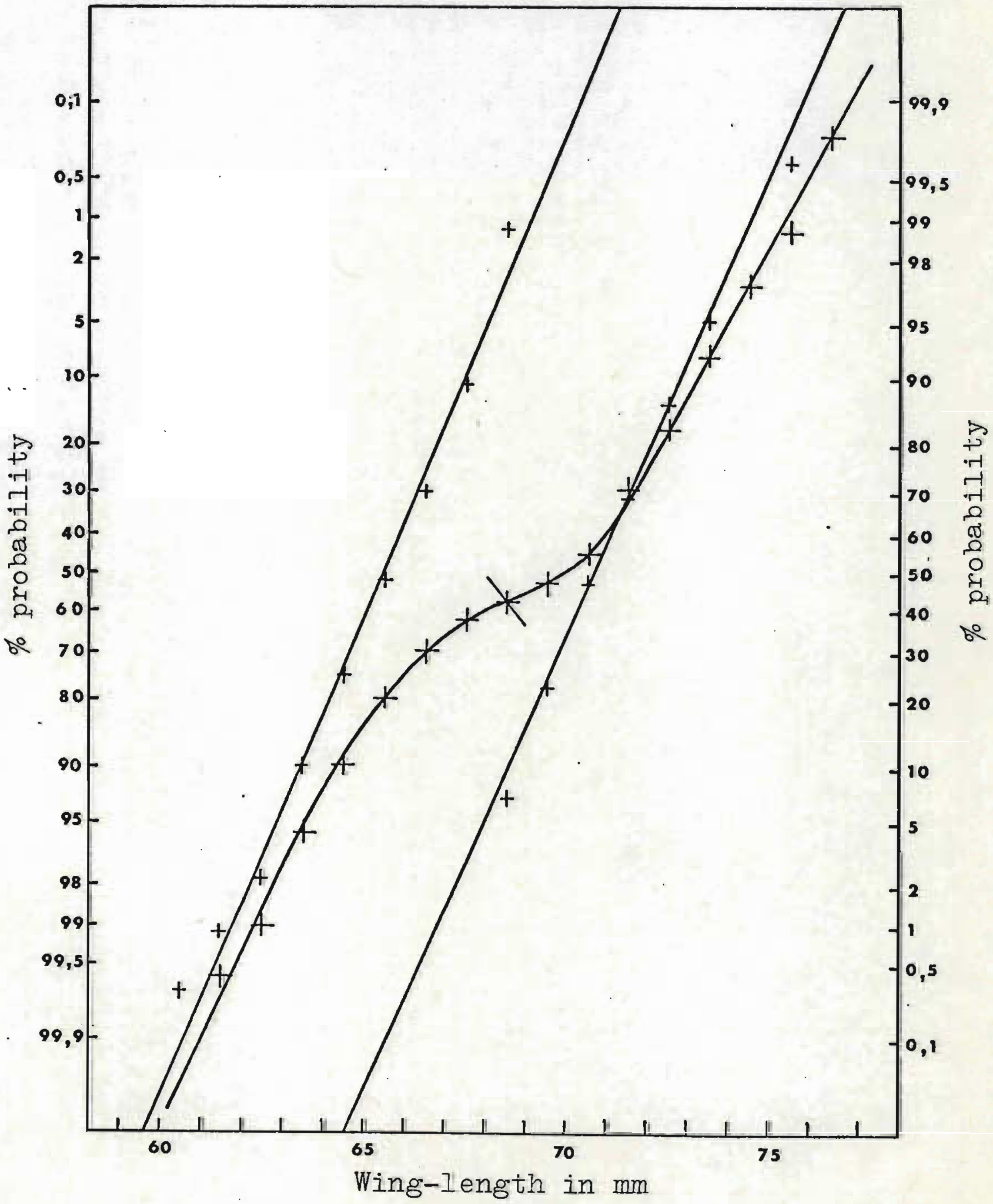


FIGURE 10

Wing-lengths of Natal Red Bishops plotted on probability paper

TABLE 5

The wing-lengths of four Euplectes species

Sex	No.	Mean (mm)	S.D.	Method	Locality
E. orix					
♂♂	396	70,5	1,6	Plumage	Rhodesia
♂♂	1018	69,2	1,9	Prob. paper	"
♀♀	940	63,2	1,6	" "	"
♂♂	102	77,1	2,1	Plumage	W. Cape
♂♂	260	76,5	2,2	Prob. paper	"
♀♀	294	70,0	1,5	" "	"
♀♀	36	70,2	1,6	Dissection	"
♂♂	312	71,9	1,7	Plumage	Natal
♂♂	578	71,2	1,8	Prob. paper	"
♀♀	436	65,0	1,7	" "	"
E. ardens					
♂♂	272	74,1	1,9	Plumage	Rhodesia
♂♂	272	74,3	2,0	Prob. paper	"
sub♂♂	246	70,0	1,3	" "	"
♀♀	560	64,5	1,5	" "	"
♂♂	87	75,0	1,9	Plumage	Natal
♂♂	72	75,0	1,7	Prob. paper	"
sub♂♂	65	71,5	1,4	" "	"
♀♀	161	64,3	1,4	" "	"
E. axillaris					
♂♂	208	88,0	6,9	Plumage	Natal
♂♂	197	88,4	3,2	Prob. paper	"
sub♂♂	190	79,0	1,9	" "	"
♀♀	316	68,7	1,7	" "	"
E. albonotatus					
♂♂	178	76,3	2,2	Plumage	Rhodesia
♂♂	176	76,0	1,7	Prob. paper	"
sub♂♂	124	69,6	2,1	" "	"
♀♀	95	63,7	1,5	" "	"

The differences between Natal and Rhodesian birds in the Red Bishop and the Red-collared Widow, however, may be due to individual differences in the method of measuring wing-length. In the Cape L.G. Underhill was ringing at the same localities as I was, and he has allowed me to use his Red Bishop data. Figure 11 compares the wing-length distributions which we recorded, showing that his measurements were consistently greater than mine. Plotting his data on probability paper gives a mean wing-length of 79,5 mm (S.D. 2,4) for male Red Bishops, and 72,2 mm (S.D. 2,4) for females. Thus it can be very misleading to compare wing-lengths recorded by different ringers, as has been emphasized by Kelm (1970).

Tail-lengths were not recorded in Natal, but measurements on the Rhodesian birds are shown in Table 6. In the Red Bishop males have significantly longer tails than females, but tail-length does not differ in eclipse and nuptial plumage. Both the White-winged Widow and the Red-collared Widow moult the rectrices during the pre-nuptial moult, resulting in very long tails amongst males in nuptial plumage. This measurement can also be used to sex the birds, but wing-length is easier to record consistently accurately, and the tail feathers are more easily abraded or lost.

Sex ratio

My catches of Red Bishops in the Cape were concentrated in the breeding months, with a few samples at other times for the examination of the gonads. L.G. Underhill and G. Wilson have allowed me to use their figures, which are made up of catches at irregular intervals over several years. They also sexed the birds primarily on the basis of wing-length, and I have checked the sexing, allowing for the differences in our measurement of wing-length. Our combined data show a 1:1 sex ratio (Table 7).

In Natal I have samples for all months of the year, and since there were no differences between the same months in different years, all the data have been combined in Table 8. As in the previous table, subadult and adult males were only distinguished in the months when most

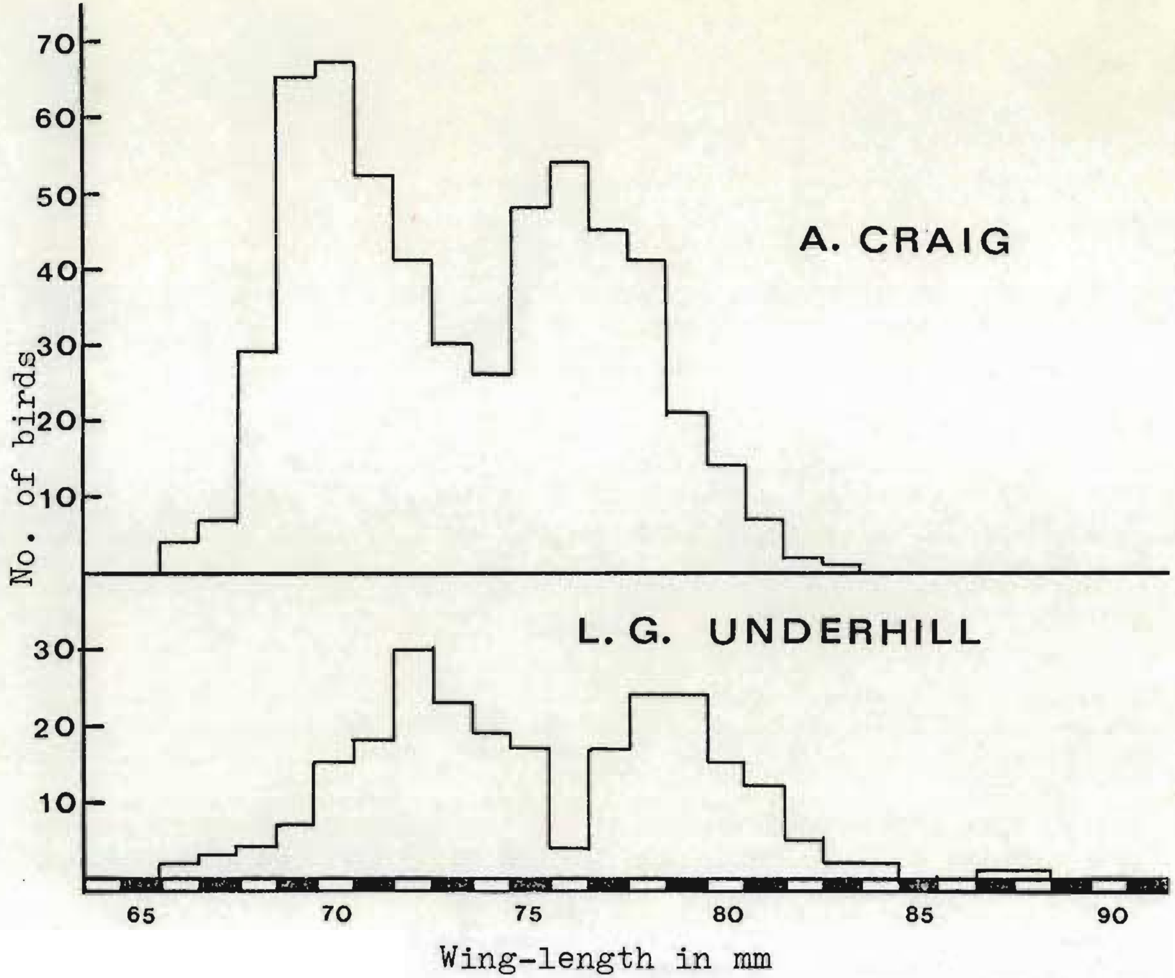


FIGURE 11

Wing-lengths of Cape Red Bishops measured by different ringers

TABLE 6

The tail-lengths of some Rhodesian *Euplectes*

Species	Sex	No.	Tail (mm)	S.D.
albonotatus	♂ b.d.	50	88,3	6,7
	♂ e.p.	50	51,3	4,0
	♀	50	42,3	2,2
ardens	♂ b.d.	30	238,5	28,0
	♂ e.p.	50	51,9	3,5
	♀	50	43,3	2,3
orix	♂ b.d.	50	39,2	1,6
	♂ e.p.	50	39,0	1,9
	♀	50	35,6	1,6

Note: b.d. = breeding dress; e.p. = eclipse plumage.

TABLE 7

The sex ratio of Cape Red Bishops

Month	ad. ♂♂	sub. ♂♂	♂♂	♀♀	χ^2
May 1972			19	33	3,25
June 1972			49	67	2,49
July 1972	4	1	5	11	1,56
Aug. 1972	13	13	26	50	6,96
Sept. 1972	21	22	43	20	7,68
Oct. 1972	23	19	42	23	4,98
May 1973			18	12	0,83
June 1973			41	38	0,05
Aug. 1973			11	10	0
Total	61	55	254	264	0,16
All (L.G.U.)			112	123	0,43
All (G.W.)			295	268	1,20
Total			661	655	0,02

Note: L.G.U. indicates the records of Dr. L. Underhill, G.W. those of Mr. G. Wilson.

males were in full nuptial plumage. There are clear seasonal variations in the numbers of each sex captured. At the start of the pre-nuptial moult in October, more males than females were captured, and there was again a significant excess of males in November. During December and January the sex ratio was balanced, but in February and March when breeding ends and the post-nuptial moult begins, there was again an excess of males. From April until September there was no significant deviation from a balanced sex ratio. Juvenile birds were also sexed on the basis of their measurements, and in this case there was no significant deviation from a 1:1 ratio (Table 8). The sexing of juveniles is probably less accurate than that of adults, since size is greatly influenced by age, and this may explain the greater number of females recorded.

Samples for all years are also combined in the Red Bishop data from Rhodesia (Table 9), since the numbers caught in some months were small because of infrequent catches, but there were no obvious differences between years. Here the seasonal variations in sex ratio do not follow as clear a pattern as in Natal. There is an excess of males in September but not in October, in November but not in December. For the rest of the summer there is a very large excess of males, but by March there is an excess of females, which recurs in June and in August. These results are difficult to interpret, but they may be caused by irregular movements on the part of the population being studied. The totals for the juveniles show significant variations in the different years, but the samples are small and the overall sex ratio is balanced.

Of the other Rhodesian species, the Cape Bishop catch consisted of 47 males and 47 females; a perfect 1:1 ratio! The White-winged Widows comprised 283 adult males, 126 subadult males and only 195 females - thus 67,7% males. However, this imbalance is probably caused by selective sampling of the population - A.J. Manson informs me that very little catching was done in the area where the birds were breeding, and most of the males were caught while roosting with the Red Bishops and Red-collared Widows.

TABLE 8

The sex ratio of Natal Red Bishops

Month	ad. ♂♂	sub. ♂♂	♂♂	♀♀	χ^2
Jan.	17	12	29	35	0,39
Feb.	82	25	107	70	7,32
Mar.	80	5	85	43	13,10
Apr.			45	45	0
May			51	43	0,26
June			49	44	0,17
July			32	40	0,68
Aug.			41	30	1,16
Sept.			20	14	0,73
Oct.			99	52	14,01
Nov.	70	21	91	44	15,67
Dec.	48	30	78	63	1,59
Total	297	93	727	523	32,97

Year	juv. ♂♂	juv. ♀♀	χ^2
1975-1976	23	25	0,02
1976-1977	59	74	1,47
Total	82	99	1,41

TABLE 9

The sex ratio of Rhodesian Red Bishops

Month	ad. ♂♂	sub. ♂♂	♂♂	♀♀	χ^2
Jan.	85	52	137	83	12,77
Feb.	101	97	198	93	37,89
Mar.	42	106	148	189	4,75
Apr.	58	117	175	196	1,08
May	56	29	85	107	2,30
June			60	95	7,46
July			110	99	0,31
Aug.			44	71	5,88
Sept.			79	55	3,95
Oct.			66	51	1,67
Nov.			91	65	4,01
Dec.	42	10	52	42	0,86
Total	444	411	1245	1146	4,02

Year	juv. ♂♂	juv. ♀♀	χ^2
1972	5	2	
1973	24	11	4,11
1974	70	107	7,32
1975	104	135	3,76
1976	134	123	0,39
1977	2	0	
Total	339	378	2,01

This species was only recorded in certain months of the year, which is an additional source of bias. Of 13 juveniles ringed, there were six males and seven females.

The Red-collared Widow shows a much more consistent pattern in both areas. In Rhodesia there is a significant excess of females in January, but the ratio for all other months of the year is approximately balanced (Table 10). Only 29 juveniles were caught in the six years of ringing - 11 males and 18 females. From the Natal data there appears to be an excess of females in the winter months of June to August, but at other times of the year there is no significant difference in the numbers of the sexes, and the sex ratio of the juveniles is balanced (Table 11).

Male Red-shouldered Widows predominate in January and February, but in April during the post-nuptial moult there is an excess of females. For the rest of the year the sex ratio is balanced, and the sex ratio of the juveniles does not differ significantly from the expected 1:1 ratio (Table 12).

Overall the large samples of the Red Bishop show an excess of males in both Natal and Rhodesia. The catches of the Red-shouldered Widow in Natal also contain a significant excess of male birds, but the sex ratio of the Red-collared Widow appears to be 1:1.

The numbers of adult and juvenile birds caught during the summer months in Natal are shown in Table 13. The numbers of Red-collared Widows caught during 1976 are too small to warrant comparison with 1977, although it appears that the birds were more abundant at the netting sites in 1977. In the case of the Red-shouldered Widow the proportion of juveniles in the two years is identical, though the sample for 1976 is small. The numbers of Red Bishops caught are very similar in 1976 and 1977, but the proportion of juveniles is three times as high in 1977. This might reflect more breeding activity, which was certainly the case at the study colony, where four times as many young were fledged in 1977 as in 1976. Thus with large samples, the proportion of juveniles caught may provide a measure of recruitment in different years.

TABLE 10

The sex ratio of Rhodesian Red-collared Widows

Month	ad. ♂♂	sub. ♂♂	♂♂	♀♀	χ^2
Jan.	20	39	59	87	4,99
Feb.	15	22	37	28	0,98
Mar.	4	11	15	11	0,35
Apr.	3	6	9	9	0
May	1	6	7	14	1,71
June	10	10	20	11	2,06
July	20	14	34	28	0,40
Aug.	24	7	31	24	0,65
Sept.	18	11	29	15	3,84
Oct.	43	52	95	78	1,48
Nov.	84	61	145	176	2,80
Dec.	48	29	77	90	0,86
Total	290	268	558	571	0,13

TABLE 11

The sex ratio of Natal Red-collared Widows

Month	ad. ♂♂	sub. ♂♂	♂♂	♀♀	χ^2
Jan.	6	4	10	16	0,96
Feb.	6	8	14	14	0
Mar.	13	6	19	14	0,48
Apr.	6	12	18	20	0,03
May	11	4	15	12	0,15
June	6	6	12	26	7,53
July	0	0	0	5	
Aug.	6	3	9	23	5,28
Sept.	4	4	8	8	0
Oct.	25	5	30	21	1,25
Nov.	20	4	24	19	0,37
Dec.	19	5	24	22	0,03
Total	118	65	183	200	0,66

Year	juv. ♂♂	juv. ♀♀	χ^2
1975-1976	1	0	
1976-1977	50	52	
Total	51	52	0

TABLE 12

The sex ratio of Natal Red-shouldered Widows

<table>
<tr><th>Month</th><th>ad. ♂♂</th><th>sub. ♂♂</th><th>♂♂</th><th>♀♀</th><th>χ^2</th></tr>
<tr><td>Jan.</td><td>20</td><td>19</td><td>39</td><td>21</td><td>4,82</td></tr>
<tr><td>Feb.</td><td>18</td><td>30</td><td>48</td><td>27</td><td>5,33</td></tr>
<tr><td>Mar.</td><td>14</td><td>18</td><td>32</td><td>31</td><td>0</td></tr>
<tr><td>Apr.</td><td>4</td><td>7</td><td>11</td><td>25</td><td>4,69</td></tr>
<tr><td>May</td><td>22</td><td>6</td><td>28</td><td>16</td><td>2,75</td></tr>
<tr><td>June</td><td>6</td><td>10</td><td>16</td><td>15</td><td>0</td></tr>
<tr><td>July</td><td>5</td><td>0</td><td>5</td><td>3</td><td rowspan="2">0</td></tr>
<tr><td>Aug.</td><td>5</td><td>8</td><td>13</td><td>16</td></tr>
<tr><td>Sept.</td><td>10</td><td>8</td><td>18</td><td>19</td><td>0</td></tr>
<tr><td>Oct.</td><td>70</td><td>46</td><td>116</td><td>96</td><td>1,70</td></tr>
<tr><td>Nov.</td><td>42</td><td>26</td><td>68</td><td>56</td><td>0,97</td></tr>
<tr><td>Dec.</td><td>28</td><td>25</td><td>53</td><td>58</td><td>0,14</td></tr>
<tr><td>Total</td><td>244</td><td>203</td><td>447</td><td>383</td><td>4,78</td></tr>
</table>

Year	juv. ♂♂	juv. ♀♀	χ^2
1975-1976	3	5	
1976-1977	28	33	
Total	31	38	0,52

TABLE 13

The numbers of juvenile Euplectes caught in Natal

Month	Species	No. caught	No. juv.	% juv.
January 1976	axillaris	1	0	0
	orix	15	0	0
February 1976	ardens	5	0	0
	axillaris	19	4	21,0
	orix	149	19	12,8
March 1976	ardens	4	1	25,0
	axillaris	15	4	26,7
	orix	104	24	23,1
Total 1976	ardens	9	1	11,1
	axillaris	35	8	22,8
	orix	268	43	16,0
January 1977	ardens	45	16	35,5
	axillaris	61	1	1,6
	orix	51	23	45,1
February 1977	ardens	49	25	51,0
	axillaris	75	17	22,7
	orix	108	61	56,5
March 1977	ardens	44	14	31,8
	axillaris	78	32	41,0
	orix	71	20	28,2
Total 1977	ardens	138	55	39,8
	axillaris	214	50	23,4
	orix	230	114	49,6

Dominance and sex hormones

In most species of birds kept in groups in aviaries, a hierarchy is soon established in which some birds dominate the others. In a group of Orange Bishops kept in aviaries at the University of Bielefeld, a linear ranking order was identified, and the highest-ranking birds had preferential access to food and perches.

Table 14 compares the behaviour of the top-ranking female, bird 78, with two low-ranking birds before and after treatment with testosterone. "Nesting" refers to the amount of time spent manipulating nest-building material - females often picked up the coconut fibres provided in the aviary and manipulated them, even threading them through the wire mesh. This behaviour was apparently not stimulated by testosterone. The time spent feeding was also not increased - bird 78 still spent far more time feeding than either of the others. The increase in preening shown by bird 38 might have been due to irritation at the site of the injections, since this was the area which was preened most frequently. There was no increase in calling, and no male-type vocalizations were ever heard from females.

The only obvious effect was on aggressive behaviour. Success in aggressive encounters with other females improved dramatically for both birds 38 and 85. Within a month of their last injection, the effect had worn off, and they were once more the two lowest-ranking birds. It is interesting to note that the actual number of aggressive encounters was not affected, but instead of giving way when threatened by another bird, the experimental birds after treatment would return the threat with great vigour.

Although males in breeding plumage normally dominated all eclipse-plumaged birds, one incident suggested that under the artificial conditions of captivity individual recognition may play a role in dominance. After the conclusion of this experiment, female 78 was removed for laparotomy, and kept singly for a few days. During this time the adult male was moved to another aviary and

TABLE 14

The effect of testosterone on female Orange Bishops

	♀ 78	♀ 38 before	♀ 38 after	♀ 85 before	♀ 85 after
Hours observed	11	6	16	7	27
% time feeding	9,5	2,5	4,1	4,6	4,2
% time preening	10,0	7,0	11,0	2,1	2,3
% time nesting	9,2	0	0	0	0
Aggressive encounters with ♀♀	124	31	145	51	164
No. won	72	3	116	1	52
% won	58,1	9,7	80,0	2,0	31,7
Total no. aggressive	194	61	207	150	515
Enc./hr.	17,6	10,2	12,9	21,4	19,1

replaced by a strange male in nuptial plumage, which took over the top-ranking position. When bird 78 was returned to the aviary, she refused to be dominated by the new adult male and soon outranked him, although she remained subordinate to the subadult male in the aviary, as had been the case before her removal.

Observations on castrated birds have also shown that they still perform normal threat displays, and are not necessarily dominated by all other males. However, in all-male groups in captivity, one bird usually established itself as a "tyrant", and during the breeding season spent much of its time chasing other occupants of the aviary, in the manner of a male displacing intruders from its territory. It is clear that gonadal hormones alone are not the key to dominance in these species.

Mortality rates and survival

The Rhodesian ringing data extend over a sufficient period for an analysis of the recaptures to give some information on the mortality rates of the species concerned. Haldane's method as described by Seber (1973: pp. 247-249) has been used, since it makes allowance for the possibility that some of the ringed birds are still alive. The last date of recapture of each bird is assumed to represent the time when that bird left the population permanently - this means that the calculated mortality rates are likely to be higher than the true rates, since birds which have emigrated are treated as though they have died. Only birds ringed as adults and recaptured more than two months after ringing have been included, and the age classes have been grouped; all birds last recaptured between three and 12 months after ringing are said to be one year old, those last recaptured between 13 and 24 months after ringing two years old, etc.

The results for the Rhodesian Red Bishops are shown in Table 15. There is no evidence that the mortality rates differ for the two sexes. If the data in Table 15 are analysed using the chi-squared test for a 2 x n table, there is no significant difference between the numbers of males and females recaptured (χ^2 = 1,92 d.f. = 3 p > 0,5).

TABLE 15

The survival of Rhodesian Red Bishops

Year ringed	Age in years at last recapture 1	2	3	4	5	6	Total
1971	0	2	1	0	0	2	5
1972	77	68	73	25	12	1	256
1973	61	76	27	10	2		176
1974	54	25	9				88
1975	102	22					124
1976	45	2					47
1977	1						1
Total	340	195	110	35	14	3	697

Mean annual mortality = 47% ± 1,6

TABLE 16

The survival of Rhodesian Red-collared Widows

Year ringed	Age in years at last recapture 1	2	3	4	5	6	Total
1971	3	0					3
1972	12	9	12	6			39
1973	19	10	5	1			35
1974	16	14					30
1975	9	2					11
1976	5						5
Total	64	35	17	7			123

Mean annual mortality = 46% ± 3,7

Moreover it is known that more males than females were ringed initially (see above). The estimated mortality rate for the Red-collared Widow is very similar (Table 16).

The recoveries of dead ringed Red Bishops recorded at the National Unit for Bird-ringing Administration are analysed in Table 17. Since the accuracy of the sexing is not known, it is not possible to treat the two sexes separately, and only birds ringed as free-flying adults are included. The same conventions have been used in aging the birds. The mortality rate for adult birds is lower that that calculated from the Rhodesian recaptures, and is probably closer to the true rate, since the data have been collected over a much longer period. Of 19 birds ringed as nestlings, ten were recovered within a month of ringing, a further six within the first year, two birds two years later and one bird four years later. This suggests that the mortality in the first year of life is higher than in subsequent years.

The longest interval between ringing and recovery was eight years and six months, and it seems likely that ten years is the maximum lifespan of these birds under natural conditions. The recoveries provide little evidence for large-scale movements, but the recovery rate is low. Most birds were ringed during the breeding season and recovered during a subsequent breeding season (59%); only 24% of the recoveries were during the non-breeding season, so that the chances of recovery at the breeding colonies (and perhaps of males in nuptial plumage) are greatest. Only six birds out of 129 were recovered more than 50 km from the ringing site, the greatest distance between ringing site and recovery site being 104 km, with 50% of all the recoveries occurring at the ringing site, and a further 35% within 10 km of it.

TABLE 17

The survival of South African Red Bishops

Year ringed	Age in years on recovery 1	2	3	4	5	6	7	8	9	Total
1963	1	0	0	1	0	0	1	0	1	4
1964	0	1							1	2
1965	2	2	1	0	1	1				7
1966	0	1	1	0	1					3
1967	4	2	2	1						9
1968	0	0	1	0	1					2
1969	7	3								10
1970	0	4								4
1971	11	1	1							13
1972	7	7	1	0	1					16
1973	3	1	2							6
1974	2									2
1975	2									2
1976	1									1
Total	40	22	9	2	4	1	1	0	2	81

Mean annual mortality = 44% $\pm$ 4,5

Discussion

Seasonal movements

The field identification of the Euplectes species in eclipse plumage is difficult, except in the case of males which retain the black wing feathers and epaulets as in the Red-shouldered Widow. The large mixed flocks which often occur complicate matters further. Nevertheless many authors have suggested that some of the species leave the breeding areas during the winter, only returning the following spring.

Stark (1900) states that the Golden Bishop E. afer appears to migrate in South Africa, and Skead (1965) remarks that this species visits the Eastern Cape very irregularly. Lynes (1924) was convinced that they left the Sudan district where he lived immediately after the breeding season and did not reappear until the following year, but Reichenow (1904) refers to this species as resident in Ethiopia. My limited experience of the Golden Bishop suggests that it remains only to breed and then disappears from the area (see Chapter 4).

The White-winged Widow also leaves the breeding areas in the Sudan at the end of summer (Lynes 1924), and in Rhodesia seems to move north after breeding (Hornby 1967). A.J. Manson's ringing data confirm its absence for most months of the year in the Salisbury area. I mentioned above that this species roosts at Cedara in winter, but is not found there in summer. At Malton I have recorded it in all months of the year, but the numbers in winter are much smaller than those in the breeding season, and adult males are often not seen for several months.

In Katanga the Red-collared Widows seem to remain in the same localities throughout the year and their roosting sites in the swamps are used regularly (de Bont et al. 1965), though Ruwet (1964a) refers to local movements in the savannah. Newton (1937) states that the birds disappear from the breeding areas at the onset of the post-nuptial moult in Nigeria, and are then to be found in mixed flocks with other species. This species was caught in all months of the year in Natal and Rhodesia, but adult males were seldom seen at Malton during the winter.

Skead (1959) states that the Red-shouldered Widow does not move far from its breeding areas in the Eastern Cape; this is also the case in Natal. Large numbers of both males and females can be seen at Malton and Cedara at all times of the year.

The Cape Bishop appears to be resident in the Congo basin (de Bont et al. 1965) and in East Africa, although it may move about according to the availability of food (Van Someren 1956). In the Cape I have caught them around the breeding areas during winter, as has L.G. Underhill. The only specimen actually handled in Natal was caught at the Cedara roost during winter - I have not seen them in this area in summer, and they are only common in the foothills of the Drakensberg.

Several authors refer to local movements in Red Bishop populations (Delacour & Edmond-Blanc 1933; Mackworth-Praed & Grant 1962; Vincent 1949), and both Skead (1965) and Rowan (1964) report that the flocks move widely and erratically during the dry season. The males tend to return to the same nesting areas in subsequent seasons, as found from the recaptures in Natal and in Rhodesia, and in the study described by Rowan (1964). The birds are certainly present in large numbers throughout the year in Natal, but it is quite probable that the same birds do not remain all winter. Only a long-term ringing study, preferably with a grid of workers spread over several districts, will provide the necessary information.

There are no references to the non-breeding dispersal of the Long-tailed Widow in the literature. A small flock of 10-12 birds seems to frequent Malton at all seasons, and during the winter I have seen large flocks in the Nottingham Road area, where the birds are particularly common in the summer.

The remaining members of the genus do not occur in South Africa, and I have no personal experience of them in the field. The available information in the literature will be reviewed briefly. There are no data for Euplectes aureus, diadematus, gierowii and hartlaubi. E. jacksoni has a very restricted distribution in East Africa, and is almost certainly resident (Van Someren 1956).

The Orange Bishop is said to be locally migratory (Mackworth-Praed & Grant 1955, 1973); according to von Boetticher (1952) it does not follow regular routes in East Africa, but reappears from the interior at the start of the rainy season. In Darfur Lynes (1924) showed that it was resident, although it is uncertain whether the same birds were present throughout the year.

Local movements are also reported for the Fire-crowned Bishop E. hordeaceus (Verheyen 1953). In the permanent swamps of the Sudan there appear to be small resident populations, but those birds breeding in grassland during the rainy season are classed as "partial migrants" by Lynes (1924). This species leaves the East African breeding areas during the dry season according to Moreau & Moreau (1938)

East African populations of the Yellow-backed Widow E. macrourus are resident (von Boetticher 1952), but the large roosting flocks may break up into small groups which wander erratically, if the swamps dry out or the reeds are burnt (Reichenow 1904). A.J. Manson has caught a few birds breeding near Salisbury, but they are not present every year.

Moreau & Moreau (1938) reported that the Black-bellied Bishops E. nigroventris left the breeding areas during the dry season for an unknown destination.

It seems that, with a few possible exceptions such as the Long-tailed Widow, the Euplectes species generally move about during the dry season, and may be absent from their breeding areas for varying periods. Only a part of the population may be involved at any one time, and the extent of the movements probably varies from year to year under the influence of drought and fire. There is as yet no evidence that these movements follow any regular routes. The distances covered are also unknown, but recently Jones & Ward (1977) have measured lipid content in Orange Bishops and Golden Bishops in Nigeria when the birds are moving south at the start of the rainy season, and they suggest that the Orange Bishop has reserves for a flight of some 600 km.

Sexual dimorphism

In many birds the degree of sexual dimorphism is related to the mating system of the species. Thus from the plumage characters of the Long-tailed Widow, Darwin (1871) correctly inferred that this species was likely to be polygynous. Even in monogamous species, small sexual differences in body size may be important in maintaining particular dominance relationships between the members of the pair (Selander 1972).

The colourful nuptial plumages of the Euplectes species must play a role in mate selection by the female and species isolation. However, when the male enters eclipse plumage after the post-nuptial moult, it remains considerably larger than the female. Such dimorphism in body size may also have important effects on the ecology of the species.

In many species size dimorphism is associated with differences between the sexes in feeding behaviour (reviewed by Selander 1972). Female birds of prey are often larger than the males, and it has been suggested that they take different prey. Balgooyen (1976), however, proposes that the size differences in this group are related to the conservation of energy; size dimorphism is most marked when there is division of labour during breeding, with the female remaining at the nest and being fed by the male. A smaller male needs less energy for the capture and transport of food, so that a larger proportion of the food collected can be given to the female. The feeding ecology of the Euplectes species has yet to be studied in detail, but both these explanations may prove relevant. If a female is rearing young alone, smaller size may be selected for in the female, so that she can devote a larger proportion of her foraging time to collecting food for the nestlings.

From a study of the Geospizinae, Downhower (1976) has produced a hypothesis that sexual dimorphism in body size influences the timing of reproduction in fluctuating and seasonal environments. Assuming that breeding is triggered by a variable environmental factor, and that the energy for egg production is derived from the food available and not from stored reserves, then smaller birds should be able to accumulate the necessary energy more rapidly than larger ones. Thus they will be able to breed over a longer period, and in a fluctuating environment may have more opportunities. This model suggests that the energetics of reproduction in the genus Euplectes would be a rewarding field for study.

In the present case wing-length and weight were the only physical characters which were recorded, primarily as a means of sexing the birds. It has been demonstrated for many species of birds that the males have significantly longer wings than the females, but in some cases such as the Tree Sparrow Passer montanus the difference is not sufficient to permit sexing of individual birds (Clausing 1976). Niemeyer (1969a) estimated that Willow Warblers Phylloscopus trochilus could be sexed on the basis of wing-length alone with an error of no more than 5%. Wilson (1973) has described the sexing of Red Bishops and Cape Bishops on the basis of wing-length, and the present study has confirmed that this is a useful method in the field. However, it must be emphasized that individual workers may obtain significantly different measurements on the same birds. For this reason the use of probability paper is most valuable, since it enables one to assess the degree of sexual dimorphism present in the population being studied, and provides estimates of the mean measurements of the components of the population. Comparison with other methods of sexing as described above has shown that the values obtained from probability paper are very accurate, considering that the original wing-lengths were only correct to the nearest millimetre.

Many passerines also show significant differences in wing-length between adult and juvenile birds. This is found both in species with a partial post-juvenile moult where the juvenile wing feathers are retained, such as the Siskin *Carduelis spinus* (Abs 1964) and the Blue Tit *Parus caeruleus* (Stewart 1963), and in species which replace their wing feathers during the post-juvenile moult such as the House Sparrow *Passer domesticus* (Stewart 1963; Folk & Novotný 1970). Where a marked degree of sexual dimorphism is present, the subadult and adult males differ much more than subadult and adult females, as in the Boat-tailed Grackle *Quiscalus mexicanus* (Selander 1958). Verheyen (1956) has shown that in the Long-tailed Widow there are marked differences between the wing-lengths of subadults and adults of both sexes, and he suggests that the longest wings, and the longest tails of males in nuptial plumage, belong to the oldest birds.

Among the *Euplectes* species described here, sexual dimorphism is not as great as in the Long-tailed Widow, and even using probability paper failed to show up any differences between adult and subadult females once they had completed the post-juvenile moult. However, there were obvious differences in the wing-lengths of adult and subadult males in the Red-collared, Red-shouldered and White-winged Widows, and it is probable that there is a slight difference in the case of the Red Bishop. As will be discussed further in the next chapter, there is some evidence that the oldest male Red-shouldered Widows have the longest wings.

The sex ratio

Darwin (1871) was the first to pay serious attention to the sex ratio in animals, and he evidently appreciated what large numbers are required to arrive at an unbiased estimate, since he writes of cattle "I have received returns from nine gentlemen of 982 births, too few to be trusted; ...". He described a balanced sex ratio (487 ♂♂: 514 ♀♀) in domestic chickens, and noted that the general impression of naturalists and bird catchers was that the males were more numerous than the females in wild birds.

In 1939 Mayr again drew attention to the importance of accurate information on the sex ratios of wild birds.

He distinguished three categories of sex ratio: the primary ratio at the time of fertilisation, the secondary ratio at the time of birth, and the tertiary sex ratio during adult life. Where the complete clutch of eggs hatches, the secondary sex ratio is equal to the primary ratio. Mayr (1939) discusses the sources of error in establishing the true sex ratios of birds and notes that large samples are required, but then cites a number of small samples (e.g. 20 ♀♀:7 ♂♂ in the Sparrowhawk Accipiter nisus) which provide little support for his surprising conclusion that the primary sex ratio in birds is frequently very unequal. Lack (1954) had few new data at his disposal, and he concluded that in birds the sex ratio is normally about equal in the young, but that there is often a small excess of males among the adults. More recently Trivers (1972) noted that in most animal groups when the sex ratio is unbalanced, there are more females than males, except for birds, in which males tend to predominate.

There are still very few data on the secondary sex ratios of birds. The largest samples come from Landauer's (1957) analysis of clutches of domestic fowls in which all the eggs hatched. He found no significant deviation from the expected 1:1 ratio. McIlhenny (1940) claimed to have found an excess of females in nestlings of the Boat-tailed Grackle and an excess of males in nestlings of the Red-winged Blackbird Agelaius phoeniceus. However, his method of sexing was apparently based on size differences between the nestlings, and Selander (1960) found no evidence for an unbalanced sex ratio in nestlings of the Boat-tailed Grackle which were sexed by dissection, and cited evidence that the same was true of the Red-winged Blackbird. Kessel (1957) also found a balanced sex ratio in nestlings of the European Starling Sturnus vulgaris, and this has been demonstrated for the Red-billed Quelea (Ward 1965c) and the Cape Weaver Ploceus capensis (Elliott 1973). Havlín (1975) quotes studies of the House Sparrow which showed a slight excess of males amongst the nestlings, but the differences are not statistically significant. There is no evidence for any bird species that the secondary sex ratio differs significantly from the predicted 1:1 ratio.

A study of the California Quail Lophortyx californica by Emlen (1940) provided the first detailed information on the sex and age structure of a bird population. Emlen found an overall sex ratio of 112 ♂♂:100 ♀♀, but showed that the sex ratio of immature birds was 1:1 and males predominated only in the adult population. Females suffered a higher mortality, especially during the summer breeding season. This situation appears to apply to many other game birds, such as the Bob-white Quail Colinus virginianus (Leopold 1945) and the European Partridge Perdix perdix (Pullianen 1968). The sex ratios of ducks in the northern hemisphere also show an excess of males (Aldrich 1973). Once again the sex ratios of juveniles seem to be balanced, but during the breeding season there is a high female mortality. This is partly compensated for by higher losses of males during the hunting season.

Fry (1972) has suggested a correlation between nesting dispersion and sex ratio in the bee-eaters, since there appears to be an excess of males in the colonial species, but not in solitary breeders. In the Cape Shelduck Tadorna cana Siegfried (1976) has demonstrated an excess of females, in contrast to the usual trend in waterfowl described above. This may be related to the "reversed" sexual dimorphism and courtship behaviour found in this group of ducks, where the females are more brightly coloured, and actively court the males. A most unusual mating system is found in the Tasmanian Native Hen Tribonyx mortierii (Maynard Smith & Ridpath 1972). In the population studied there was an excess of males amongst the immature birds, so that many of the breeding groups comprised two males and one female - most commonly two brothers and an unrelated female. It is suggested that this system has evolved due to the unbalanced sex ratio, but the cause of the excess of males is unknown.

Several passerine birds such as the European Starling (Kessel 1957) have balanced sex ratios in the first year, but thereafter males predominate. In the Brown-headed Cowbird Molothrus ater Hill (1976) found a 1:1 sex ratio in some four thousand first-year birds, while Darley (1971) had described an adult population of this species containing 96 ♂♂:47 ♀♀. Darley (1971) estimated from his ringing returns that females had a higher mortality than males once they started breeding. Ward (1965c) described seasonal changes in the sex ratio of the Red-billed Quelea, leading to a marked excess of males by the end of the dry season, despite balanced sex ratios in nestlings and fledglings.

Table 18 lists the sex ratios of some passerines for which the sample size is greater than 500 birds, and the collecting seems to have been unbiased. Many ringing stations have recorded the sex ratios of migrants on passage, but these are not considered reliable, since there is good evidence of differences in the migratory behaviour of the two sexes for many species. Thus Niemeyer (1969b) analysed the captures of the Willow Warbler on Heligoland, and found that during the autumn migration the sex ratio of both first-year and adult birds was 1:1, but there was a highly significant excess of females during the return migration in spring. He suggests that this may be due to males not stopping over on Heligoland in the spring. Similarly spring catches of the Redstart Phoenicurus phoenicurus on Heligoland contain more females than males (Vauk & Schröder 1972).

There is a large excess of males for all the species in Table 18, except the Red-collared Widow and the Boat-tailed Grackle. The Boat-tailed Grackle is the only species with significantly more females than males. McIlhenny's (1940) data are taken from ringing records. More recently Selander (1965) has also provided evidence for an excess of females in the Boat-tailed Grackle, although his methods of counts at roosts visually and by means of photographs of the flocks seem less reliable. Selander's (1965) data do suggest that the sexes may flock separately in this species, and the possibility of bias in the trapping should be checked.

TABLE 18

The sex ratio of some passerine birds

Species	Sample size	% ♂♂	Author
Carduelis chloris	837	64,0	Havlín 1975
Fringilla coelebs	517	63,1	Havlín 1975
Parus major	1418	53,4	Havlín 1975
Sturnus vulgaris	1225	60,4	Coulson 1960
Sturnus vulgaris	2522	68,0	in Coulson 1960
Sturnus vulgaris	1359	57,8	Kessel 1957
Sitta pygmaea	710	63,5	Norris 1970
Passerina cyanea	2376	59,4	Johnston 1970
Agelaius phoeniceus	6480	84,4	McIlhenny 1940
Agelaius phoeniceus	68248	75,2	Burtt & Giltz 1970
Quiscalus mexicanus	5333	33,1	McIlhenny 1940
Passer domesticus	20931	53,2	Piechocki 1954
Passer domesticus	1494	54,7	Folk & Novotný 1970
Passer domesticus	2877	57,4	in Folk & Novotný 197
Ploceus capensis	3537	54,2	Elliott 1973
Quelea quelea	2602	60,8	Ward 1965c
Euplectes ardens	1512	49,0	this study
Euplectes axillaris	830	53,8	this study
Euplectes orix	4957	53,1	this study

It has often been assumed that in polygynous species there is an excess of females in the population, but Verner (1964) and other workers have demonstrated that unmated territorial males may be present while other birds have several mates (see further discussion in Chapter 4). The breeding sex ratios will certainly be unbalanced, but the existence of an appreciable number of non-breeding males has often been overlooked. Mayr (1939) wrote of the Orange Bishop and the Fire-crowned Bishop "...it is well known that in these species the females outnumber the males at least 2:1". This was based on the impressions of early observers such as Gurney (1860, 1861), who noted that in the flocks the males in nuptial plumage were greatly outnumbered by brown-plumaged birds. Although Davies (1910) had shot a flock of Long-tailed Widows and reported that many of the "browns" were immature males, the myth of the male accompanied by a large harem has been perpetuated by many recent authors (e.g. Mackworth-Praed & Grant 1962). Even Lack (1968) has fallen into the same trap, concluding from Moreau & Moreau's (1938) figures of one male to six browns in the flocks that there is definitely a surplus of females in the <u>Euplectes</u> species.

The data presented here show that there is no surplus of females in at least three of the species, and a small excess of males is probably usual. The sex ratio of nestlings has not been examined, but the suggestion of Priest (1936) that the Red Bishop is polygynous because more females than males are hatched can safely be dismissed. Seasonal variations in the sex ratio, as were found here, occur in a number of other species (e.g. Burtt & Giltz 1970; Havlín 1975; Ward 1965c). It appears that the numbers of adult and subadult males in the population are generally about equal, so that the breeding sex ratio is 2 ♀♀:1 ♂. However, in Natal adult males greatly outnumbered the subadults in both the Red Bishop and the Red-collared Widow. This may be because large numbers of adult males return to the roost at the start of the breeding season, then disperse more widely as the territories in the immediate vicinity are occupied. Many Red Bishops may reappear at the roost at the start of the moult.

An imbalance in the sex ratio of a species implies differences in the mortality rates of the sexes. This may occur at any stage of the life cycle. For many species there is evidence that females suffer a higher mortality than males during their first breeding season. Yom-Tov & Ollason (1976) suggest that intersexual competition for food in sexually dimorphic species may result in an imbalanced sex ratio. However, both these topics belong to the next section. In the Great Tit Parus major more males than females fledge when conditions are unfavourable for the nestlings (Dhondt 1970). This species is monogamous, but in polygynous species where there is a high degree of competition between the males for mates, males in poor condition will stand little chance of reproducing successfully. Thus Trivers & Willard (1973) note that a male in good condition at the end of the period cf parental care, or "parental investment", will be able to produce more young than a female, while if they are both in poor condition the female will produce more young, since all surviving females are likely to breed each year. Therefore selection should favour parental ability to adjust the sex ratio of their offspring according to prevailing conditions.

Howe (1976) has tested this hypothesis in a study of the Common Grackle Quiscalus quiscula, a polygynous icterid in which incubation starts before the clutch is complete; this favours the young hatching earliest - if food supplies are scarce, the last-hatched chicks will die. This results in a nestling sex ratio skewed to favour females. If the eggs are removed on laying and temporarily replaced by models, it is possible to ensure that incubation starts only when the clutch is complete. In this case the nestling sex ratio is balanced. Howe proposes that the sex ratio of the nestlings will vary as a function of the physiological condition of the females and the ecological conditions during the breeding season.

These results suggest that Trivers & Willard's (1973) model may apply to other polygynous species, provided that there is a relationship between laying sequence, egg size and nestling sex as is the case in the Common Grackle. The most likely alternative explanation would be a higher female mortality during the breeding season for species such as the Red-winged Blackbird and the Red Bishop, where there is a surplus of males. Howe's (1976) findings may provide an explanation for the excess of females in the Boat-tailed Grackle.

The role of social dominance

In bird species whose males are socially dominant over the females throughout the year, the population structure may be markedly affected. Thus Kluyver (1957) showed that in the Great Tit the birds roost singly in nest boxes during the winter, and the increased survival of males seems to be correlated with their dominance over the females, which results in more males acquiring nest boxes to roost in.

Crook & Butterfield (1970) have examined the social status of the sexes in captive Red-billed Quelea, in relation to Ward's (1965c) findings on the sex ratio of wild populations. Crook & Butterfield (1970) found that luteinizing hormone rather than testosterone determined the success of both sexes in aggressive encounters, as recorded in individual distance infringements among captive birds. Subsequently, however, Dunbar & Crook (1975) demonstrated that, among male Red-billed Queleas, dominance over food does not correlate with dominance in individual distance infringements. Nevertheless females are always subordinate to males in competition for food. They suggest that in the wild females could be displaced from food items by the males and forced to feed on the periphery of the flock where there is less food, and where they are secondarily exposed to heavier predation. This would explain the increasing imbalance in sex ratio in favour of the males during the dry season period of food shortage.

Luteinizing hormone has not been tested on the

Euplectes species, but even the present data suggest that dominance is not solely due to testosterone. These species live in less arid environments than the Red-billed Quelea, so that food shortages are likely to be less acute, but dominance of males over females in competition for food could account for the small observed excess of males in the populations studied.

It is also possible that the dominance of the adult birds may inhibit reproductive development in the subadults, and so result in deferred sexual maturity. First-year birds of the monogamous Eastern Rosella *Platycercus eximius* show a very similar gonadal development to that of adults, and Smith & Brereton (1976) conclude that the failure of first-year birds to breed in this species is behavioural rather than physiological. An experimental study of the polygynous Red-winged Blackbird also indicates that the slower physiological development of first-year males is not regulated by the presence of adult males (Wiley & Hartnett 1976).

Butler (1905) reported that a group of hand-reared Orange Bishops first came into nuptial plumage at the age of eight months, although their plumage was much duller than that of the adults. This may, however, have been due to an unusual diet in captivity. Duncan (1906) states that captive male Red Bishops were several years old before they assumed full nuptial plumage. Nevertheless birds in brown plumage displayed sexual behaviour during the breeding season. Lynes (1924) described the plumage sequences of the Orange Bishop, and confirmed that males moult into nuptial plumage only in their second summer. Bates (1927) decided that this was also the case in the Fire-crowned Bishop and the Yellow-backed Widow.

From her analysis of recaptures of the Red Bishop, Rowan (1964) suggested that some males may breed in their first year, and others not until the third year after hatching. The recaptures in the present study indicate that in the Red Bishop, Red-collared Widow and Red-shouldered Widow males normally come into nuptial plumage in the second summer after hatching. Lack (1968) accepts that deferred maturity is general in male *Euplectes*, whereas females breed in their first year. While this is essential to an explanation of the observed breeding sex ratios, there is no good evidence from field studies that females do breed in the first summer after hatching - Lynes (1924) thought that both sexes showed deferred maturity. The only observations on birds of known age have been made on captive specimens - Schifter (1967) records that a male Red Bishop in Schönbrunn Zoo mated with a daughter from the previous season. The problem of deferred maturity in polygynous species will be discussed again in the following chapters.

Survival and mortality

Recently Botkin & Miller (1974) have challenged the general assumption that adult birds have a constant mortality rate, since this results in large discrepancies between observed longevity and predicted longevity in many species. A study of the Kittiwake *Rissa tridactyla* by Coulson & Wooller (1976) supports their conclusion that the mortality rates of wild birds increase with age. However, for species with a potential longevity of less than 25 years and a calculated mortality rate of more than 30%, the old age-independent models are reasonably accurate. This applies to all the passerine species which will be considered here.

A European Starling aged 20 years (Botkin & Miller 1974) is probably one of the longest-lived passerines recorded in field studies. For most other species 10-12 years appears to be the maximum age attained by wild birds. The oldest Red Bishop recovered to date was about nine years old, and the other longevity records for the genus are based on captive birds. The 20-year-old Golden Bishop and Fire-crowned Bishop cited by Adlersparre (1938) are open to question. However, a male Long-tailed Widow lived for 18 years in the Schönbrunn Zoo (Schifter 1970), and aviculturalists record an age of 18 years 10 months for a Cape Bishop (Donnelly 1965) and 15 years for a Golden Bishop (Musil 1969). Both the Long-tailed Widow and the

Cape Bishop were flightless in their last years, which suggests that 15 years may represent the maximum age attainable under natural conditions.

Mortality rates have been calculated for a number of species, but it should be noted that the method used is likely to over-estimate the true mortality rate, and that many of the figures quoted are based on relatively small samples. The lowest mortality rate recorded for any passerine is 11% for the White-bearded Manakin (Snow 1962). This appears to be quite exceptional, since the next lowest values are around 30%, as in some American woodland passerines (Savidge & Davis 1974). The average annual mortality of the Blackbird Turdus merula in Britain is about 44% (Coulson 1961), and for the European Starling about 53% (Coulson 1960). At the other end of the scale, a mortality rate of 70% has been reported for the Blue Tit (Snow 1956) and the Red-billed Firefinch (Morel 1969). For some South African estrildids Skead (1975) also found mortality rates of 60-70% in a more limited study.

Few data are available for South African passerines. In the Cape Sparrow Passer melanurus the mortality rate appears to be around 50% in the males (Rowan 1964, 1966), and also in male Masked Weavers Ploceus velatus (Rowan 1964). The rates calculated for the Euplectes species in this study are close to 50%, which seems to be common in medium- and small-sized passerines, although the rate of 25-39% estimated by Rowan (1964) for male Red Bishops is much lower.

Juvenile mortality rates are usually considerably higher than those calculated from birds caught as adults, as discussed by Lack (1954). In both the Blue Tit (Snow 1956) and the Blackbird (Coulson 1961) the mortality of juveniles is higher only in the first months after fledging and soon equals that of the adults. The available data on the Red Bishop suggest that the mortality rate of juveniles is much higher than that of the adults, but it is not possible to determine at what age this mortality occurs.

Coulson (1960) was able to analyse some 7000 recoveries of the European Starling, and could show that the cause of death affected the estimates of annual mortality. The mortality rate also varied in different years from 40% to 66%. Similarly the mortality rate in the Blackbird varied from 34% to 69% (Coulson 1961). The mortality rate may also vary geographically (Coulson 1960, 1961), and in the Blue Tit Snow (1956) showed that the mortality rate of this species in Europe was correlated with its clutch size in different areas.

Another source of variation may be differential mortality of the two sexes. Females appear to suffer a higher mortality in numerous non-passerines, as discussed earlier, but in passerines the picture is complicated by the fact that in several species such as the Song Sparrow Melospiza melodia (Nice 1937) females may be less resident than the males. In the European Starling Coulson (1960) found evidence for a female mortality of 70% in the first year while males only suffered a mortality of 39% - he suggests that this is probably because more first-year females than males breed. Lack (1968) argues that adult male Euplectes incur a higher mortality while in their conspicuous nuptial plumage, and that first-year males do not breed because it is dangerous for them to do so. However, there is no evidence for this, and the observed sex ratios suggest a higher mortality amongst the females, perhaps affecting birds breeding for the first time.

Lack (1954, 1966) has maintained that starvation is the main source of mortality in populations of wild birds, but except for the work of Ward (1965a) on the Red-billed Quelea, there is little direct evidence from field studies. There is no information on the incidence of starvation in the Euplectes species, and large-scale outbreaks of disease have not been recorded.

Predation is now usually assigned a minor role in the control of natural populations. Nest predators will be dealt with in Chapter 3; the adult birds have few potential enemies. The vast colonies and drinking assemblages of the Red-billed Quelea attract a wide variety of avian predators, of which the raptors, herons and storks will also take adult birds (Leuthold & Leuthold 1972; Thiollay 1975). Of the species mentioned by these authors, only the Lanner Falcon *Falco biarmicus* was encountered in the present study. A pair often hunted over Malton, and although they were never seen with identifiable prey, the Red Bishops showed intense alarm when the Lanners passed over the colony. Lanners probably take *Euplectes* on occasion, but they are too rare to be an important threat.

The most important predators of adult birds are probably owls. The pellets of the Barn Owl *Tyto alba* may contain up to 30% bird remains, and *Euplectes* skulls have been identified in several areas (Grindley *et al*. 1973; Vernon 1972). Rowan (1964) lists the Red Bishop as one of the species where rings were recovered from Barn Owl pellets, and Vernon (1972) states that the Barn Owl often hunts over the reed-bed roosts. Vernon (1972) also found bird remains, some apparently of ploceids, in the pellets of Grass Owls *Tyto capensis*, and C. Lloyd (pers. comm.) has found a small proportion of birds in the pellets of this species in Natal, usually at times when the density of small mammals was low in his study area.

No Barn Owls were seen in my study areas, and I have only a single sight record of the Grass Owl for Malton. However, a pair of Marsh Owls *Asio capensis* was resident in the area of the roost at Cedara, and they were often seen while I was ringing there. In winter the birds were often released after dark, and during 1977 a Marsh Owl unexpectedly perched close at hand on three evenings and caught some birds in the air as they were released. Thus Marsh Owls may be a threat to late-comers to the roosts, although the bulk of the roosting population is settled before the owls appear. Vernon (1971) records Marsh Owl pellets from South West Africa which contained predominantly bird remains, apparently unidentified small seed-eaters.

Pitman (1958) has reviewed the snake predators of birds in Africa, but snakes are rarely a threat to adult ploceids, nor are mammalian predators. Struggling birds in a mist-net are very vulnerable to small mammalian predators, and in the Cape I had to trap five Cape Grey

Mongoose Herpestes pulverulentus at one ringing site. In the Orange Free State White Storks Ciconia ciconia tried to swallow birds caught in a mist-net (Craig & Burman 1973), and at Cedara I caught a Fiscal Shrike Lanius collaris and an African Marsh Harrier Circus ranivorus, which had struck at birds in the net and become entangled themselves! Mist-nets must be watched constantly lest they encourage predation.

Summary

Variations in the catch size of the Red Bishop, Red-collared Widow and Red-shouldered Widow suggest seasonal movements in the populations studied. There is evidence for seasonal movements in most Euplectes species. The wing-lengths of these three species show clear sexual dimorphism, and enable birds to be sexed accurately throughout the year. The sex ratios of the Red Bishop and Red-shouldered Widow show a small but significant excess of males, while the sex ratio of the Red-collared Widow seems to be 1:1. This may be indirectly related to male dominance over females in these species. The mortality rates of the Red Bishop and Red-collared Widow were calculated from the available data; they are less than 50%. These results are discussed in relation to the findings on other passerine species.

CHAPTER TWO

The annual cycle of the Red Bishop and related species

Introduction

All bird species experience some degree of seasonal change in their environment. Consequently it is important that the major physiological events in the life of the bird should be timed to coincide with favourable environmental conditions. The three periods which make the greatest demands on the energy reserves are breeding, moult and migration, and their relationship to each other determines the form of the annual cycle in any bird species.

Immelmann (1963, 1971) has reviewed the types of annual cycles which have been found in birds. The intervals between the initiations of successive breeding attempts by individuals range from six months to more than two years in different species, but the majority of species studied to date have a cycle of around 12 months.

The *Euplectes* species in Natal have a clearly defined annual cycle with a restricted breeding season. In spring the males commence the pre-nuptial moult and in both sexes the gonads enlarge in preparation for the summer breeding season. Full breeding condition is maintained for about four months, after which the gonads regress and all birds enter the post-nuptial moult. The males exchange their distinctive nuptial plumage for an eclipse plumage closely resembling that of the female. Both sexes replace the body plumage, wing coverts, remiges and rectrices, while the gonads become inactive. During the winter dry season the flocks may move about, as discussed in the previous chapter, reappearing in the following spring as the pre-nuptial moult begins again.

In this chapter the pre-nuptial moult and gonad cycle of the males, the post-nuptial moult, and the weight changes during the year are described for the Red Bishop *Euplectes orix*, the Red-collared Widow *E. ardens* and the Red-shouldered Widow *E. axillaris*. I have incorporated information kindly supplied by A.J. Manson, who has done extensive ringing of

Red Bishops and Red-collared Widows in Rhodesia. Some information on feeding is also included. The breeding season of the Red Bishop is discussed in detail in the next chapter.

Methods

Ringing operations at Cedara have been described in Chapter 1. Each bird caught was weighed to the nearest gram on a Pesola spring balance, which had been checked against the Mettler top-loading balance in the Department of Zoology, University of Natal (the results differed by no more than 0,3 gm). Manson (MS.) used an Ohaus triple-beam balance to weigh the Rhodesian birds.

We both used the "moult score" method described by Newton (1966) to record primary moult. An old feather is assigned a score of 0; a feather still in pin a score of 1; a feather no longer in pin but less than 1/3 grown a score of 2; a feather 1/3-2/3 grown a score of 3; a feather more than 2/3 grown a score of 4; and a new feather a score of 5. The moult score was recorded for the right wing only, unless there were marked differences between the two wings.

Recently Seel (1976) has criticised the moult score method, pointing out that it is not a proper measurement and should not be treated as such. I also found that comparing scores between different species or between different months was very misleading, and used the outermost feather in moult in each bird to show the course of moult in the population (see Figs. 13, 14 & 15).

For male Red Bishops the condition of the body plumage and the bill colour was recorded according to the system described in the attached paper (Craig 1975). For this species the testis cycle can be followed without taking specimens for histological examination. The same plumage stages were used to describe male Red-collared and Red-shouldered Widows. A small number of specimens of male Red-shouldered Widows was examined by Mendelsohn (1976), who has described the relationship between testis development, nuptial plumage and bill colour in this species. His results will be discussed below. Manson (MS.) recorded the nuptial plumage of male Red Bishops in Rhodesia as a percentage, but did not make any quantitative records of bill colour.

Feeding was not investigated in any detail, since it was not my intention to collect specimens from the population for samples of stomach contents, and a study of feeding in the Red Bishop is in progress at the University of the Orange Free State (M. Louw, pers. comm.). When feeding flocks were sighted in the field, I endeavoured to see what they were feeding on, and take specimens of the grasses. These were kindly identified for me by Professor K. Gordon-Gray of the Department of Botany, University of Natal. In addition Mr. R.K. Brooke generously allowed me to use his field notes on feeding of *Euplectes* spp. in Rhodesia. In this case the grasses had been identified by the Southern Rhodesian Government Herbarium.

Sonderabdruck aus: Journal für Ornithologie 116, Heft 1 (1975)

Aus dem Lehrstuhl für Verhaltensphysiologie der Universität Bielefeld

Hodenreife, Prachtkleid und Schnabelfärbung beim Oryxweber (*Euplectes orix*)

Von Adrian Craig

J. Orn. 116, 1975: S. 87—93

Aus dem Lehrstuhl für Verhaltensphysiologie der Universität Bielefeld.

Hodenreife, Prachtkleid und Schnabelfärbung beim Oryxweber (*Euplectes orix*)

Von Adrian Craig

Einleitung

Die Männchen der afrikanischen Webervogelgattung *Euplectes* mausern einmal im Jahr in das farbige Prachtkleid, das nur während der Fortpflanzungszeit getragen wird (BROOKE 1964). Diese Mauser wird beim Oryxweber und bei einigen anderen Arten von einer Umfärbung des Schnabels begleitet. Die Untersuchungen von WITSCHI (1936, 1938, 1961) haben gezeigt, daß beim verwandten Feuerweber *Euplectes franciscanus* das Prachtkleid von einem Hormon der Hypophyse (L. H.) abhängig ist, während Androgene, die von aktiven Hoden produziert werden, für die Schnabelumfärbung verantwortlich sind.

Ein ähnlicher Zusammenhang zwischen den männlichen Geschlechtshormonen und der Schnabelfarbe ist für *Ploceus philippinus* (SAXENA & THAPLIYAL 1962), *Passer domesticus* (LOFTS, MURTON & THEARLE 1973), *Fringilla coelebs* (NOWIKOW 1939) und *Spinus tristis* (MUNDINGER 1972) beschrieben worden. Auch wenn beide Geschlechter eine Schnabelumfärbung zeigen, wie bei *Sturnus vulgaris* (WYDOSKI 1964) und *Fringilla montifringilla* (NOWIKOW 1939) sind männliche Hormone für deren Regulation verantwortlich.

Obwohl die Höhe der Androgenproduktion nicht aus der Schnabelfarbe geschlossen werden kann (siehe Diskussion in LOFTS, MURTON & THEARLE 1973), weisen einige Autoren darauf hin, daß der Grad der Färbung sich mit dem Hodenzyklus korrelieren läßt (HAASE 1973; MUNDINGER 1972; VAUGIEN 1952). Nachfolgend soll der Zusammenhang zwischen den Entwicklungsstadien der Hoden, dem Grad der Schwarzfärbung des Schnabels und der Entwicklung des Prachtkleides bei *Euplextes orix* beschrieben werden.

Material und Methode

Von August bis Oktober 1972 und von Mai bis August 1973 wurden insgesamt 47 ♂ an einem Schlafplatz in der Nähe von Kapstadt, Südafrika (34,01° S / 18,45° E) gesammelt. Hier legen im Juli die ersten Vögel das Prachtkleid an; die Brutaktivität erreicht im September-Oktober ihren Höhepunkt. Aus diesem Grund kann man während des obgenannten Zeitabschnittes Vögel in allen Stadien des Fortpflanzungszyklus antreffen.

Die Köpfe der ♂ wurden zu Bälgen präpariert, die Hoden in Bouinscher Flüssigkeit fixiert. Danach wurden sie in Paraffin eingebettet und 6 µm H. E. gefärbte Schnitte hergestellt.

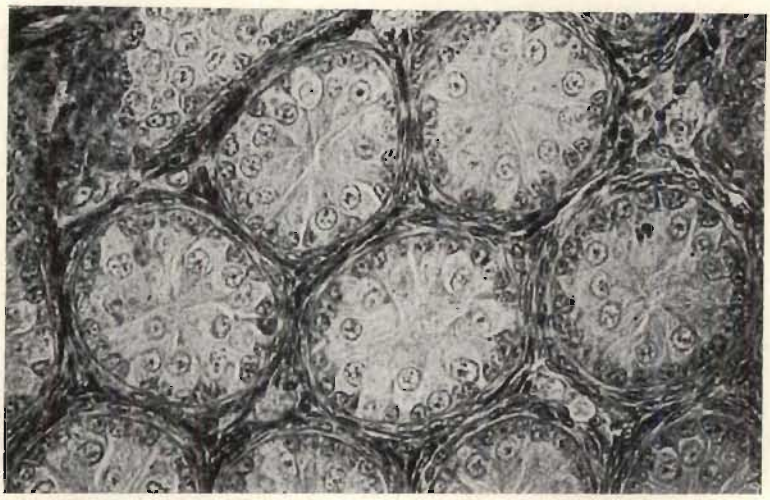


Abb. 1. Reifestadium 2 bei ♂ (8); Gefiederstadium 1 und Schnabelfarbewert 2. (× 450).

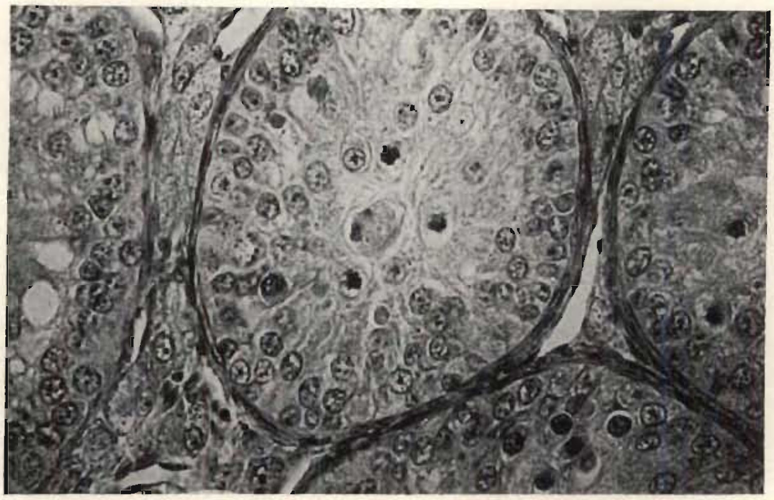


Abb. 2. Reifestadium 4 bei ♂ (18); Gefiederstadium 1 und Schnabelfarbewert 3. (× 450).

Das Reifestadium der Hoden wurde nach der Einteilung von BLANCHARD(1941) bestimmt; eine weitere Beschreibung der dort unterschiedenen Stadien 1 bis 7 findet sich bei SOSSINKA (1970). Abb. 1 bis 3 zeigen typische Stadien für *Euplectes orix*.

Unter Berücksichtigung der individuellen Variation wurde das Körpergefieder in fünf Stadien eingeteilt:

Stadium 1: Ruhekleid; ausschließlich braune Federn.

Stadium 2: erste rote und schwarze Federn des Prachtkleides sichtbar, die jedoch weniger als $^1/_4$ des Körpers bedecken.

Stadium 3: Prachtkleid über $^1/_4$ bis $^3/_4$ der Körperoberfläche.

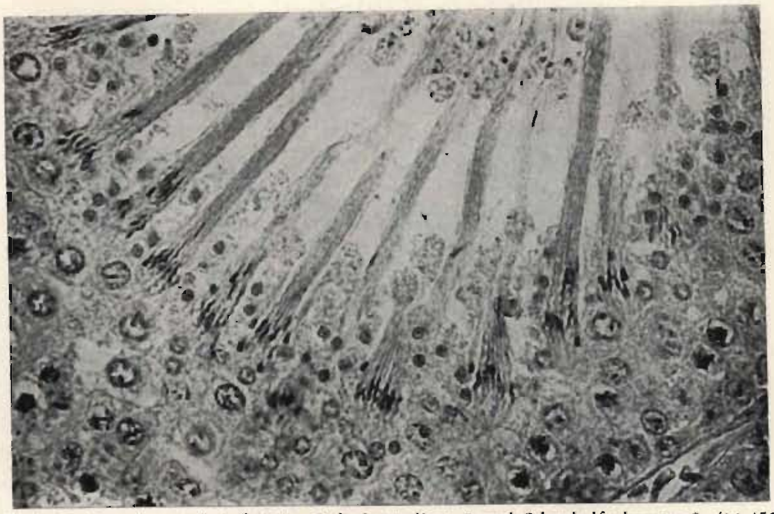


Abb. 3. Reifestadium 7 bei ♂ (26); Gefiederstadium 5 und Schnabelfarbewert 8. (× 450).

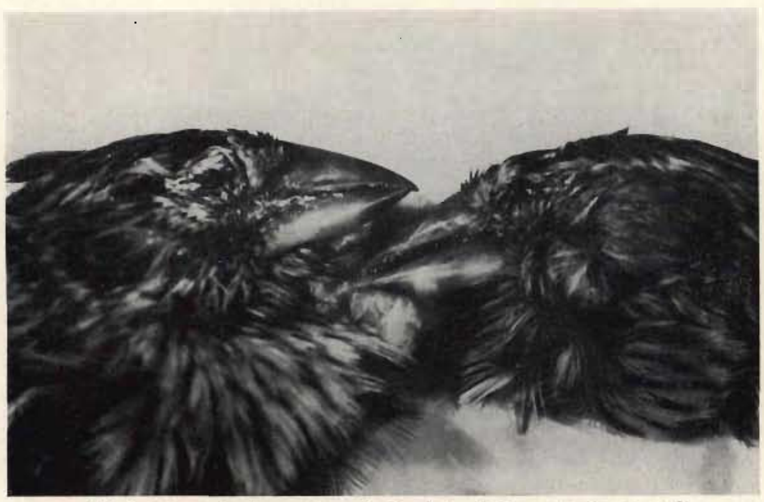


Abb. 4. Schnabelfarbewert 2; links Kopf des ♂ (8), rechts der eines ♀.

Stadium 4: Prachtkleid über mehr als 3/4 der Körperoberfläche, nur noch einzelne braune Federn sichtbar.

Stadium 5: vollendetes Prachtkleid; keine braunen Federn.

Für die Schnabelumfärbung konnten — obwohl Messungen von einem Genauigkeitsgrad wie bei Mundinger (1972) nicht durchführbar waren — die folgenden vier Stadien unterschieden werden:

Stadium 1: Schnabel braun; nicht von dem des ♀ zu unterscheiden (Abb. 4).

Stadium 2: vereinzelte Stellen von Melaninablagerungen erkennbar.

Stadium 3: Schnabel überwiegend schwarz gefärbt.

Stadium 4: Schnabel völlig schwarz (Abb. 5).

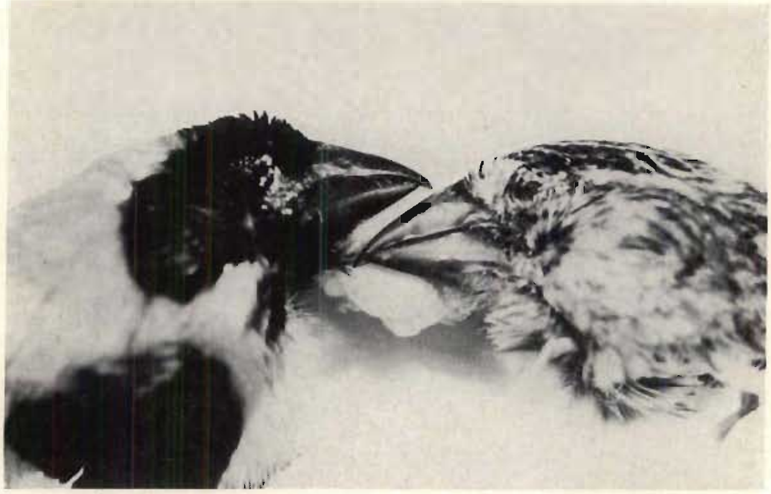


Abb. 5. Schnabelfarbewert 8 im Vergleich zu 2; links Kopf des ♂ (26), rechts der eines ♀.

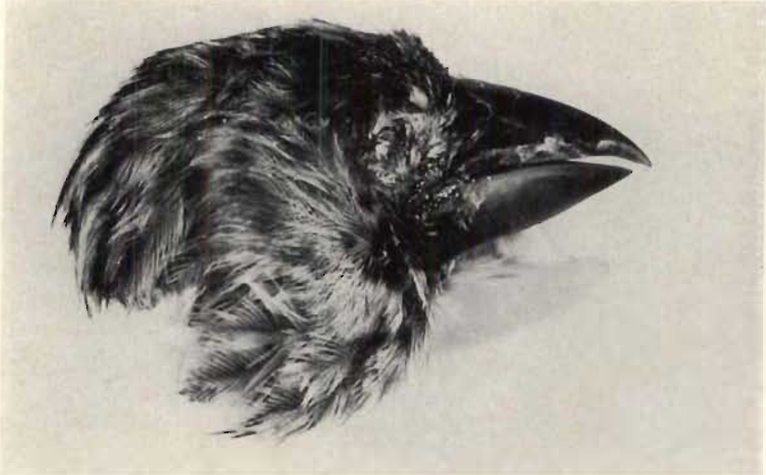


Abb. 6. Kopf des ♂ (12) mit Schnabelfarbewert 7; Reifestadium 7, aber Gefiederstadium 1.

Weil sich Ober- und Unterschnabel unterschiedlich durchfärben, wurden sie einzeln ausgewertet; aus diesem Grund gibt es für den gesamten Schnabel Werte von 2 bis 8.

Den Fang der Vögel verdanke ich großenteils den Herren Dr. C. Elliott und Dr. M. Connor. Für ihre Hilfe bei der Auswertung und Vorbereitung des Manuskriptes danke ich Herrn Dr. R. Sossinka und Prof. Dr. K. Immelmann. Mein besonderer Dank gilt Frl. E. Stockmann für die Durchführung der histologischen Arbeiten.

Ergebnisse und Diskussionen

Ein Schnabelfarbewert von 5 oder mehr deutet auf Hoden mit freien Spermien hin, während im Gefiederzustand ein größeres Ausmaß an individueller Variabilität feststellbar ist (Tab.). Abb. 6 zeigt einen Fall, wo der Unterschied zwischen Schnabelfarbe und Gefieder besonders auffallend ist. Auch bei *Passer domesticus* fand STEINBACHER (1952), daß Brutkleid und Schnabelfarbe oft nicht gleich weit entwickelt waren.

Tab. Zahl der ♂, die die angegebene Gefiederstadium-Schnabelfarbe- und Reifestadium werte zeigten.

Reifestadium		2	3	4	5	6	7
Schnabelfarbewert	2	14	6				
	3		2	4	1		
	4						1
	5				1		3
	6						1
	7						3
	8						7
Gefiederstadium	1	14	6	2			1
	2		2	2	1		3
	3				1		1
	4						3
	5						7

Vier ♂, deren Hoden bereits Anzeichen von Degeneration zeigten, wurden in die Auswertung nicht mit einbezogen. Mit der Rückbildung der Hoden wird der Schnabel wieder hell. Zur gleichen Zeit erfolgt auch die Erneuerung der Schwungfedern und die Umfärbung ins Ruhekleid.

Um die Zusammenhänge zwischen den drei Faktoren festzustellen, wurde der Korrelationsfaktor „r" für das Verhältnis Reifestadium: Schnabelfarbe ($r = 0{,}86$), Schnabelfarbe: Gefieder ($r = 0{,}77$) und Reifestadium: Gefieder ($r = 0{,}74$) berechnet. In allen Fällen ergibt sich eine sehr starke positive Korrelation ($p < 0{,}001$) mit keinen signifikanten Unterschieden zwischen den r-Werten.

Für die Kontrolle der Schnabelumfärbung gibt es drei mögliche hormonelle Mechanismen: (1) ausschließlich durch Hormone der Hypophyse; (2) ausschließlich durch Hormone der Keimdrüsen; (3) durch die Mitwirkung der Hormone beider Organe. WITSCHI fand, daß kastrierte ♂ von *Euplectes franciscanus* eine normale Mauser ins Prachtkleid durchführen. Ihre Schnäbel blieben hell gefärbt, wurden jedoch nach Androgenspritzen wieder schwarz. Keine Ergebnisse mit hypophysektomierten Vögeln sind vorhanden und, da in allen bisher ausgeführten Untersuchungen das Vorhandensein der hypophysären Hormone angenommen werden muß (siehe weitere Diskussion in LOFTS, MURTON & THEARLE 1973), ist nur die erste Möglichkeit ausgeschlossen. Trotzdem macht der enge Zusammenhang zwischen Schnabelfarbe und Prachtkleid es sehr wahrscheinlich, daß bei *Euplectes orix* die Mitwirkung von Hormonen der Hypophyse und der Keimdrüsen die Schnabelumfärbung bestimmt.

Das Alter der ♂ ist nicht bekannt, jedoch waren alle mindestens fünf Monate alt, da die vorausgegangene Brutzeit spätestens im Dezember zu Ende war. Das Reifestadium 1 nach BLANCHARD ist wahrscheinlich nur während der Jugendentwicklung zu finden; PAYNE (1969) erwähnt, daß dieses Stadium in mehreren Untersuchungen nicht feststellbar war. Wiederfänge von beringten Vögeln haben gezeigt, daß ♂ von *Euplectes orix* in der Regel erst im zweiten Lebensjahr ins Prachtkleid mausern (ROWAN 1964). PAYNE (1969) fand bei *Agelaius phoeniceus*, einer Icteriden-Art, bei der die ♂ sich ebenfalls im ersten Lebensjahr nicht verpaaren, daß die Hoden trotzdem eine langsame Entwicklung bis zur Spermienproduktion durchmachten. Das Verhalten der ♂ von *Euplectes orix*, die noch nicht im Prachtkleid sind (CRAIG unveröffl.), läßt darauf schließen, daß auch hier in der ersten Brutsaison eine gewisse Hodenentwicklung stattfindet. Jedoch sind weitere Untersuchungen abzuwarten.

CHAPIN (1954) erwähnt, daß sich bei *Euplectes capensis* die Schnabelfarbe während der Mauser ins Prachtkleid veränderte, obwohl die Gonaden noch sehr klein waren und die Brutzeit erst drei Monate später begann. BROOKE (1964) beobachtete, daß sich ♂ von *E. capensis* bereits längere Zeit im Prachtkleid befanden, bevor die ersten Nester und Gelege vorhanden waren. Im Gegensatz dazu zeigen die vorliegenden Untersuchungen, daß die Hodenentwicklung bei *Euplectes orix* den sekundären Geschlechtsmerkmalen deutlich voraus geht und daß die ♂ bereits fortpflanzungsreif zu sein scheinen, ehe die Umfärbung in das Prachtkleid abgeschlossen ist. Revier- und Nestbauverhalten (CRAIG, im Druck) sind jedoch erst voll entwickelt, nachdem die ♂ das volle Prachtkleid angelegt haben. Die Ergebnisse zeigen, daß bei dieser Art regelmäßige Protokolle der Schnabelfarbe freilebender Vögel einen wertvollen Überblick über den Gonadenzyklus vermitteln können.

Zusammenfassung

Die Hodenentwicklung des südafrikanischen Webers *Euplectes orix* wurde histologisch untersucht und zur Entwicklung des Prachtkleides und zur Umfärbung des Schnabels in Beziehung gesetzt. Es zeigte sich, daß alle drei Faktoren miteinander positiv korreliert sind, daß jedoch die Schnabelfarbe am besten geeignet ist, als Indikator für die Fortpflanzungsreife bei freilebenden Populationen dieser Art zu dienen.

Summary

Testis development, nuptial plumage and bill colour in the Red Bishop *Euplectes orix*.

The histological stage of testis development in South African *Euplectes orix* was investigated in relation to the development of nuptial plumage and the change in bill colour. All three factors are strongly correlated with each other, but bill colour seems best suited for use as an indicator of breeding condition in natural populations of this species.

Literatur

BLANCHARD, B. D. (1941): The white-crowned sparrows (*Zonotrichia leucophrys*) of the Pacific seaboard: environment and annual cycle. Univ. Calif. Publ. Zool. 46/1. • BROOKE, R. K. (1966): Nuptial moult, breeding season and clutch size of Rhodesian red bishops *Euplectes orix* and congeners in relation to rainfall. Ostrich Suppl. 6: 223—235. • CHAPIN, J. P. (1954): The birds of the Belgian Congo, Part 4. Bull. Am. Mus. Nat. Hist. 75 B. • CRAIG, A. J. F. K. (in Druck): Reproductive behaviour of the male Red Bishop Bird. •

Testis development, nuptial plumage and bill colour in the Red Bishop

HAASE, E. (1973): Zur Kontrolle von Fortpflanzungszyklen bei Vögeln; Untersuchungen an Bergfinken. J. comp. Physiol. 84: 375—431. • LOFTS, B., R. K. MURTON & R. J. P. THEARLE (1973): The effects of testosterone propionate and gonadotropins on the bill pigmentation and testes of the House Sparrow *(Passer domesticus)*. Gen. Comp. Endocrinol. 21: 202—209. • MUNDINGER, P. C. (1972): Annual testicular cycle and bill colour change in the eastern American goldfinch. Auk 89: 403—419. • NOWIKOW, B. G. (1939): Einfluß der Gonaden auf die Entwicklung der Geschlechtsmerkmale bei *Fringilla montifringilla* (L.). C. R. Ac. Sci. URSS. 25: 550—553. • PAYNE, R. B. (1969): Breeding seasons and reproductive physiology of Tricoloured Blackbirds and Redwinged Blackbirds. Univ. Calif. Publ. Zool. 90. • ROWAN, M. K. (1964): An analysis of the records of a South African ringing station. Ostrich 34: 160—187. • SAXENA, R. N., & J. P. THAPLIYAL (1962): Male hormone and beak pigmentation in the Baya (*Ploceus philippinus*). Proc. 2nd All India Congr. Zool.: 8. • SOSSINKA, R. (1970): Domestikationserscheinungen beim Zebrafinken *Taeniopygia guttata castanotis* (GOULD). Zool. Jb. Syst. 97: 455—521. • STEINBACHER, J. (1952): Jahreszeitliche Veränderungen am Schnabel des Haussperlings (*Passer domesticus* L). Bonn. zool. Beitr. 3: 23—30. • VAUGIEN, L. (1952): Sur l'activité testiculaire, la teinte du bec et la mue du moineau domestique soumis, en hiver, a l'éclairement artificiel continu. Bull. Soc. Zool. France 77: 395—407. • WITSCHI, E. (1936): Effect of gonadotropic and oestrogenic hormones on regenerating feathers of weaver finches (*Pyromelana franciscana*). Proc. Soc. Exp. Biol. Med. 35: 484 bis 489. • WITSCHI, E. (1938): Hormonal control of seasonal phenomena in birds. Proc. IXth Int. Orn. Congr.: 431—435. • WITSCHI, E. (1961): Sex and secondary sexual characters. In: MARSHALL, A. J.: Biology and comparative physiology of birds. Vol. 2, 115—168. Academic Press, London & New York. • WYDOSKI, R. S. (1964): Seasonal changes in the colour of starling bills. Auk 81: 542—550.

Anschrift des Verfassers: Dept. of Zool., University of Natal, P.O. Box 375, Pietermaritzburg 3201, South Africa.

Results

Pre-nuptial moult

In the Red Bishop the pre-nuptial moult affects the body plumage alone, with the wing coverts, remiges and rectrices being retained. At the same time the bill colour changes from horn to black. The first red and black feathers emerge on the head and near the vent, while the last brown feathers are usually on the chest and belly. The plumage and bill colour changes for both years in Natal are shown in Table 19; there was no indication of any difference between the two years. The Rhodesian records also indicate that the pre-nuptial moult takes place at about the same time each year.

Natal birds start to moult in late September, but the first birds in full breeding dress were not caught until November. Recaptures of birds during the pre-nuptial moult suggest that it lasts for four to six weeks, but there may be considerable individual variation. Two birds ringed on the same day in October 1975 with their plumage at stage 2 were recaptured together exactly a month later. One had progressed to plumage stage 5, the other no further than plumage stage 3.

By December all the adult males had completed their moult, and no intermediates between non-breeding dress (subadult males) and full breeding dress were found in December and January. In February, however, numerous birds showed the first signs of breeding plumage, only to enter the post-nuptial moult without completing the plumage change. Recaptures have shown that in the following spring these birds underwent a full pre-nuptial moult at the start of the season, and then bred for the first time.

The Red Bishops in the aviary were caught early in October, when they had just started the pre-nuptial moult. However, the transfer into captivity affected them to the extent that none of them acquired full breeding plumage that year. In the following year they all moulted normally, at about the same time as the wild population, but it is

TABLE 19

The numbers of Natal Red Bishops showing particular bill and plumage scores during the period of nuptial plumage

Plumage score	Bill colour score 2	3	4	5	6	7	8
Sept							
1	15	0	2				
2		2	1				
Oct							
1	44	11	2	3			
2	2	7	1	14	2	1	1
3				3		8	1
4			1				3
Nov							
1	23						
2			2	7	1	4	
3				2		3	6
4							14
5							38
Dec							
1	39						
5							53
Jan							
1	11						
5							15
Feb							
1	15	14	2	2	1		
2		1	3	3	1	2	
3				1			
4							
5						1	68

TABLE 19 (continued)

The numbers of Natal Red Bishops showing particular bill and plumage scores during the period of nuptial plumage

Plumage score	Bill colour score 2	3	4	5	6	7	8
Mar							
1	8	4	4	2		4	2
2		1	4	4	2	4	
3			1	12	1		
4				3	4	18	
5							14
Apr							
1	13	15	1	1			
2		1		1			
May							
1	46	4					
2	3						

clear that estimates of the duration of the moult based on captive birds are likely to be very inaccurate. Three birds were castrated while in full breeding dress, but they retained their nuptial plumage as already noted by Witschi (1961). The bills became flesh-coloured, even paler than the bills of non-breeding birds.

Male Red-shouldered Widows also began the pre-nuptial moult in September, but most birds were in full breeding plumage by October (Table 20). During this month there was a marked difference between the two years - in October 1975, 31 of 47 males caught were in full breeding plumage, but in October 1976 only 3 out of 26 males. Nevertheless by November there was no difference between the two years, and this may be a sampling error. In addition to the moult of the body plumage, the rectrices are replaced by much longer black feathers - the fanning of the tail is a conspicuous part of many male displays during the breeding season. There were no recaptures of birds at different stages of the pre-nuptial moult, but Table 20 suggests that the moult may be more rapid than in the Red Bishop. In this species the subadult males did not develop any trace of nuptial plumage.

The number of Red-collared Widows caught during the pre-nuptial moult was too small to warrant tabulation. The first signs of moult appeared in September, and the first birds in full breeding dress were recorded in November. This species also moulted the rectrices, and the very long tail was often not fully grown when the body moult was already complete. A few subadult males began to grow elongated tail feathers towards the end of the breeding season, but the moult was much less extensive than in the Red Bishop.

The gonad cycle

In the Red Bishop testis development can be monitored by following the changes in bill colour (Craig 1975). Thus Table 19 shows that by October many birds have sperm present in the tubules (histological stage 7, indicated by a bill colour score of more than 5). The maximum size of the

TABLE 20

The numbers of Natal Red-shouldered Widows showing particular plumage scores during the period of nuptial plumage

Month	Plumage score				
	1	2	3	4	5
September	8	4			
October	5	19	9	6	34
November			1	1	40
December					34
January					27
February					24
March		2	7	1	4
April	6				
May	15				

testes was reached when the males were in plumage stage 5, that is during November. In the space of just over a month the testis increases in volume by a factor of 300 - 400, from the non-breeding size of 0,8 mm^3 to the breeding condition of 300 mm^3. As in Western Cape birds, bill colour and testis development proceeded more rapidly than the pre-nuptial moult. In adult males, testis regression began in March. The bill colour score was not closely correlated with the precise stage of regression, and the first signs of a loss of bill colour indicated that regression was well under way. By the end of April the testes had regressed to the non-breeding condition, although traces of dark pigment remained on the bill until early May.

Subadult males started testis development in February, at the same time as the first indication of a pre-nuptial moult appeared. The bill colour scores of Table 19 suggest that some of them continued testis development during March, when bill colour scores of 8 have been recorded for birds in non-breeding plumage. A small number, however, showed no signs of pre-nuptial moult or bill colour change. This may be related to the age of the birds; males hatched early in the previous breeding season may show the greatest development of secondary sexual characters, whereas those hatched at the end of the season retain eclipse plumage and undeveloped testes. Unfortunately size differences among male Red Bishops are too small to enable one to distinguish different age classes. Most of the subadults probably achieve spermatogenesis before the post-nuptial moult and its accompanying testis regression.

Mendelsohn (1976) examined a small sample of male Red-shouldered Widows taken at different times of the year. He found that, as in the Red Bishop, histological stage 7 had been reached long before the pre-nuptial moult was completed, but the testes had then not yet reached their maximum size. The increase in volume was of the same order as that of the Red Bishop. The four subadult males taken late in the breeding season showed no sign of testis development.

The bill of the male Red-shouldered Widow in nuptial plumage is a steel blue colour, whereas that of females and subadult males is brown. McLachlan & Liversidge (1958) state that the male in non-breeding dress has a brown bill. Consequently the lack of any apparent correlation between bill colour and testis development in Mendelsohn's (1976) work was puzzling. However, careful examination of my ringing records provided the explanation. Adult males retain the blue bill at all seasons. The birds which show a bill colour change in spring during the pre-nuptial moult are males coming into breeding condition for the first time; at their last post-nuptial moult (see below) they acquired the black primaries which make their plumage indistinguishable from that of males which have bred in previous years. The change in bill colour takes place in two stages: first all pigment appears to be withdrawn from the brown bill, leaving it almost white; then the blue colour appears, starting from the tip. The legs also become black during the breeding season, and these scales are shed during the post-nuptial moult.

The bill of the male Red-collared Widow turns black during the pre-nuptial moult, and this may be correlated with testis development as in the Red Bishop. Adequate data are still lacking.

The post-nuptial moult

During the post-nuptial moult the males, females and juveniles of all three species replace their entire plumage. The males shed their nuptial plumage and moult into an eclipse plumage similar to that of the females, while the juveniles lose the buff-tinged body plumage which identifies newly-fledged young, and the females regrow the feathers covering the brood patch.

As shown in Table 19, adult male Red Bishops started losing their nuptial plumage in March, and by May the body plumage had been replaced by the eclipse plumage. This part of the moult lasts approximately four weeks in individual birds. Table 20 suggests that replacement of the body plumage is even more rapid in adult male

Red-shouldered Widows, since March was the only month in which intermediate plumage stages were recorded, but the sample for April is very small. In the Red-collared Widow the transition from nuptial plumage to eclipse plumage also takes no more than a month. The male Red Bishops lose their head feathers first, almost simultaneously, so that in the last weeks at the breeding colonies apparently bald birds may be seen briefly. At this stage they finally abandon their territories.

The first primary feather is dropped either as the body moult starts, or when the plumage score is 4. The primary moult follows the typical sequence, proceeding from number one to number nine (Stresemann & Stresemann 1966). The tenth primary is much reduced in the Ploceidae. I disregarded it in recording the moult. The moult of the secondary feathers and the rectrices follows the usual passerine pattern: the first secondary is dropped when the primary moult has reached primary 4 or 5, but the sequence of secondary replacement is not regular, with a second central moult focus; the rectrices are moulted in a regular sequence, starting with the central feathers (Stresemann & Stresemann 1966).

By the time the moult of the primary feathers commences, the wing feathers are noticeably abraded. Figure 12 shows the mean wing-lengths of male and female Red Bishops during different months of the year, and it is clear that in both sexes the wing is 1-2 mm shorter in the months immediately preceding the moult. In the Red-shouldered and Red-collared Widows the wing feathers of the adult males are black, and this together with the wing-length enables age classes to be distinguished among the males, as described in Chapter 1. The sequence of plumages for a male Red-shouldered Widow is as follows: on fledging the young male already has a wing in excess of 70 mm, but the body plumage has a distinct buff tone, marking it as a juvenile. Two or three months later it enters the post-juvenile moult, replacing the body plumage with the normal eclipse plumage, and acquiring new brown wing feathers. The wing-length is now in the range 75-82 mm. The following summer it does not undergo a

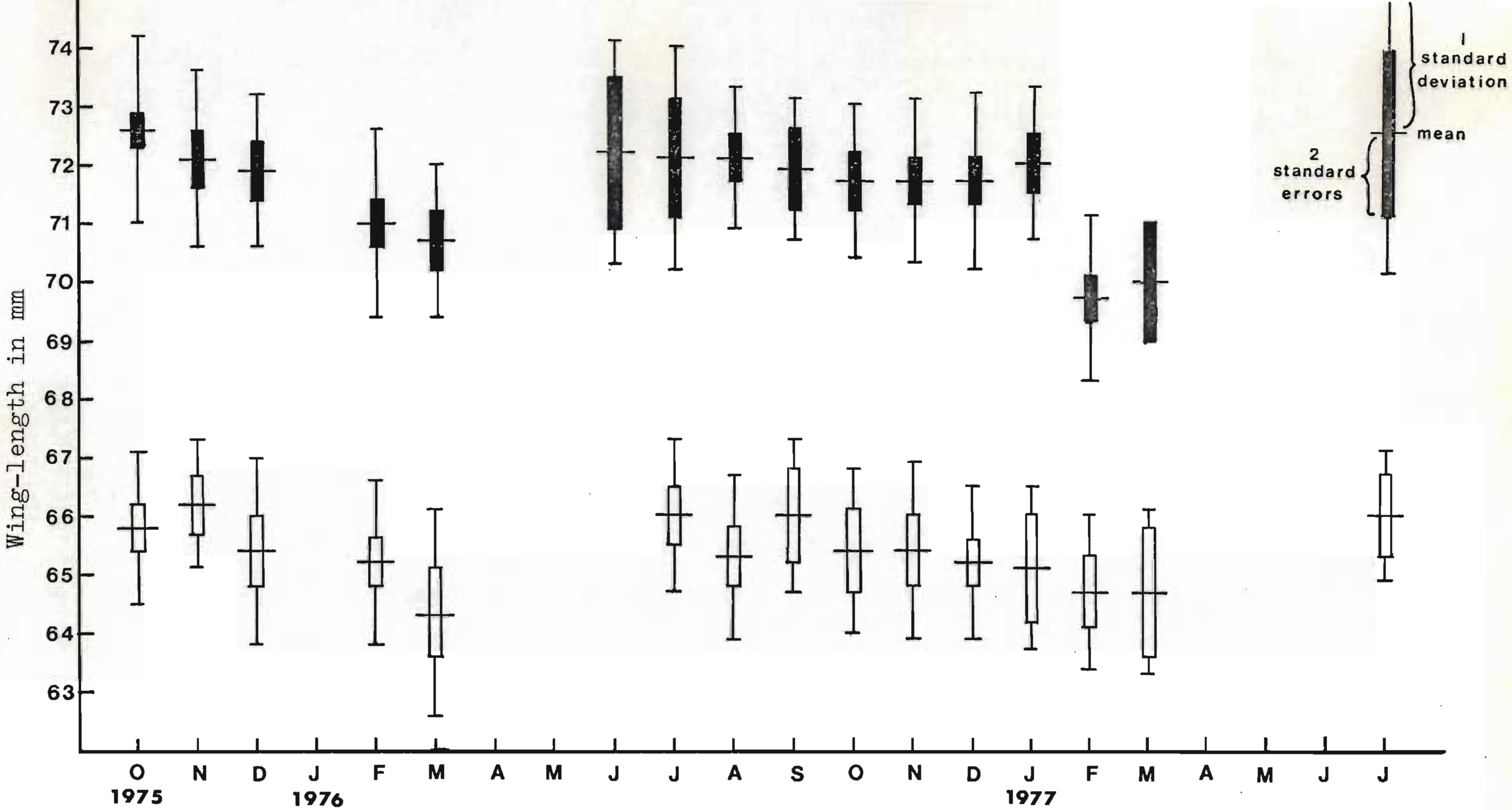


FIGURE 12

Mean monthly wing-lengths of Natal Red Bishops pre-nuptial moult, but at the end of the breeding season it loses its brown wing feathers and replaces them with the black wing feathers and bright shoulder patch characteristic of the adult, while the wing-length increases to 80-85 mm. The bill may temporarily become paler, but soon reverts to its brown colour. In the next spring, the bird undergoes its first pre-nuptial moult, during which the bill changes to blue. After this first active breeding season, there may be a further increase in wing-length at the post-nuptial moult, so that the adult males, which retain blue bills throughout the year, have a wing-length in the range 84-96 mm.

The castrated male Red Bishops appeared to undergo a normal wing-moult, but one bird retained partial nuptial plumage, while the other two produced new feathers on the head and upper chest which were intermediate in type between the eclipse plumage and the nuptial plumage. The moult of the aviary birds was not followed in detail due to the disturbance involved in catching the birds for examination. It has also been shown by other workers that the moult of captive birds differs significantly from that of the wild population (e.g. Zeidler 1966).

There is no evidence of any difference between the sexes in the date on which the moult starts. The juveniles undergo a complete moult, replacing both the body plumage and the wing feathers during the same period as the adults. The date on which they start their moult probably depends on the date of fledging; juveniles are often amongst the first birds to show signs of moult, but late-moulting individuals also tend to be juveniles, presumably from late broods. Since the breeding season extends from December to the end of March in Natal, and the start of the moult from the end of February to May, all juveniles must commence their post-juvenile moult within about three months of leaving the nest. There have been no recaptures of birds ringed as nestlings to provide a more precise estimate.

It is clear from Figures 13 & 14 that there was little

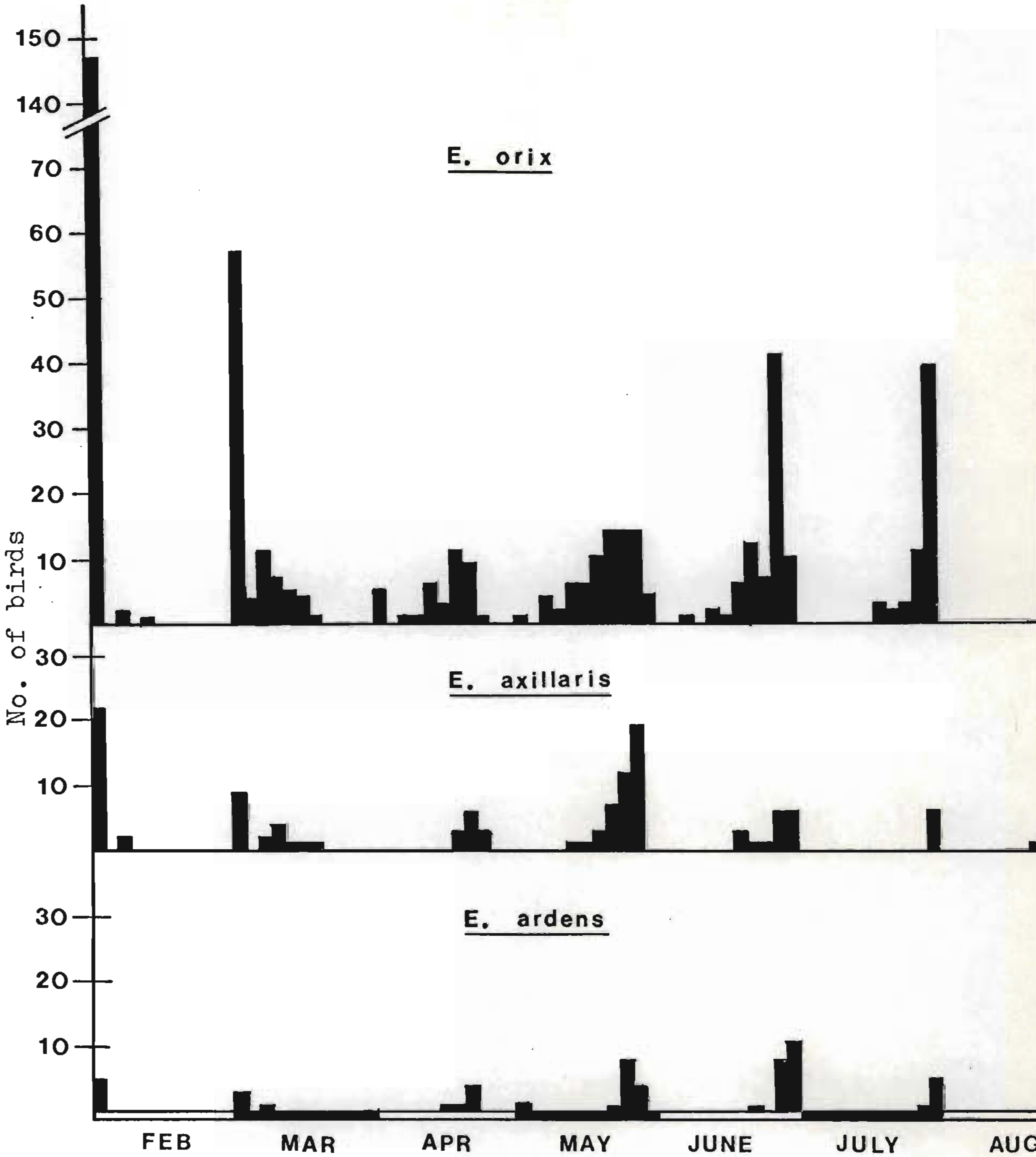


FIGURE 13

The moult of three <u>Euplectes</u> species in Natal during 1976

For each month the column on the extreme left shows the number of birds with no moult, the next nine columns birds in which the moult has reached primaries 1-9, and the last column birds which have completed their moult. All sex and age classes are combined.

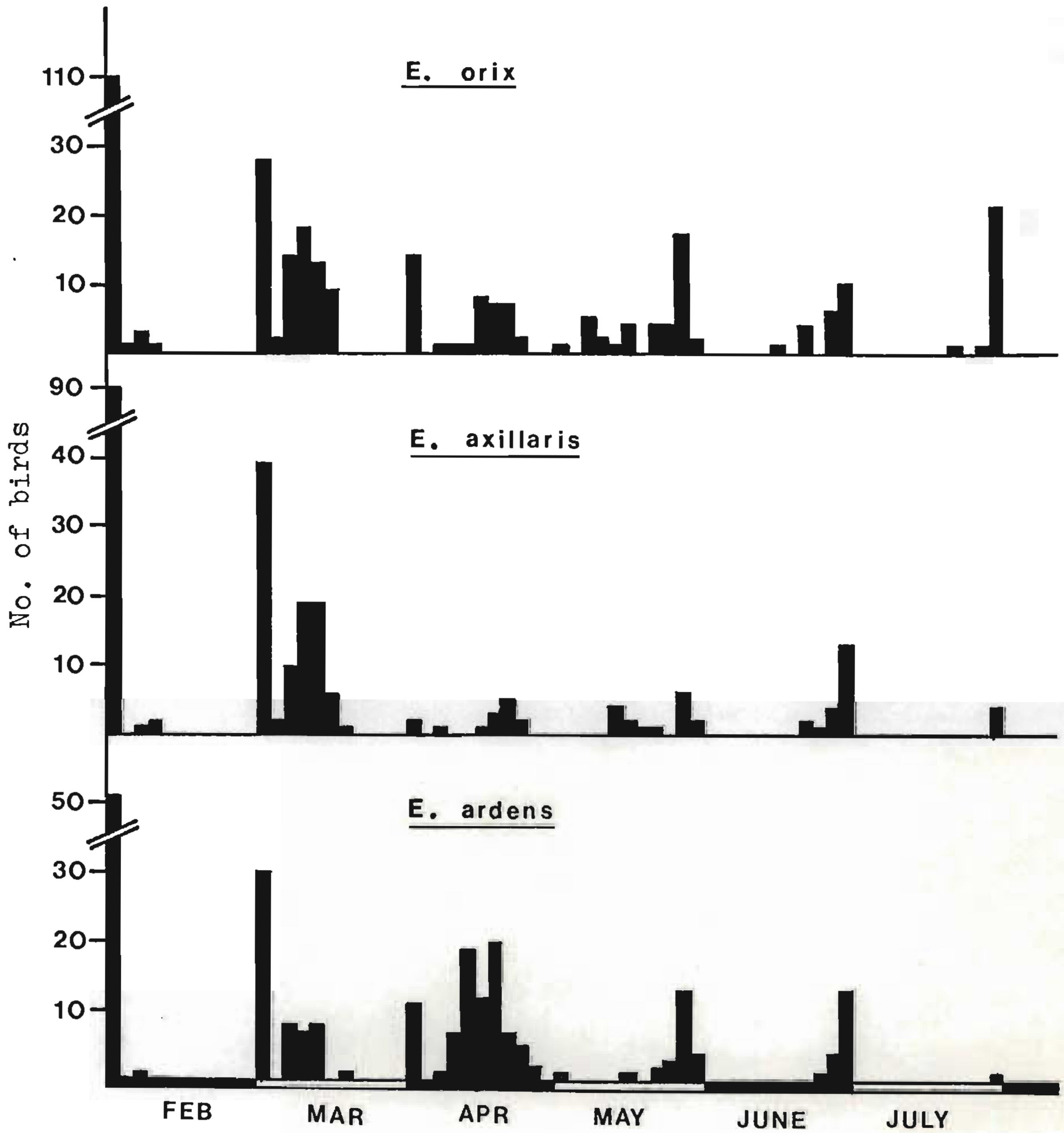


FIGURE 14

The moult of three Euplectes species in Natal during 1977 difference in the course of the moult in 1976 and 1977, and the pattern was essentially similar for all three species. In both years the first birds in moult were caught in the last week of February, and the last birds with no wing-moult were recorded in May. During May the first birds with completely new feathers appeared in the catches, and by August virtually all individuals had completed their moult. The Rhodesian records are less complete, due to small catches during the winter months, but Figure 15 compares the moult of the Red Bishop in three different years. There is again no indication that the period of the moult differed markedly from year to year. The duration and timing of the breeding season may have some influence, particularly in determining at what time particular "cohorts" of juveniles will start moulting.

These figures show only the outermost growing feather in each bird, but in general more than one feather is growing at a given time. Table 21 shows the number of growing primaries recorded in the three species; only birds with at least one old feather distal to the growing feathers are included. There is a tendency for more growing feathers to be present in the early stages of the moult, with the number decreasing as primary 9 is approached. The figures in Table 21 were compared with respect to sex and species, using the chi-squared test for a 2 x n table.

There is no significant difference in the number of growing primaries between male and female Red Bishops, male and female Red-collared Widows, or subadult and adult male Red-shouldered Widows. Consequently these figures can be combined. However, there is a significant difference between male and female Red-shouldered Widows ($\chi^2 = 4,34$ d.f. = 1 $p < 0,05$). Comparing the different species shows that there is a highly significant difference between the Red Bishop and the other two ($p < 0,001$ in both cases). There is also a significant difference between Red-collared Widows and male Red-shouldered Widows ($\chi^2 = 7,27$ d.f. = 2 $p < 0,05$), but not between Red-collared Widows and female Red-shouldered Widows. This suggests that the duration of

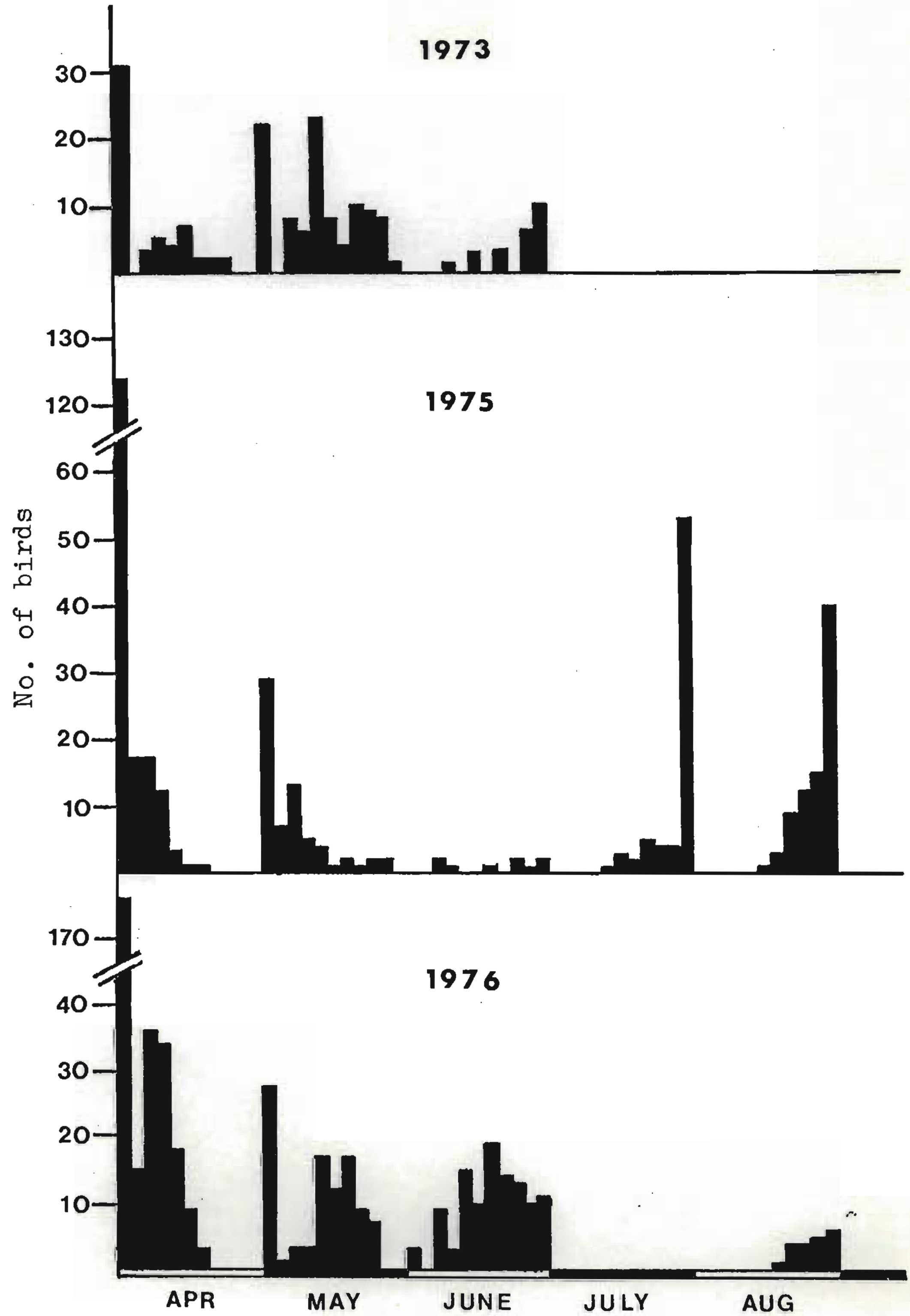


FIGURE 15

The moult of the Red Bishop in Rhodesia in different years

TABLE 21

The number of birds moulting several primaries simultaneously in three *Euplectes* species.

Species	No.	No. of growing primaries 1	2	3	4
♂ *orix*	406	82	242	71	11
♀ *orix*	412	95	252	60	5
♂ *ardens*	63	5	24	31	3
♀ *ardens*	64	2	26	29	7
sub. ♂ *axillaris*	36	3	21	12	0
ad. ♂ *axillaris*	47	3	26	17	1
♀ *axillaris*	68	2	29	29	8
orix	818	177	494	131	16
ardens	127	7	50	60	10
♂ *axillaris*	83	6	47	29	1
♀ *axillaris*	68	2	29	29	8

the moult should be longest in the Red Bishop, followed by male Red-shouldered Widows, and shortest in the Red-collared Widow and female Red-shouldered Widows.

The estimated duration of the moult in individual birds is shown in Table 22. Three different methods were used. For birds caught twice during a single period of moult, the moult score and the moult stage (the outermost primary in moult) were plotted on graph paper against date, and the line joining the two values extrapolated to give the date of start and completion of the moult. The third method is illustrated in Figure 16. In this system, the moult stages represented in each sample are plotted against date, and the slope of the lines bounding the scatter of points obtained is regarded as representing the average rate of moult in the population (see Snow 1976).

Table 22 shows that the three methods give very different values for the duration of the moult. The graphical method of Figure 16 only gives a very rough estimate of the time taken; Snow (1976) used it where data on individual birds were lacking. Both the moult score and moult stage methods are inaccurate when the second capture is shortly after the first, and especially when both captures fall in the first or second "halves" of the moulting period. The moult initially proceeds rapidly, so that two values early in the moulting period will underestimate the total duration, but later proceeds more slowly, so that two values in the final stages of moult will overestimate the duration of the process. In one case of a Red Bishop caught three times during the moult, the first two values gave an estimate of 70 days in moult, and the last two values an estimate of 220 days!

The most accurate estimates of the duration of the moult will be obtained from birds caught shortly after the start of the moult, and recaptured just before its completion. Only three Red Bishops, one Red-collared Widow and a male and a female Red-shouldered Widow met these criteria, to provide the following figures: 110-120 days for the Red Bishop, about 100 days for the male Red-shouldered Widow,

TABLE 22

The duration of moult in three *Euplectes* species

Species	No. of birds	Method	Mean no. days	S.D.
orix	16(R)	moult score	115	48
orix	10(N)	moult score	121	47
orix	14(R)	moult stage	133	36
orix	10(N)	moult stage	118	25
orix		graph	93	
ardens	6	moult score	56	16
ardens	7	moult stage	66	26
ardens		graph	90	
♂ *axillaris*	3	moult score	83	
♂ *axillaris*	3	moult stage	101	
♀ *axillaris*	1	moult score	72	
♀ *axillaris*	1	moult stage	86	
axillaris		graph	98	

Note: the Natal and Rhodesian data are treated separately for *E. orix*; there are no Rhodesian data for the other two species.

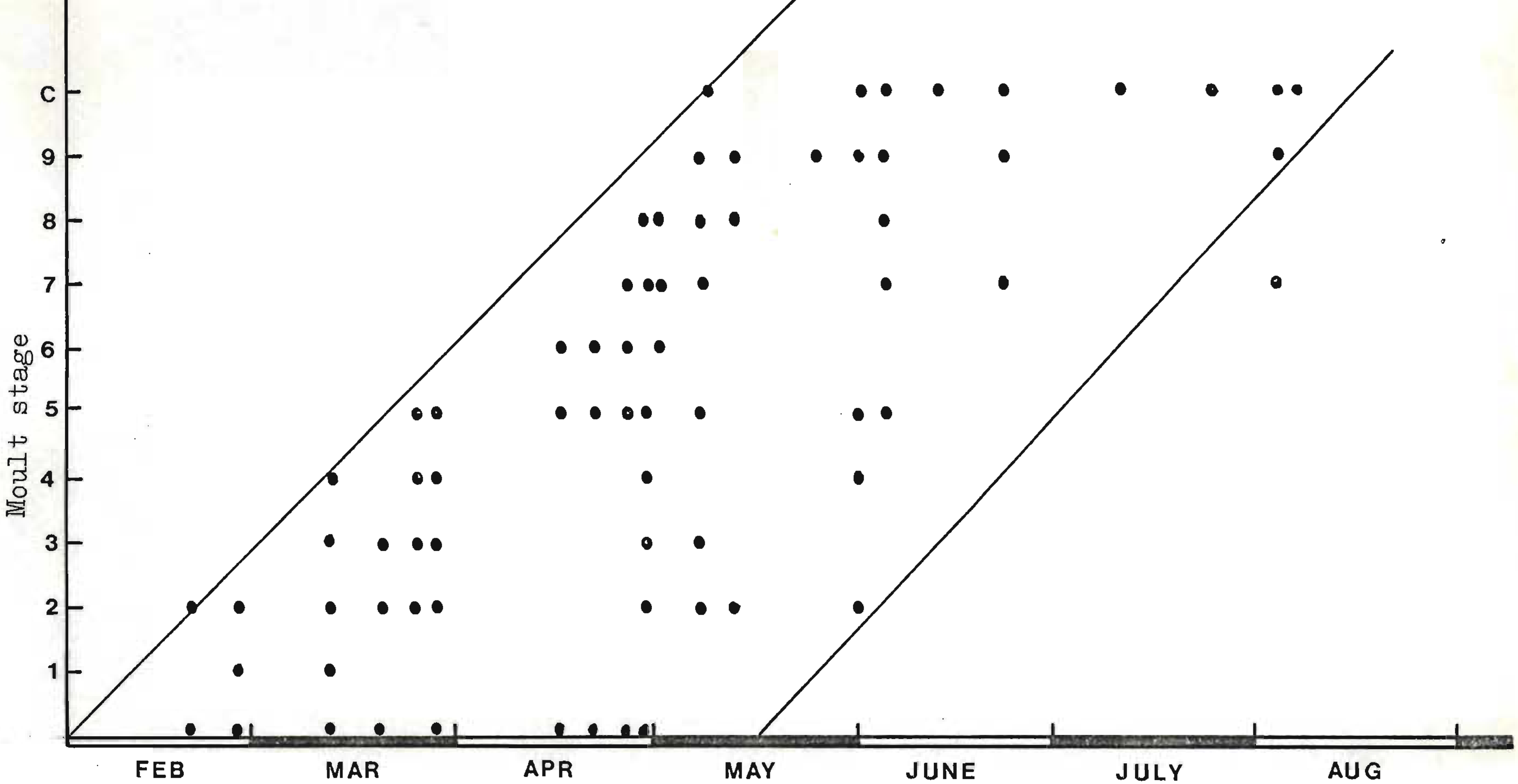


FIGURE 16

The moult stages represented in catches of the Red Bishop in Natal during 1977 and about 80 days for the Red-collared Widow and the female Red-shouldered Widow. This is in agreement with the predictions made on the basis of the number of growing primaries in the different species.

Weights

Since the weight of a bird can be expected to fluctuate on a daily basis as well as seasonally, the weight data from Natal are all drawn from birds caught at roosts in the evenings. Some weights were recorded for the Red Bishop in the Cape during a previous study (Craig 1973), and are tabulated separately (Table 23). The Rhodesian data are listed in Table 24 for the Red Bishop, and Table 25 for the Red-collared Widow, since they were taken at different times of the day, and not in all months, so that comparisons throughout the year are not possible.

As discussed in Chapter 1, Red Bishops in the Western Cape are considerably larger than those in other regions, and their weights were also much greater than any recorded in Natal or Rhodesia. In all months males weighed more than females, but there are no significant differences in weight between birds caught during the day, and birds caught in the evening. There is some indication that weights of both males and females were at their maximum level at the start of the breeding season (around August), declining during the course of the year in 1972 (Table 23).

The Rhodesian Red Bishop data again show that the males were at all times heavier than the females. It is also possible to compare weights at different times of day during the same months. In all cases the birds caught in the late afternoon and evening are heaviest. There is relatively little change in weight during the day, and in most cases the weights for the two periods 0900-1200h and 1200-1500h have been combined. The most surprising feature of the records is that weights of birds caught early in the morning are not significantly lower than those of birds caught during the day, and are in fact often greater. No seasonal trends can be established (Table 24).

The same patterns appear in the weights of Rhodesian

TABLE 23

Some Red Bishop weights from the Western Cape

Month	Sex	No. caught	Mean wt. (gm)	S.D.
May 1972	♂	10	29,5	1,8
	♀	22	25,5	1,7
June 1972	♂	50	32,6	2,1
	♀	67	26,5	1,5
August 1972 (evening)	♂	19	31,1	2,4
	♀	10	25,9	2,7
August 1972 (day)	♂	23	29,4	1,8
	♀	42	24,6	2,1
September 1972 (evening)	♂	10	29,0	2,0
	♀	4	25,0	1,4
September 1972 (day)	♂	33	28,7	1,6
	♀	16	25,1	2,6
October 1972 (evening)	♂	18	29,0	3,1
	♀	11	24,5	2,6
October 1972 (day)	♂	20	28,5	2,2
	♀	14	24,7	2,3
November 1972	♂	10	27,0	2,7
	♀	11	24,3	3,0
May 1973	♂	19	29,3	2,0
	♀	11	25,0	1,5
June 1973	♂	43	29,4	1,6
	♀	39	23,6	1,4
August 1973	♂	11	32,8	2,8
	♀	11	25,4	1,8

TABLE 24

Some Red Bishop weights from Rhodesia

Month	Sex	Time	No. caught	Mean wt. (gm)	S.D.
June 1972	♂	2	12	21,1	1,4
	♂	3	11	20,9	1,2
	♀	1	9	17,6	0,7
	♀	2	14	16,4	1,0
	♀	3	17	17,2	1,0
July 1972	♂	2	17	20,6	1,1
	♂	3	34	20,9	1,0
	♀	2	31	17,5	1,0
	♀	3	36	17,9	1,2
September 1972	♂	4	17	22,2	1,5
	♀	4	11	19,3	1,4
October 1972	♂	2+3	40	22,2	1,5
	♀	2+3	14	17,4	1,1
November 1972	♂	2+3	20	21,5	1,1
	♂	4	20	22,6	1,2
	♀	2+3	16	17,5	0,8
	♀	4	24	18,7	0,8
December 1972	♂	2+3	23	22,1	1,3
	♀	2+3	13	17,2	1,1
January 1973	♂	2+3	25	20,7	1,2
	♂	4	14	20,9	1,0
	♀	2	11	17,5	1,3
February 1973	♂	1	16	19,8	1,5
	♂	2	10	20,1	1,5
	♂	3	16	20,4	1,2
	♂	4	20	21,7	1,2
	♀	1	18	17,4	1,1
	♀	2+3	12	17,5	1,2
	♀	4	9	19,1	1,7

TABLE 24 (continued)

Some Red Bishop weights from Rhodesia

Month	Sex	Time	No. caught	Mean wt. (gm)	S.D.
March 1973	♂	1	20	20,1	1,4
	♂	3	23	19,9	0,9
	♂	4	11	20,4	1,3
	♀	1	18	17,1	1,7
	♀	2	32	17,1	1,3
	♀	3	24	16,7	1,3
	♀	4	15	17,8	1,2
April 1973	♂	2+3	14	20,2	1,5
	♀	2+3	17	16,6	1,2
May 1973	♂	1	18	19,8	1,4
	♂	2+3	12	21,1	2,0
	♂	4	19	22,7	1,0
	♀	1	18	16,4	1,1
	♀	2+3	19	17,0	1,0
	♀	4	25	19,8	1,2
September 1973	♂	2+3	20	20,5	1,1
	♀	2+3	27	17,4	0,8
March 1974	♂	2+3	26	20,6	1,0
	♀	2+3	26	17,0	0,9
	♀	4	9	19,0	1,2
April 1974	♂	1	11	19,9	0,7
	♂	2+3	20	20,5	1,1
	♂	4	14	22,1	1,3
	♀	2+3	27	17,2	1,3
	♀	4	24	18,7	1,2
April 1975	♂	2+3	27	19,3	1,1
	♀	2+3	32	15,9	1,1
May 1975	♂	2+3	16	19,2	1,3
	♀	2+3	19	16,3	1,2

TABLE 24(continued)

Some Red Bishop weights from Rhodesia

Month	Sex	Time	No. caught	Mean wt. (gm)	S.D.
July 1975	♂	1	31	20,0	1,0
	♂	2	10	19,8	1,5
	♀	2	18	16,5	0,9
August 1975	♂	2+3	19	19,7	1,3
	♀	1	10	16,7	0,6
	♀	2+3	27	16,8	1,0
November 1975	♂	1	20	19,9	1,8
	♂	2+3	17	18,6	1,5
	♀	3	12	14,4	0,7
December 1975	♂	1	14	22,1	1,6
	♂	2+3	13	19,9	1,9
	♀	2	11	15,9	0,8
January 1976	♂	1	27	20,3	1,1
	♂	2	27	20,0	1,5
	♂	4	14	21,0	1,1
	♀	1	24	16,8	1,1
	♀	2	26	16,9	1,6
	♀	4	21	18,6	1,9
February 1976	♂	1	57	19,3	1,2
	♂	2	63	19,0	1,1
	♂	4	29	20,7	1,3
	♀	1	23	17,7	1,5
	♀	2	31	17,4	1,6
March 1976	♂	1	19	20,2	1,2
	♂	2	24	18,9	0,9
	♂	3	23	19,1	1,1
	♀	1	12	17,8	1,4
	♀	2	22	16,6	1,1
	♀	3	28	16,8	1,3

Note: the day is divided into four time periods.
1 = 0600–0900; 2 = 0900–1200; 3 = 1200–1500; 4 = 1500–1900.

TABLE 25

Some Red-collared Widow weights from Rhodesia

Month	Sex	Time	No. caught	Mean wt. (gm)	S.D.
October 1972	ad.♂	1	15	21,9	1,3
	ad.♂	2+3	16	21,1	2,1
	ad.♂	4	15	21,5	1,0
	sub.♂	1	14	19,9	1,1
	sub.♂	4	12	21,1	1,8
	♀	1	17	18,5	1,0
	♀	2+3	28	16,9	1,2
	♀	4	13	18,0	0,9
November 1972	♀	2+3	24	16,5	0,8
	♀	4	12	17,3	1,4
November 1973	ad.♂	4	24	24,5	1,9
	sub.♂	4	16	21,2	1,2
	♀	4	52	18,6	1,5
December 1973	ad.♂	4	12	20,8	1,5
	sub.♂	4	11	18,9	1,9
	♀	2+3	12	16,8	0,9
	♀	4	13	17,4	0,5
November 1974	ad.♂	1	15	20,8	1,0
	ad.♂	2+3	10	21,3	1,1
	ad.♂	4	15	22,5	1,2
	sub.♂	1	12	19,3	0,7
	sub.♂	4	23	20,7	1,0
	♀	1	19	16,7	1,0
	♀	2+3	15	17,4	0,8
	♀	4	39	18,0	0,8
January 1976	ad.♂	1	18	19,0	0,8
	sub.♂	1	13	17,7	1,0
	♀	1	35	15,5	1,0

Time periods as in Table 24.

Red-collared Widows (Table 25). Males are always heavier than females, both sexes are heaviest in the evening, and early morning weights are not especially low - in fact in October 1972 they were slightly greater than evening weights. In addition, subadult males weigh less than adult males.

The weight cycles of the Red Bishop, Red-collared Widow and Red-shouldered Widow in Natal over a period of 21 months are shown in Figures 17, 18 and 19. For the Red-collared Widow (Fig. 17) the data are not complete. The weights of the females showed little variation, with the only distinct peak occurring in December 1975. Male weights appeared to be greatest at the start of the breeding seasons, in October 1975 and 1976. In both sexes weight appeared to fall off in February, just before the post-nuptial moult, but then increased again and remained relatively constant through the winter.

There are even more gaps in the record for the Red-shouldered Widow, particularly during the winter of 1977 (Fig. 18). Female weights peaked in the breeding season of both years (December 1975 and January 1977). They were lower during the remainder of the summer, increasing again as the post-nuptial moult began. During the winter of 1976 there was a clear decrease until September, when weights began to increase again. The adult males reached their maximum weights at the start of the breeding season, in October 1975 and October-November 1976. By the end of the summer their weights had dropped considerably, but they increased again during the post-nuptial moult. In the winter of 1976 there was some indication of another drop in weight before the spring increase. The weights of the subadult males showed a remarkably similar pattern, except that the increase in weight at the start of the breeding season was hardly noticeable.

In the case of the Red Bishop the means are based on the weights of at least ten birds of each sex for all months, except January 1976 when there were no evening catches (Fig. 19). The male pattern closely resembles that

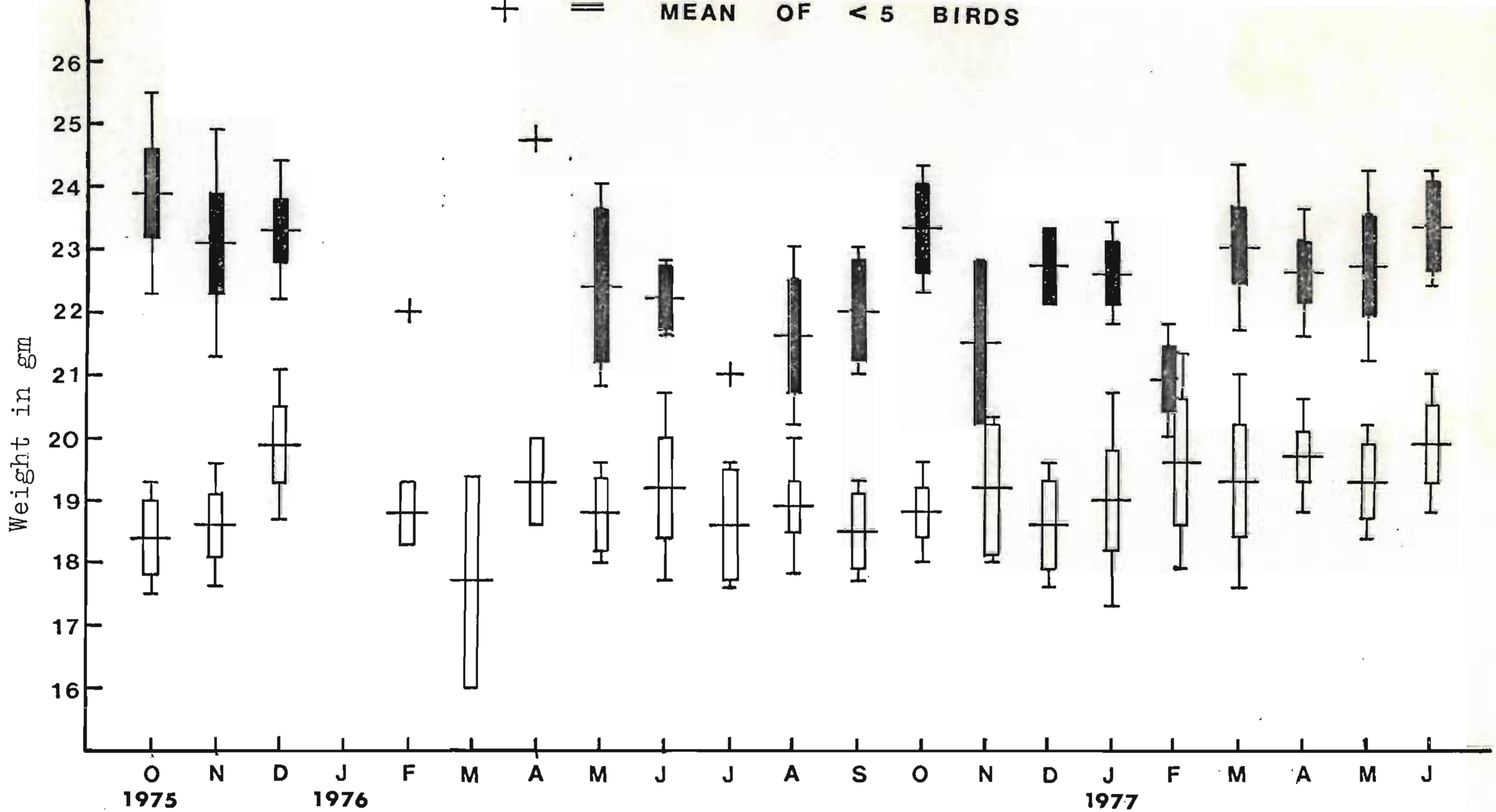


FIGURE 17

Mean monthly weights of Natal Red-collared Widows

(Conventions as in Fig. 12)

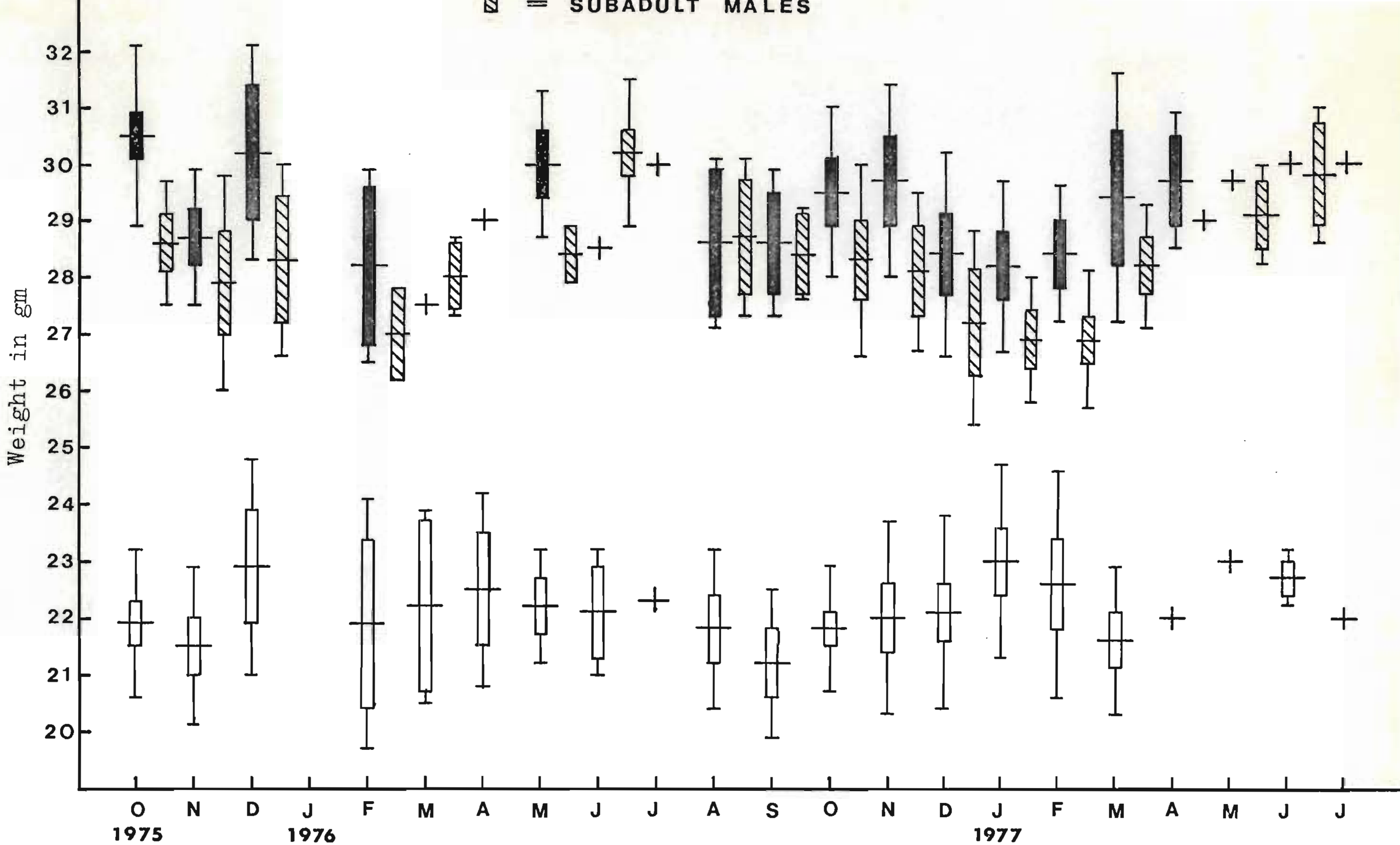


FIGURE 18

Mean monthly weights of Natal Red-shouldered Widows

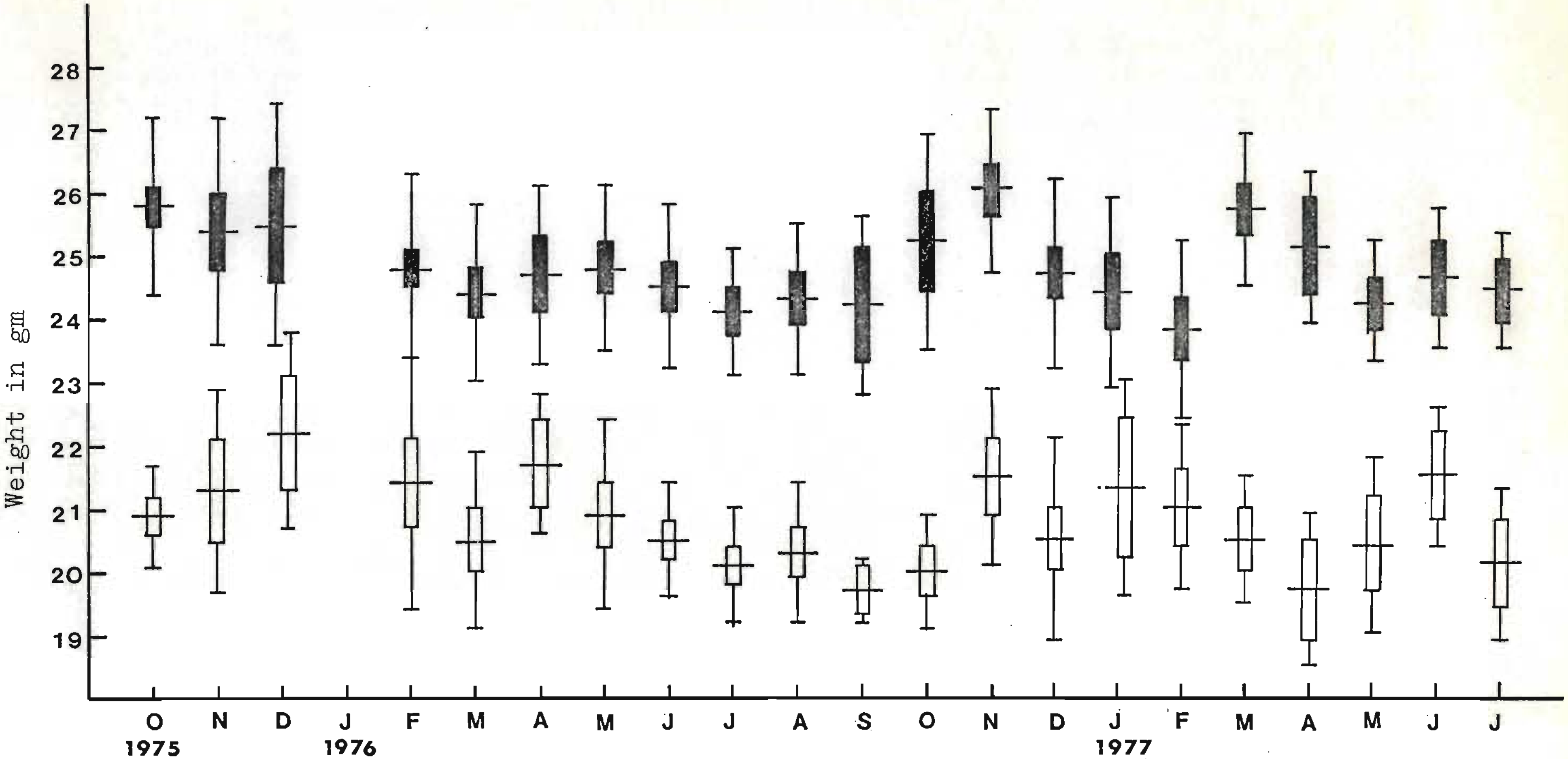


FIGURE 19

Mean monthly weights of Natal Red Bishops described for the two previous species. The weights showed a peak at the start of the breeding season in October 1975, declined until March 1976, and then increased slightly during the post-nuptial moult. Male weights were slightly lower during the winter, but increased dramatically in the spring of 1976, reaching their peak in November. During the ensuing breeding season the males' weights dropped sharply, but increased very abruptly in March as the post-nuptial moult started. They then fell off, but remained fairly constant during the winter months of May to July.

Female Red Bishops reached their maximum weights in December 1975, and then lost weight until March. Another peak in April coincided with a much smaller increase in male weights, but after that female weights decreased steadily through the winter, reaching their minimum in September. During the 1976-1977 breeding season there were two clear peaks in November and January, which corresponded to the two peaks in egg-laying in early December and mid-January described in Chapter 3. As in the previous year, weights then dropped, and surprisingly started to increase only in May, reaching a new peak in June. This suggests that very different factors might be controlling the weights of the two sexes.

Feeding

The available information on the seeds taken by the three species studied in Natal is given in Tables 26, 27 and 28. During the summer they seemed to favour seeds which were still green and milky; birds handled for ringing often regurgitated this white mush, and females were seen feeding it to the chicks. The flowering tassels of the mealies were often the part of this plant which these species fed on, though I found crushed mealies (possibly from the poultry section at Cedara) in the crops of male Red-shouldered Widows collected by J. Mendelsohn. Millet was a special favourite, and my aviary birds definitely preferred millet to any other seed mixtures.

Oatley & Skead (1972) in their review of nectar feeding

TABLE 26

Some food-plants of the Red Bishop

Species	Source
Zea mays	personal observation
Millet	" "
Wheat	" "
Amarantus paniculatus	Commins 1953
Batriochloa insculpta	personal observation
Digitaria spp.	Skead 1965
Echinochloa colonum	personal observation
Echinochloa crus-pavonis	" "
Echinochloa pyramidalis	Brooke pers. comm.
Hyparrhenia dregeana	personal observation
Hyparrhenia sp.	Woodall 1971
Hypoxis obtusa	Woodall 1971
Leersia hexandra	Brooke pers. comm.
Paspalum commersonii	" " "
Paspalum urvellei	Woodall 1971
Rhynchelytrum repens	Skead 1975
Setaria angustifolia	Brooke pers. comm.
Setaria pallidifusca	" " "
Setaria sphacelata	" " "
Setaria spp.	Skead 1965
Sporobolus africanus	personal observation
Tagetes minuta	Brooke pers. comm.
Tithonia sp.	" " "
Urochloa panicoides	personal observation

TABLE 27

Some food-plants of the Red-shouldered Widow

Species	Source
Zea mays	personal observation
Millet	" "
Batriochloa insculpta	" "
Digitaria sp.	Skead 1965
Echinochloa colonum	personal observation
Echinochloa crus-pavonis	" "
Hyparrhenia dregeana	" "
Paspalum dilatatum	" "
Setaria sp.	Skead 1965
Sporobolus africanus	personal observation

TABLE 28

Some food-plants of the Red-collared Widow

Species	Source
Zea mays	personal observation
Millet	" "
Batriochloa insculpta	" "
Digitaria sp.	Ruwet 1965
Echinochloa colonum	personal observation
Hyparrhenia dregeana	" "
Setaria sp.	Ruwet 1965

record a Red-collared Widow feeding on Aloe candelabrum in the Pietermaritzburg district, but this is evidently a rare event. These birds certainly do not frequent flowers as often as the Ploceus weavers, but the Red-collared Widow tends to establish territories on steep slopes and hillsides where aloes are quite common.

Insects were fed to the chicks regularly and might form an important item in the diet of all species in summer. Skead (1956) saw Red Bishop chicks being fed on spiders, grasshoppers, beetles and lepidopterous larvae. I have seen females bringing dragonflies, grasshoppers and caterpillars to the young. Woodall (1971) found that the stomachs of two chicks contained beetles and seeds in equal proportions, but Reed (1968) noted that from the age of six days onwards the chicks were fed chiefly on grass seeds. In captivity the young are initially fed insects such as mealworms and ant pupae (Rutgers 1973). Neunzig (1921) states that a captive female Red-shouldered Widow also fed the young on mealworms, ant pupae and egg mixture, and even caught flies and spiders in the aviary. According to Skead (1965) the Red-collared Widow feeds the chicks on seeds alone, but Reichenow (1904) reports that animal food and greenstuff are essential in captivity.

Ruwet (1965) writes that the Red-collared Widow is probably more insectivorous than is generally assumed. Of 12 specimens examined by Chapin (1954), three had insects in their stomachs - ants, beetles and a small caterpillar. Stark (1900) suggested that the Red-shouldered Widow might feed extensively on insects. I have found beetle remains in their stomachs, and Neunzig (1921) referred to wild birds taking termites and locusts. In the aviary I have twice seen a Red Bishop catch a hover fly (Syrphidae) in flight.

Termites are undoubtedly the most important seasonally available insects, and in the summer months large numbers of birds of many species will gather to feed at a termite emergence. Brooke (1970) and Brooke et al. (1972) give many records of birds which feed on termites, and most of the Euplectes species are mentioned. At Malton I have watched Red Bishops, Red-collared Widows and Red-shouldered

Widows feeding together on emerging termites, and they were adept at catching the insects in the air. Brooke (1970) notes that the Red Bishop in particular will employ a variety of different "hunting methods" in dealing with termites.

Discussion

The pre-nuptial moult

The timing of the pre-nuptial moult in relation to environmental conditions was first discussed by Brooke (1966). He has suggested that rainfall in November in Rhodesia determines both the timing of the pre-nuptial moult and the start of breeding in the Red Bishop and other species, but his data do not show any striking differences in the timing of the moult in different years. The records of the pre-nuptial moult in A.J. Manson's ringing data are unfortunately incomplete, but there is no indication that the time of onset of the moult differs markedly from year to year. Despite the spring rains being a month earlier in 1975 than in 1976, the moult of the birds in Natal took place at the same time in both years as described above.

Unusually dry conditions may reduce the number of sight records of birds in nuptial plumage, since the birds will avoid dry areas in favour of those where rain has already fallen, but I consider it highly unlikely that the timing of moult in individual birds is dependent on rain. I would suggest that individual birds tend to start the pre-nuptial moult at about the same time each year, but my recaptures to date do not provide any clear proof.

The laboratory experiments of Brown & Rollo (1940) and Rollo & Domm (1943) have shown that the pre-nuptial moult in some _Euplectes_ species can be induced by artificially increased photoperiods. However, daylength is relatively constant in the tropical environments which most of the genus normally inhabit, and this result tells us little about the controlling factors in their natural habitat. Photoperiodic control of the annual cycle in birds will be discussed in Chapter 3.

In a series of experiments Witschi (1961) demonstrated that luteinising hormone (LH), if injected into male Euplectes in eclipse plumage, resulted in new feathers of nuptial-type plumage being produced. Thus it was suggested that the change of plumage was under the control of the gonadotrophic hormones and directed by the hypothalamus. However, the experiments of Ralph et al. (1967) failed to confirm any of the proposed mechanisms by which these hormones might determine the appearance of nuptial plumage. Thus the physiological basis of the pre-nuptial moult remains unclear.

Adlersparre (1939) noticed that Orange Bishops Euplectes franciscanus in captivity showed marked individual differences in the intensity of red colour in the nuptial plumage. He showed that the colour could be modified to some extent by varying the amount of carotenoid in the diet, but the individual differences remained. However, a male Golden Bishop E. afer showed no response to changes in the diet, with the yellow areas of the plumage remaining unchanged. The chemical investigations of Kritzler (1943) showed that in Red Bishops and Orange Bishops the red feathers of wild birds contained three different carotenoid pigments, while those of captive birds contained only two of these, accounting for their paler colouration. The Spotted-back Weaver Ploceus cucullatus and the Golden Bishop have only two yellow pigments, and there were no differences between wild and captive specimens. Kritzler found that rich stores of pigment were maintained in the liver and in adipose tissue, and he concluded that the amount of pigment appearing in the nuptial plumage is only a small fraction of what is absorbed in the diet in the course of the year. It is not known from what food source the birds normally obtain these pigments, but some of them may be produced by the oxidative decomposition of dietary carotenoids. In a recent study, Brush & Power (1976) have shown that in the House Finch Carpodacus mexicanus the carotene taken in from the food is converted to a new compound before being deposited in the feathers. They also found evidence of an interaction between diet and hormone levels at the time when the feather follicles are active - this need not occur in the Euplectes species, if relatively large amounts of pigment are constantly present in the body.

In wild Red Bishops I have also noticed striking individual variation in the intensity of the red colours in the nuptial plumage, and the red collar of the Red-collared Widow varies from deep crimson to orange. White feathers are occasionally to be found in the red areas of the nuptial plumage of Red Bishops, and I once saw a male with large white patches in its red plumage. Sage (1965) describes a female Red Bishop which apparently lacked the normal brown pigment, so that the body plumage was almost entirely a dull white colour. He also mentions a male Fire-crowned Bishop Euplectes hordeaceus in which the forehead, wings and tail were white instead of black, while the red areas of the plumage were unaffected. A male Red-collared Widow at Cedara provided a striking example of partial albinism: the outer rectrices were snow white, while the two central feathers and the remainder of the plumage were black as usual, except for the red crescent on the throat. Two cases of melanism have also been recorded. Lawson (1965) reported a totally black male Red-shouldered Widow near Durban. Rollin (1962) had a captive male Orange Bishop in which large areas of the red plumage had been replaced by black, but the eclipse plumage was normal.

Females may also develop a few feathers of nuptial plumage type. Bates (1927) has described a female Yellow-backed Widow E. macrourus with some black feathers and an elongated tail. The aviaries at the University of Bielefeld had a female Orange Bishop with partial male plumage, and at Cedara I caught two female Red-shouldered Widows (sexed by laparotomy) which had black feathers on the face, some black primaries, and partly blue bills. Thus plumage abnormalities occur in both sexes and may affect any of the feather regions, though they are undoubtedly rare.

The gonad cycle

The gonad cycle of the male Red Bishop follows the typical pattern of a seasonally breeding bird, as described by Blanchard (1941) for the White-crowned Sparrow *Zonotrichia leucophrys*. The testis development of subadult males resembles that found in several other species in which males do not breed in their first year. Wright & Wright (1944) and Payne (1969) showed that the testes of first-year Red-winged Blackbirds *Agelaius phoeniceus* start their development later than those of adult males and are consistently smaller, even when they reach their maximum size and achieve spermatogenesis. The same has been found for the Tricoloured Blackbird *Agelaius tricolor* (Payne 1969) and the Great-tailed Grackle *Quiscalus mexicanus* (Selander & Hauser 1965). Elliott (1973) suggests that "deferred adult plumage" should be used to describe the "immature" males of the Cape Weaver *Ploceus capensis*, since most of them are sexually mature.

Mendelsohn's (1976) work on the Red-shouldered Widow shows that the subadult males may not follow the same cycle of testis activity as in the Red Bishop, and more data are required for the other *Euplectes* species. The ovarian cycle has yet to be investigated in any member of the genus.

The post-nuptial moult

The timing of the major annual moult in any bird species may be expected to be subject to the same selection pressures as the timing of the breeding season (Immelmann 1963). However, there is evidence that in many species the period of the moult does not vary with changes in environmental conditions to the predicted degree.

Gwinner *et al*. (1971) showed experimentally that changes in photoperiod could modify the moult and other cyclic events in two European warblers, but they also found evidence of control by endogenous mechanisms. Subsequently Berthold *et al*. (1972a) demonstrated a circannual rhythm of moult in Garden Warblers Sylvia borin kept under constant environmental conditions, and Gwinner & Biebach (1977) have shown that the moult of the Red-backed Shrike Lanius collurio is under endogenous control.

Field observations indicate that the moult of many species may show a regular periodicity. Keast (1968) in the arid regions of Australia and Snow (1976) in tropical America both found that the moult was much more regular in its occurrence than breeding, and in Australia the "post-nuptial" moult would take place whether breeding had occurred or not. Since the duration of the moult is relatively constant for any species, Snow (1976) proposed that the moult season, rather than the breeding season, should be fixed: "If two mutually exclusive processes, one of fixed and the other of variable length, have to be fitted together into an annual cycle, the simplest way is for the process which takes a fixed length of time to recur at the same, or nearly the same time, each year, and the variable process to take place at such other times as conditions are suitable". With respect to the Cotingidae, he concluded that the availability of food acts as the main proximate factor, but an endogenous circannual cycle may be involved in many species.

The hormonal control of moult was reviewed by Assenmacher (1958) and there appears to have been little advance in our understanding of the process since then. Assenmacher concludes that the activitation of the hypophyseal-thyroid axis is critical in initiating the moult, which is also facilitated by the inhibition of the hypophyseal-gonadal axis. The detailed interrelationships of the various endocrine rhythms have yet to be established for any bird species, and much of the work has been done on poultry, which may differ from Passerines in many respects.

The extent of the post-nuptial moult in the genus Euplectes was often disputed by early workers. Thus Duncan (1906), while acknowledging that the change in plumage of the Red Bishop at the start of the breeding season takes place by a moult, writes later "In the month of March the autumnal moult is commenced, and it should at once be stated that, though the birds change colour from their brilliant black and scarlet to dull brown, the feathers are not cast." Fitzsimons (1927, 1931) was also of the opinion that the eclipse plumage was assumed by resorption of the pigment from the feathers, although he admitted that the rectrices of species such as the Red-collared Widow were moulted. However, it is now accepted that the males renew their body plumage completely during the post-nuptial moult (e.g. Stresemann & Stresemann 1966). In captivity old birds may show moulting abnormalities. Schifter (1967) reported that a male Long-tailed Widow _Euplectes progne_ underwent only a partial nuptial moult once it had reached the age of 16 years. In contrast, Adlersparre (1938) found that males of the Golden Bishop, Orange Bishop and Fire-crowned Bishop, all more than ten years old, remained in nuptial plumage throughout the year.

Stresemann & Stresemann (1966) point out that Verheyen (1953) wrongly states that the Fire-crowned Bishop moults its remiges twice a year, and they emphasize that in all _Euplectes_ the only complete moult involving the entire plumage is the post-nuptial moult. Verheyen (1953) claimed that the wings of the breeding male Fire-crowned Bishops were shorter than normal, specially adapted for the "butterfly flights" performed during their courtship. It is more likely that the wings were shorter due to wear during the preceding year, as was found in the Red Bishop. Bell (1970) mentions that in the Reed Bunting _Emberiza schoeniclus_ the wing-length is 2-3 mm shorter than the normal average when the birds commence the post-nuptial moult. Folk & Novotný (1970) followed the changes in wing-lengths of the House Sparrow _Passer domesticus_ throughout the year, and also showed that just before the moult the wings of both sexes are significantly shorter than at other times of the year.

In many species the timing of the moult may vary between the sexes and between different age groups. Bell (1970) found that in the Reed Bunting the males tend to terminate breeding activity earlier than the females, and consequently start to moult earlier. Adult male Cape

Weavers start their post-nuptial moult some three weeks earlier than adult females (Elliott 1973). However, in the Euplectes species there is no evidence of sexual differences in the onset of the moult, though there may be considerable individual variation. The recaptures do not show whether the same birds start to moult at about the same time in different years or not. Snow (1962) found that individual White-bearded Manakins Manacus manacus moulted at different times in successive years, but other manakins showed very little variation (Snow & Snow 1964).

The post-juvenile moult of the Reed Bunting (Bell 1970) and of various European finches (Newton 1972) does not include the remiges. Late broods tend to moult later, but since the moult is less extensive than that of the adults, the juveniles complete their moult during the same period. Morel (1969) showed that in the Red-billed Firefinch Lagonosticta senegala all juveniles commence their moult six weeks after leaving the nest, but the subsequent rate of moult varies in the different "cohorts". Juveniles from early broods moult more slowly than those from later broods, so that they all complete their moult at about the same time. There is still insufficient information on the Euplectes species, but since late-moulting birds are almost invariably juveniles, the date of fledging almost certainly determines the date on which the moult starts.

The duration of the wing-moult in a number of small and medium-sized passerine species is shown in Table 29. The shortest periods of moult are found in migratory species such as the Snow Bunting Plectrophenax nivalis, and the longest periods in some of the tropical species. In the equatorial forest of Sarawak, Fogden (1972) recorded that some birds of many species may not moult every year, and the moult was slow, occupying 17-20 weeks in most species. The moult of the Sociable Weaver Philetairus socius is the slowest yet recorded for a passerine bird (Maclean 1973). It appears that the moult of the Euplectes species studied takes longer than in most of the palaearctic passerines, and falls at the lower end of the range

TABLE 29

The average duration of moult in some passerine birds

Species	Locality	No. days	Author
Luscinia luscinia	Germany	35	Stresemann & Stresemann 1966
Plectrophenax nivalis	Canada	35	Hussell 1972
Acanthis flammea	England	56	Evans 1966
Emberiza schoeniclus	England	60	Bell 1970
Agelaius phoeniceus	U.S.A.	63	Payne 1969
Acanthis cannabina	England	70	Newton 1972
Acanthis flavirostris	England	70	Newton 1972
Carduelis spinus	England	70	Newton 1972
Fringilla coelebs	England	70	Newton 1972
Agelaius tricolor ♀	U.S.A.	71	Payne 1969
Carduelis carduelis	England	77	Newton 1972
Manacus manacus	Trinidad	80	Snow 1962
Passer domesticus	Germany	82	Zeidler 1966
Carduelis chloris	England	84	Newton 1972
Pyrrhula pyrrhula	England	84	Newton 1968
Agelaius tricolor ♂	U.S.A.	84	Payne 1969
Quiscalus mexicanus ♀	U.S.A.	90	Selander 1958
Pipra erythrocephala	Trinidad	100	Snow & Snow 1964
Carpodacus mexicanus	U.S.A.	105	Stresemann & Stresemann 1966
Ploceus capensis	Cape	107	Elliott 1973
Quiscalus mexicanus	U.S.A.	110	Selander 1958
Lagonosticta senegala	Senegal	125	Morel 1969
Ortygospiza nigricollis	Rhodesia	180	Stresemann & Stresemann 1966
Philetairus socius	Kalahari	270	Maclean 1973

recorded for tropical species. It is rather surprising that the Red Bishop should have a slower moult than the Cape Weaver, which is a much larger bird. In two species the moult period is shorter in females than in males - the Tricoloured Blackbird and the Boat-tailed Grackle. These are both polygynous icterids, in which the males are larger than the females. Of the three Euplectes species, sexual dimorphism is most marked in the Red-shouldered Widow, which is also the only one in which there is some evidence that the females moult more rapidly.

In his study of the moult of the Bullfinch Pyrrhula pyrrhula Newton (1966) noted that the rate of moult might vary in the same individual at different stages, mainly due to variations in the number of growing feathers. In this species at the start and the finish of the moult there is usually only one growing primary in each wing, but at other times there are two or three feathers growing, and one bird had six primaries growing simultaneously. Evans (1966) found Redpolls Acanthis flammea at the start of their moult with five growing primaries, and recorded variations in the number of growing primaries in different years, with an average of two or three feathers growing simultaneously. The very slow moult of the Sociable Weaver is due to only one primary being moulted at a time, and each feather taking a month to grow (Maclean 1973). In the Cape Weaver Elliott (1973) recorded the following numbers of birds moulting one or more primaries: 1 (56); 2 (94); 3 (16); 4 (1). In the Red Bishop the number of growing primaries is generally lower than in the other species, and this accords with its slower rate of moult.

The rate of the moult may also vary due to the growth periods of the different feathers. The detailed investigation of the moult of the House Sparrow by Zeidler (1966) revealed that the growth periods of the innermost primaries are several days shorter than those of the outermost primaries. Newton (1972) has also shown that the growth periods of the primaries in the Bullfinch, the Greenfinch Carduelis chloris, the Siskin Carduelis spinus, and the Redpoll increase from the first to the ninth primary, so that there may be a difference of more than a week in the growth periods of these two feathers. Thus my impression that the rate of moult is initially more rapid in the Euplectes species, slowing down as the moult proceeds outwards along the wing, is in agreement with the findings of other workers.

Weights

The biological significance of bird weight records was first stressed by Zedlitz (1926), who described seasonal variations in weight of both resident and migrant species in Europe. Later Baldwin & Kendeigh (1938) reviewed the available data on bird weights. They noted that, in addition to individual variations, the sex and age of the birds, the time of day and the season, and the prevailing temperatures all produce fluctuations in the weights of birds under natural conditions.

Variations due to age have not been investigated in any detail in small passerines, owing to the difficulty of aging birds in the field. In most cases juveniles weigh less than adult birds (Baldwin & Kendeigh 1938), and this was found in the present study, where identifiable juvenile birds weighed less than the adults, so that their weights were excluded from Figures 17, 18 and 19. However, soon after the start of the post-juvenile moult they can no longer be separated from the adults by weight or wing-length. First-year birds may be smaller and lighter than adults in species which mature slowly such as the Boat-tailed Grackle (Selander 1958), and this applied to male Red-shouldered Widows in Natal, and to male Red-collared Widows from Rhodesia.

Differences in weight between the sexes vary from species to species. Females may be consistently heavier than the males, but this appears to be rare (Baldwin & Kendeigh 1938). A commoner situation is for the sexes to be about the same weight during most of the year, except during the breeding season, when females are heavier than the males. This is the case in the Bullfinch and the Greenfinch (Newton 1972), the House Sparrow (Folk & Novotný

1970; O'Connor 1972), and the Pied Flycatcher Ficedula hypoleuca (Winkel & Winkel 1976). The largest group comprises those species in which the male is heavier than the female, with the most marked differences in species showing extreme sexual dimorphism. The male birds are consistently heavier than the females in the Song Sparrow Melospiza melodia (Nice 1937), the European Starling Sturnus vulgaris (Coleman & Robson 1975), the Reed Bunting (Haukioja 1969), and polygynous species such as the Red-winged and Tricoloured Blackbirds (Payne 1969) and the Boat-tailed Grackle (Selander 1958). Males of the Red Bishop, Red-collared Widow and Red-shouldered Widow are significantly heavier than the females at all times.

Several authors have investigated weight changes during the course of the day. The pattern of weight change varies, but in all cases the maximum weights have been recorded in the late afternoon. Baldwin & Kendeigh (1938) cite a number of early studies, and species for which field records have been published include the Song Sparrow (Nice 1937), the American Goldfinch Spinus tristis (Wiseman 1975), the Siskin Carduelis spinus (Abs 1964) and the Citril Finch Serinus citrinella (Märki & Biber 1975). The Rhodesian records discussed earlier show the same late afternoon peak in weights for the Red Bishop and the Red-collared Widow. Wiseman (1975) found that the mean weights of the American Goldfinch were significantly lower during the early hours of the day in the cold months but not in the hot months, which may explain why the weights of the two Euplectes species were often not as low as had been expected in the early morning. Kontogiannis (1967) followed the daily weight changes of White-throated Sparrows Zonotrichia albicollis in captivity, and he suggested that the early morning weight should be considered the basic weight and used for comparisons between seasons. However, in the field it is usually more convenient to catch birds at the roosts in the evenings as was done at Cedara, and provided they are caught at the same stage of the daily cycle on each occasion, valid comparisons are possible.

Temperature and weight show an inverse correlation in several palaearctic passerines such as the Bullfinch (Newton 1972) and the Blackbird Turdus merula (Biebach 1977). Newton (1972) does not regard the influence of daylength as important in the Bullfinch, but Biebach (1977) working on the Blackbird and O'Connor (1972) working on the House Sparrow both consider the hours of daylight available for feeding to be closely correlated with temperature. The method by which temperature affects body weight is still unclear. Marsh roosts such as those used by the Euplectes species at Cedara must undergo a considerable drop in temperature on winter nights, and this question would repay investigation.

Seasonal weight variations have been documented for a number of species. The most striking feature of the annual weight cycle in birds of the temperate zones is a peak in weight during the coldest months of the year. Maximum weights in winter have been recorded for the Blackbird (Biebach 1977), the Bullfinch and the Greenfinch (Newton 1972), the American Goldfinch (Wiseman 1975), the Song Sparrow (Nice 1937), the House Sparrow (Folk & Novotný 1970; O'Connor 1972), the Red-winged and Tricoloured Blackbirds (Payne 1969) and the European Starling in New Zealand (Coleman & Robson 1975). Newton (1969) has examined winter fattening in the Bullfinch, and showed that the increased fat deposits are not a long-term energy reserve but only meet the overnight energy requirements. He concluded that at no time could the birds have survived for more than a day without feeding. Biebach (1977) also found that the winter weight increase of the Blackbird was primarily due to fat deposition, and estimated that this much larger bird would have sufficient reserves to survive two days of starvation with normal locomotor activity.

Elliott (1973) found that the highest seasonal weights in the Cape Weaver were during the winter and in the breeding season, but there was relatively little fluctuation. His study area in the Western Cape is still in the temperate zone. At Singapore, only 1^{o} N, Ward (1969b) found that seasonal weight changes in the Yellow-vented Bulbul Pycnonotus goaivier were very small. Yet even in this environment the birds accumulated a small fat reserve each day to provide their overnight energy requirements. On the island of Aldabra C.B. Frith (1976) found much more marked seasonal variations in the weight of the Aldabran Fody Foudia eminentissima, with maximum weights in autumn, before the start of the dry season.

For the Euplectes species in Natal the lower temperatures in the winter months are probably less important than the shortage of food during the dry season, which may oblige the birds to fly farther than usual to forage. Thus their weight cycles may be directly related to food abundance.

In all the species mentioned above, the females show a peak in weight during the breeding season, shortly before egg-laying. Some authors have allowed for this by excluding the weights of females with brood-patches, but if these birds are included this is usually the highest average weight achieved by the females. This was also the case in the Red Bishop, Red-collared Widow and Red-shouldered Widow. Payne (1969) has some figures showing the changes in weight of female Red-winged and Tricoloured Blackbirds during different phases of the nesting cycle, and this period has been investigated in detail in the Pied Flycatcher by Winkel & Winkel (1976). The same trends are probably found in most species: little change in weight or even a slight increase during incubation, then a marked drop in weight while feeding the nestlings and later the fledglings. In these species the male participates to some extent in feeding the young, so that in a polygynous species where the male does not feed the young at all, as in the Red Bishop, the female may lose proportionately more weight during this period.

Territory establishment and display at the start of the breeding season may also make heavy demands on the male bird. Male Red Bishops, Red-collared Widows and Red-shouldered Widows are heaviest at the start of the breeding season, and then lose weight during the ensuing months. The drop in weight is most marked in the male Red-shouldered Widow, which spends the most time in flight displays and defends the largest territory. Both the male

Red-winged Blackbird (Payne 1969) and the male Aldabran Fody (C.B. Frith 1976) show a significant decrease in weight during the breeding season.

Both sexes of the Euplectes species in Natal also show a slight, sometimes quite distinct, increase in weight at the start of the moult. This has also been reported in several other passerine birds, including the American Goldfinch (Wiseman 1975), the Reed Bunting (Bell 1970; Haukioja 1969), and the House Sparrow (Folk & Novotný 1970; O'Connor 1972). Newton (1968) found that the weight of the Bullfinch reached a peak when the most feathers were in growth. The Redpoll differs in some respects, since Evans (1966) described an initial decrease in the weights of moulting adults, followed by an increase at the end of the moult. Juveniles of this species did not change their weights to a significant degree during moult.

Although there are numerous published lists of bird weights which include Euplectes species, these data are useless for practical purposes. In most cases they are taken in one locality over a few days, and virtually all the sources of variation discussed here have been ignored. Fry (1969) is the only author who has drawn attention to seasonal variations in the weights of members of this genus, but even he has lumped females and eclipse-plumaged males together in his totals. Many more careful studies are needed to provide a complete picture of the weight cycles of this group.

Feeding

The feeding habits of the Euplectes species are still too poorly known to warrant much discussion. They have at times attracted attention through their attacks on crops - Schlupp (1922) cited the Red Bishop, the Golden Bishop and the Long-tailed Widow as three of the chief culprits, and gave an amusing account of some impractical control measures which were proposed. To-day, however, complaints about these species are seldom heard, and the depredations of the Red-billed Quelea Quelea quelea have eclipsed their raids on crops.

The food-plants listed in Tables 26, 27 and 28 show that the three species observed overlapped to a large extent in their food preferences. Competition between the various ploceids may be important at certain times of the year. Ziswiler (1965) studied the bill structure of some Ploceidae and found that the genus *Euplectes* had a bill reflecting specialisation on grass seeds, and they could dehusk seeds much more rapidly than members of the genus *Ploceus*.

Rowan (1970) has discussed the potential importance of termites as a food source during the summer breeding period. All the Euplectes species take termites readily; Powett (1963) has recorded male Long-tailed Widows catching the insects in the air, despite the apparent handicap of their long tails. Insect protein may be vital for the spring increase in weight observed in the Red Bishop, Red-collared Widow and Red-shouldered Widow, enabling the females to build up adequate reserves for egg formation (*cf*. Jones & Ward 1976).

C.B. Frith (1976) could relate the seasonal changes in the feeding of Aldabran Fodies to their seasonal weight changes, and Ward (1965a) has described seasonal changes in the diet of the Red-billed Quelea. It is clear that a full description of the weight cycle of the Red Bishop and the other species must include quantitative information on seasonal changes in diet. There is a great deal still to be learnt about their ecology.

Summary

The pre-nuptial moult of the male Red Bishop takes approximately a month in individual birds, and involves only the body plumage. The accompanying bill colour changes are related to the presence of androgens and can be used as an index of testis development. Males of the Red-collared and Red-shouldered Widows replace both the body plumage and the rectrices during the pre-nuptial moult. There is a change in bill colour in both species, but in the Red-shouldered Widow this occurs only in males

breeding for the first time.

During the period March-August all birds of all three species undergo a complete post-nuptial moult. The rate of moult appears to be slowest in the Red Bishop and most rapid in the Red-collared Widow. There are no sexual differences in the rate of moult in these species, but in the Red-shouldered Widow females complete their moult more rapidly than the males. The time of onset and the duration of the moult does not differ in different years, but the start of the complete post-juvenile moult may be dependent on the date of fledging.

The weights of the three species show both daily and seasonal fluctuations. Maximum weights are recorded in the late afternoon and evening. Males are at all times heavier than females. The minimum annual weights were recorded during the winter, the maximum weights at the start of the breeding season in the case of males, and at the time of egg-laying in the case of females. Both sexes tended to lose weight during the breeding season, but there was often an increase in weight at the time of the post-nuptial moult. The present data on feeding are too scanty to be related to the observed seasonal weight changes.

CHAPTER THREE

Breeding in the Red Bishop

Introduction

The events of the breeding cycle are relevant to both the population structure of the species and the annual cycle of the individual birds. While mortality at the adult stage is difficult to estimate, recruitment can be determined much more readily from the number of young leaving the nest. The factors influencing breeding success may also have important effects on the timing of the whole annual cycle. The two major topics under discussion are the factors which determine the breeding season, and the breeding success of the Red Bishop *Euplectes orix*.

The breeding seasons of savannah-dwelling ploceids in Africa are closely linked to the rainy seasons. Comparing Table 30 with the rainfall figures for the particular areas in Jackson (1961), shows that the Red Bishop breeds during the summer rainy season through most of its range, except in the winter rainfall area of the Western Cape, where it starts breeding during the rains and continues into the spring, and in Kenya, where breeding apparently follows on the "long rains" of March to May. Close to the equator in East Africa the monthly rainfall shows two peaks - in November-December, and in March-May with March or April the wettest months on average (Jackson 1961).

Lack (1966) notes the paucity of information on the breeding ecology of tropical passerines. Since then more data have become available, but there are still very few studies dealing with polygynous species. This is important in discussing the theoretical models for the evolution of polygyny, which form the subject of the next chapter.

Methods

The study colony on the farm "Malton" has already been described (see Introduction). Breeding was studied in detail

TABLE 30

The breeding season of the Red Bishop

Area	Months of breeding	Authorities
Katanga	Jan-Apr	Verheyen 1953
Kenya	May-Aug	Mackworth-Praed & Grant 1955
Malawi	Dec-Apr	Mackworth-Praed & Grant 1955, 1962 Benson _et al_. 1964
Zambia	Dec-Apr	Mackworth-Praed & Grant 1962 Benson _et al_. 1964
Rhodesia	Oct-Apr	Brooke 1966 Mackworth-Praed & Grant 1955, 1962 Priest 1936, Vincent 1949 Winterbottom 1971, Woodall 1971
Maputo	Jan-Mar	Mackworth-Praed & Grant 1955, 1962 Vincent 1936
South West	Dec-Feb	Mackworth-Praed & Grant 1962 Winterbottom 1971
Botswana	Dec-Jan	Winterbottom 1971
Transvaal	Oct-Apr	Mackworth-Praed & Grant 1962 McLachlan & Liversidge 1958 Ottow & Duve 1965, Reed 1968 Winterbottom 1971
Natal	Oct-Apr	Dean 1971, Winterbottom 1971 Mackworth-Praed & Grant 1962
Eastern Province	Nov-Apr	McLachlan & Liversidge 1958 Skead 1956
Western Cape	July-Dec	Mackworth-Praed & Grant 1962 McLachlan & liversidge 1958 Vincent 1949

Note: these breeding periods represent the extreme ranges recorded in the literature.

at this site only.

During both breeding seasons the colony was visited either daily or on alternate days, depending on the amount of activity. On only three occasions was there an interval of more than two days between successive visits. Each nest was marked by wiring a small numbered metal plate to the supporting reeds. The date on which building started, the date of completion, and the height above water were recorded in each case, and the location of the nest recorded on a map of the colony. Figure 20 shows the nesting areas referred to in the following sections.

Eggs were not removed, but were counted in situ. With chicks this was more difficult, and the brood was taken out of the nest on the day after hatching. Thereafter they were counted by touch until they were removed for ringing. All chicks surviving to eight days were ringed with 2,5 mm aluminium rings provided by the National Unit for Bird-ringing Administration.

All adult Red Bishops caught at Malton were ringed with a 2,5 mm aluminium ring on the right leg, and also with a unique combination of 2,5 mm coloured plastic rings. Each colour was assigned a number for ease of recording; numbers were read off from top to bottom and from left to right. There was a maximum of two rings on the left, and one on the right leg, above the aluminium ring. A zero was used to indicate rings on different legs, when fewer than three colours were being used. Thus "10" indicated a single black ring on the left leg, while "01" meant a black ring on the right leg; "101" meant a black ring on each leg. Two rings of the same colour were not used on the same leg.

Unfortunately the ideal of having all members of the colony individually recognisable proved unattainable. Mist-netting at Malton never produced large catches, and had to be stopped once breeding had started. Walk-in traps were tried, but the bait was promptly taken by large flocks of Crowned Guineafowl Numida meleagris, which then gathered on top of the trap. Very few marked birds were re-sighted, and loss and fading of rings resulted in uncertain

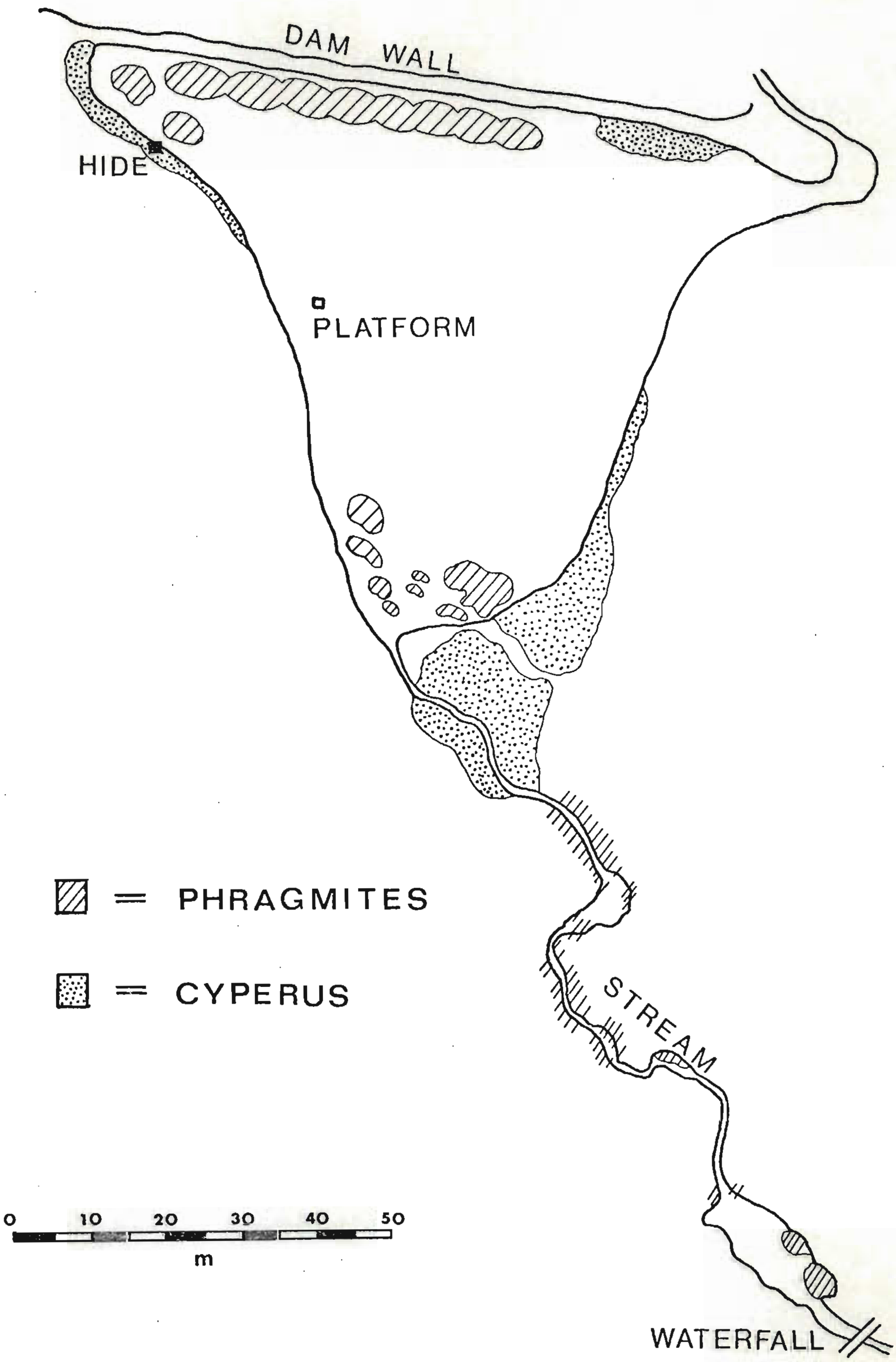


FIGURE 20

The study colony at Malton

identifications. Sealing the split in the ring with acetone was time-consuming and not always successful, as shown by recaptures of birds with missing rings. Blue and orange rings faded particularly badly.

The nest labels could be read through binoculars from the hide, which was a hessian cover supported by four tent-poles joined by diagonal cross-bars at the top. It was initially mounted on a wooden platform standing in the water of the dam, but was later moved to a site along the shoreline (see Fig. 20). A 20 x telescope was used to check the colour-ring combinations of the birds, but 10 x 50 binoculars proved more convenient for sustained observation. Behavioural observations were recorded on a cassette tape recorder, and later transcribed to printed forms.

Rainfall figures and other meteorological data were provided by Mr. W.H. Reynolds of the Agrometeorological Section at Cedara Agricultural College. The rainfall figures for "Malton" were provided by Mr. F. Essenwein of the Ciba-Geigy Tick Research Unit at Baynesdrift, about one kilometre from the study colony.

Results

Breeding and rainfall

The monthly rainfall figures for Malton and Cedara during the study period are compared in Table 31. The average values for Cedara are taken from the records over 60 years, while those for Malton are calculated from only six years of records. The pattern for the three years is the same at the two stations, with 1974-75 and 1976-77 drier than average, and 1975-76 a wet year. The monthly differences are least marked in the wet year, but Malton clearly has an overall lower rainfall, and it would be misleading to take the figures from Cedara as applying to the study colony.

In Figure 21 the weekly totals of rainfall are compared with the numbers of nests built and the numbers of eggs laid during the 1975-76 breeding season. There is some

TABLE 31

The rainfall at Malton and Cedara

Month	Cedara (mm)				Malton (mm)			
	1974-1975	1975-1976	1976-1977	Average	1974-1975	1975-1976	1976-1977	Average
July	26	2	2	18	0	0	18	6
August	8	10	24	25	0	0	0	28
September	8	116	55	42	0	109	58	45
October	32	49	145	84	17	0	138	44
November	108	99	80	110	100	115	77	87
December	116	195	126	129	134	138	56	79
January	202	207	131	136	151	256	133	184
February	119	149	25	129	120	157	0	116
March	41	244	129	111	28	257	108	106
April	58	61	31	53	0	65	8	24
May	0	34	22	30	0	32	13	23
June	0	0	10	16	0	0	14	7
Total	718	1166	780	884	550	1129	623	749

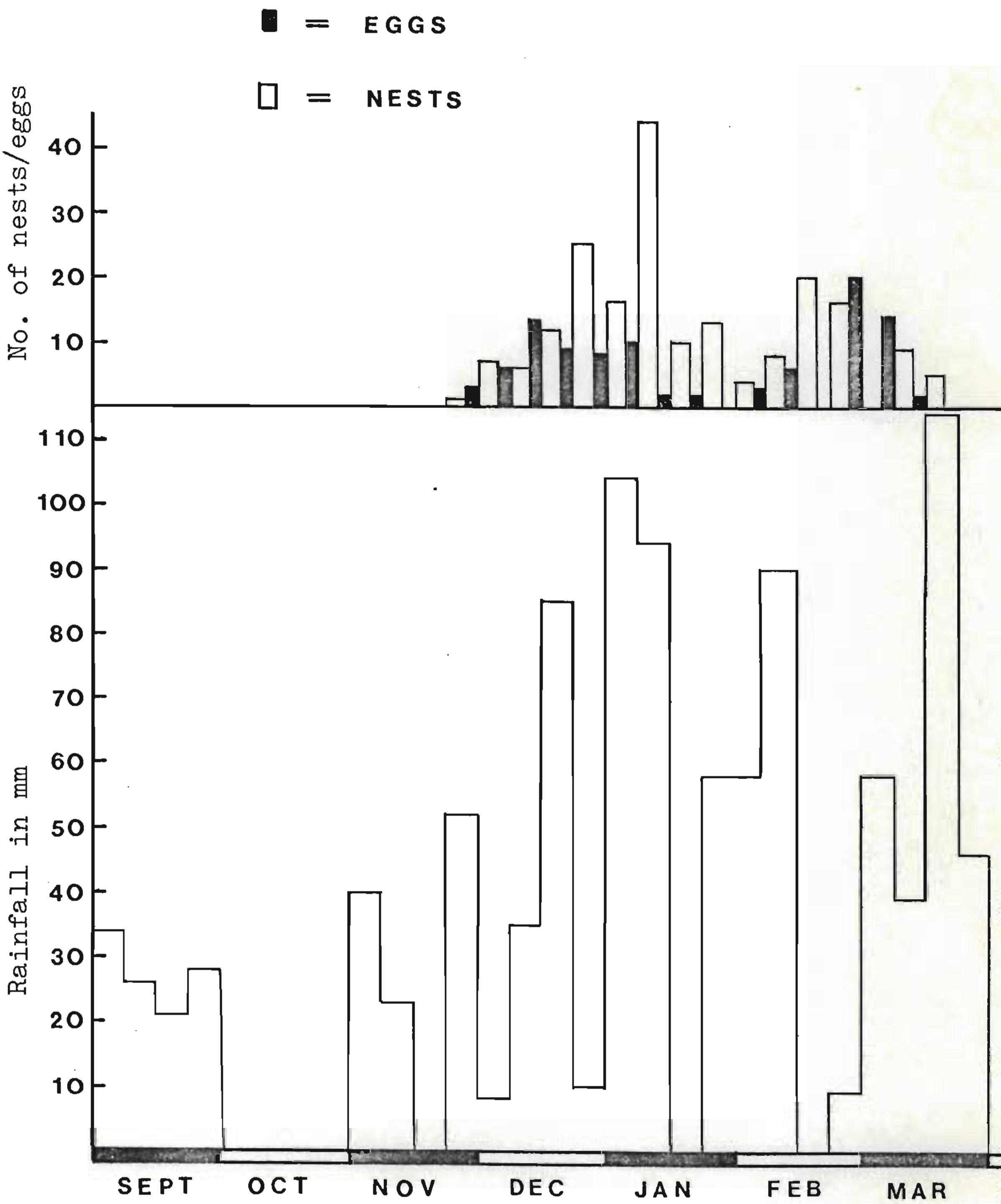


FIGURE 21

Weekly totals of rainfall and breeding activity of the Red Bish
at Malton during the 1975-1976 season

indication that peaks in nest-building activity followed a week after heavy rainfall, but there is no obvious relationship between egg-laying and periods of rain. Comparison with the results for the 1976-77 breeding season in Figure 22, shows that rainfall during the breeding season could not have been a stimulating factor. Indeed the results would seem to indicate inhibition of breeding by exceptionally heavy rains. In Figure 22 there is no correlation between rainfall and nest-building, or between rainfall and egg-laying.

The two breeding seasons are compared in Figure 23, which also shows the rainfall for the 12 months preceding breeding in each case. Here there does appear to be some correlation, since the rainfall preceding breeding in 1976-77 totals 1234 mm, as against 642 mm in 1975-76. In only two months prior to the summer of 1976-77 was no rain recorded, whereas in the previous season six months were completely dry. Examining the spring rainfall shows that in 1975 September had evenly distributed rains, while in 1976 the rains started only in the last week of September, reaching a peak in the first week of October and continuing during this month. November rainfall was almost identical in the two years (see Table 31), and in the first two weeks of November 63 mm and 72 mm were recorded in 1975 and 1976 respectively, with no rain in the third week in either year. The first eggs were recorded in the same week in both years, though nest-building began a week earlier in 1976. This was most likely related to the water level in the dam.

Figure 24a shows the dam during the dry season of 1975; the clumps of reeds on the fringes were standing on dry land, well clear of the water. In both seasons the first nests were built at the pool below the small waterfall, and along the stream leading into the dam (Fig. 20). However, in 1976 the water level in the dam had remained constant throughout the dry season (Fig. 24b) and nests were soon being built in the clumps of reeds around the dam itself. These reeds had started producing new, green leaf-blades suitable for nest-building early in September. By contrast, the first nests in these reed clumps were not

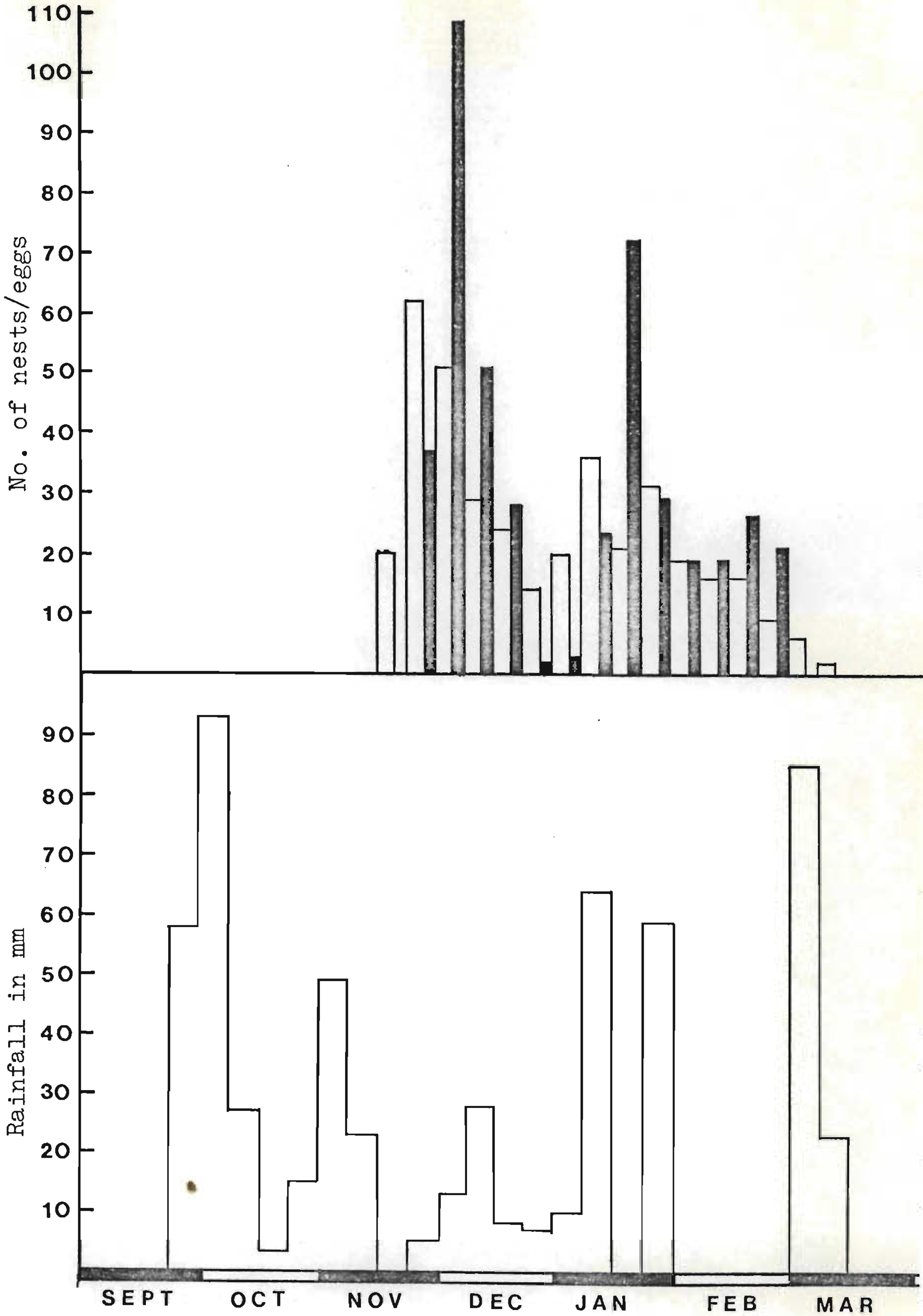


FIGURE 22

Weekly totals of rainfall and breeding activity of the Red Bish
at Malton during the 1976-1977 season

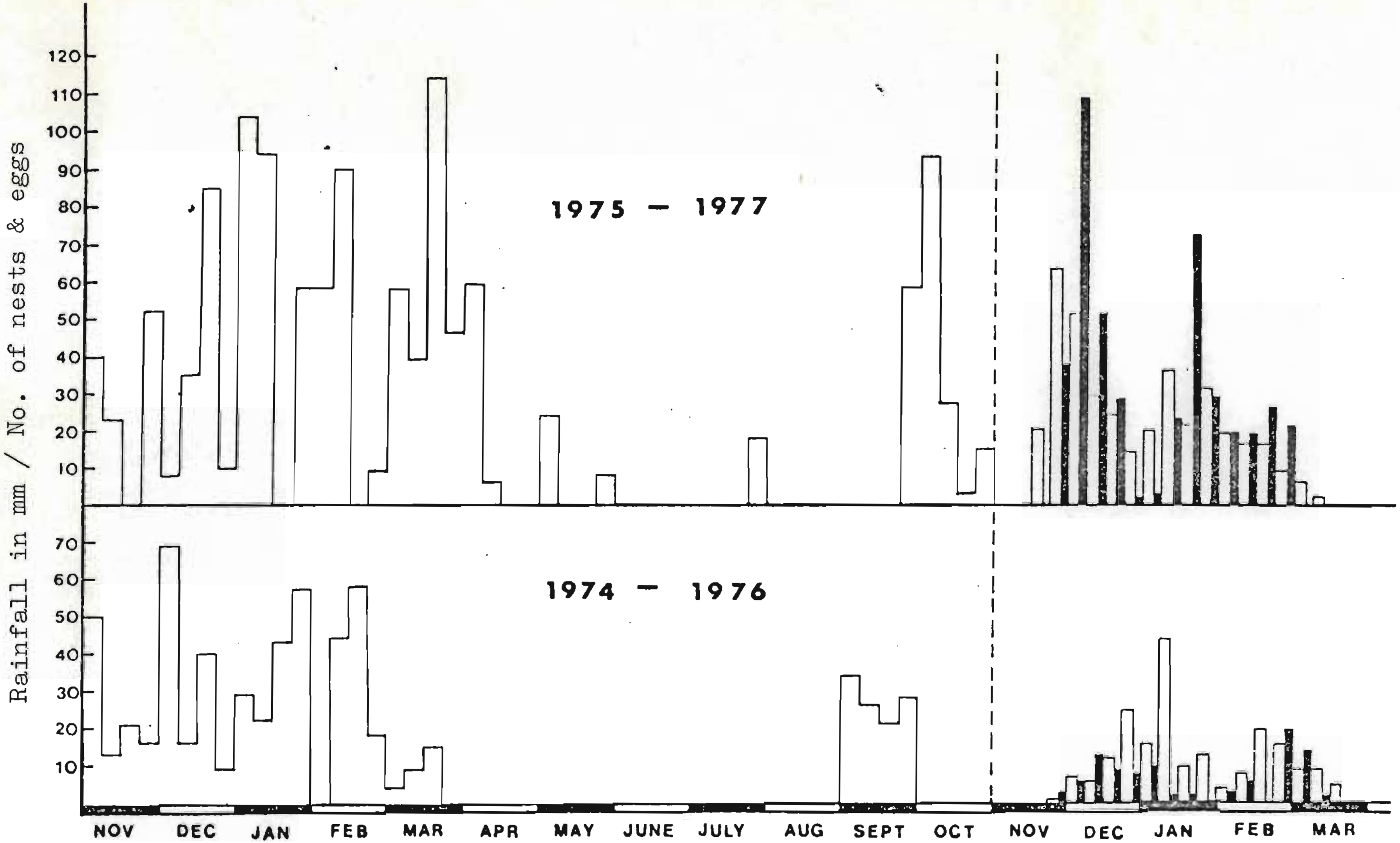


FIGURE 23

Weekly totals of annual rainfall and subsequent breeding activity of the Red Bishop at Malton

a

b

FIGURE 24

Variations in water level at the study colony

(a) the dam in winter, 1975; (b) the dam in winter, 1976 built until the third week of December 1975, when the clumps were still clear of the water and the few new leaves were thin and spiky. The dam filled up to its normal level on 21st December after a thunderstorm; intensive nest-building followed (Fig. 21). Elliott (1973) reports an interesting experiment on the Cape Weaver Ploceus capensis, in a year when the dam in which his study colony was situated dried up. He was able to pump water to the dam to fill it, and within a week the weavers were nesting.

Nest-building

As in all species of the sub-family Ploceinae studied so far, the male Red Bishop builds the nest frame from narrow strips torn off the leaf-blades of grass or similar vegetation. The method of construction has been described by Skead (1956) and Collias & Collias (1964) in some detail. It starts with a cross-bridge of knotted strips between two vertical supports; the male then works from this point during subsequent building. Both detached strips and those still attached to the supporting vegetation may be used, though the inclusion of living material is infrequent. Collias & Collias (1964) claimed to find differences in the nests of birds in the Congo basin and in South Africa; in local birds the completion of a vertical ring is always the first step. Winterbottom (1971) states that there is no porch over the entrance, but this has been present in all the nests I have examined. As I observed in a previous study (Craig 1973), males were inconsistent as regards their source of building material - they might tear off strips from the vegetation at the nest site, from somewhere else on their territory, or even from grassland away from the colony. The same bird often used all three sources during the construction of a single nest.

Both Collias & Collias (1964) and Skead (1956, 1965) mention that the practice of "leaf-stripping" is common in the Red Bishop. In this behaviour the male grasps the leaf-blade at the base, tugs briefly, repeating the process until the leaf is torn off and dropped. One finds numerous leaf-blades floating in the water below newly-built nests in a reed-bed where Red Bishops are breeding. The method of leaf-stripping is identical to the normal method of tearing off nesting material, except that the initial movement is repeated without the bird flying off trailing a strip of leaf, as is usually the case. Intensive leaf-stripping was done only by males building new nests. A spell of leaf-stripping often preceded the collection of a new piece of building material, though the two behaviour patterns were never shown at the same site. Leaf-stripping is clearly an incomplete form of the normal movement, of uncertain function.

When a female has accepted a nest, she adds an inner lining of the seed-heads of grasses, or fluffy down such as is found on the heads of bulrushes, _Typha_ spp. Hoesch & Niethammer (1940) record a lining of feathers in one nest, but this was almost certainly due to the subsequent use of the nest by some other species such as the Orange-breasted Waxbill _Amandava subflava_. Daily inspections during the present study confirmed my earlier impression that there are considerable individual variations in the amount of nest-lining material used. The sudden appearance of lining material in an empty nest was a certain indication that eggs would be laid by the next day. However, in over 60% of the nests, lining followed the laying of the first egg, and in some nests the eggs were visible from the outside through the side walls during the entire incubation period. There was no correlation between the amount of lining and the success of the nests, since both well-lined and poorly-lined nests were vulnerable to predation and flooding, the two main causes of nest-failure.

Nest sites

The most typical nesting site for the Red Bishop is in reeds such as _Phragmites australis_ standing in water. _Typha latifolia_ and other waterside vegetation may be used; Benson _et al_. (1964) record 1030 nests in _Phragmites_, 103 in _Typha_, 451 in weeds, 182 in grasses, and 219 in bushes, mostly _Populus_ sp. The distribution of the nests according to the vegetation at Malton is shown in Table 32. In spite

TABLE 32

The distribution of Red Bishop nests at Malton in relation to the vegetation

Vegetation	No. nests	No. used	% used	Mean ht. (m)	Range of hts.	S.D.
Phragmites australis	171	30	17,5	0,96	0,32-2,87	0,36
Cyperus congestus	13	2	15,4	0,78	0,30-1,38	0,31
Echinochloa crus-pavonis	14	2	14,3	1,15	0,68-1,47	0,27
Echinochloa colonum	3	0	0	0,82	0,23-1,19	0,42
Polygonum senegalense	4	0	0	0,50	0,14-0,84	0,27
Total 1975-76 season	205	34	16,6	0,95	0,14-2,87	0,36
Phragmites australis	364	165	45,3	1,34	0,41-2,52	0,39
Cyperus congestus	12	2	16,7	1,05	0,44-1,48	0,41
Echinochloa colonum	1	0	0	0,97		
Polygonum senegalense	1	1	100	0,51		
Total 1976-77 season	378	168	44,4	1,33	0,41-2,52	0,43

of the great increase in nest numbers during 1976-77, fewer nests than in the previous season were in vegetation other than *Phragmites*. The grass *Echinochloa crus-pavonis* sprang up along the edges of the dam in both years, but reached a height suitable for nest-building only by the end of February. In 1976, 23 nests were built during March (Fig. 21) and all the nests in *Echinochloa crus-pavonis* were built at this time. However, during March 1977 only eight nests were built, with nest-building activity tailing off much earlier. The number of nests built and occupied in the sedge *Cyperus* was virtually the same in both years, and there was a colour-marked male, which nested in this area in both years. Another colour-marked male occupied an identical patch in the *Phragmites* reed-bed along the dam wall (Fig. 20) during the two breeding seasons. This shows that some birds may exhibit site tenacity, and there may be individual vegetation preferences.

During the 1975-76 season, the nests in *Echinochloa crus-pavonis* were on average the highest, but this is probably misleading because of the very rapid growth of this grass, and the small number of nests concerned. Generally the nests in *Phragmites* were higher than in any other vegetation at the dam. The usual nest height of the Red Bishop is given in the literature as 1,2 - 1,5 m (Collias & Collias 1964; Delacour & Edmond-Blanc 1933; Neunzig 1921; Vincent 1936; Winterbottom 1971), while extremes of 0,6 m (Vincent 1949) and 2,4 m (Emlen 1957; Woodall 1971) have been recorded. In the present study the difference in mean nest height between the two seasons is highly significant ($t = 11,51$ $p = 0,001$). This is due to the differences in water level of the dam mentioned earlier. I have often heard it said by farmers that if the weavers build their nests higher than usual, one can expect a wet season. This would not apply unless there were two successive wet seasons - during 1976-77 there were no significant variations in water level, and the nests were never in danger of flooding. However, during the previous summer on the farm "Gartmore" the nests of

Red Bishops and Cape Weavers in the ox-bows of the Karkloof River were submerged to a depth of up to 2 m during the floods, most nests having been built within 1 m of the water surface.

Figure 25 shows the frequencies of different nest heights in the two seasons, and the proportions of nests which were occupied. For both breeding seasons there is no significant difference between the observed number of nests of each height which were occupied by females, and the expected numbers: for 1975-76 the chi-squared value is 2,59 (d.f. = 4 ; $p > 0{,}5$) and for 1976-77 chi-squared is 4,78 (d.f. = 15 ; $p > 0{,}99$). Thus there is no evidence that nest height is a factor influencing female choice. Nest quality does play an important role, however. I did a subjective rating of nests that to my eye were poorly built (i.e. loosely woven). No nest which I had rated as "poorly built" was laid in, but in three cases a male later added new material to an old frame, strengthening and improving it, and these nests were then accepted by females.

The age of the nest on the date when the first egg was laid is shown in Table 33. It is of course unlikely that the egg-laying date represents the date on which the female accepted that nest; in one instance where behavioural observations were made from the period of nest-building onwards, the female accepted the nest and copulated three days before laying the first egg. However, there were also records of eggs being laid within one day of completion of the nest, and these eggs hatched. This seems to indicate that some females will accept a mate before the nest is complete (building normally takes only one or two days). Table 33 does suggest that the freshness of the nest is not as important in the Red Bishop as I had assumed on the basis of work on other weavers (Collias & Collias 1970). It is evident from Figure 23 that in 1976-77 peaks in egg-laying followed about one week after peaks in nest-building, while there is no such relationship for 1975-76. At all times there was a surplus of nests available for females to choose from.

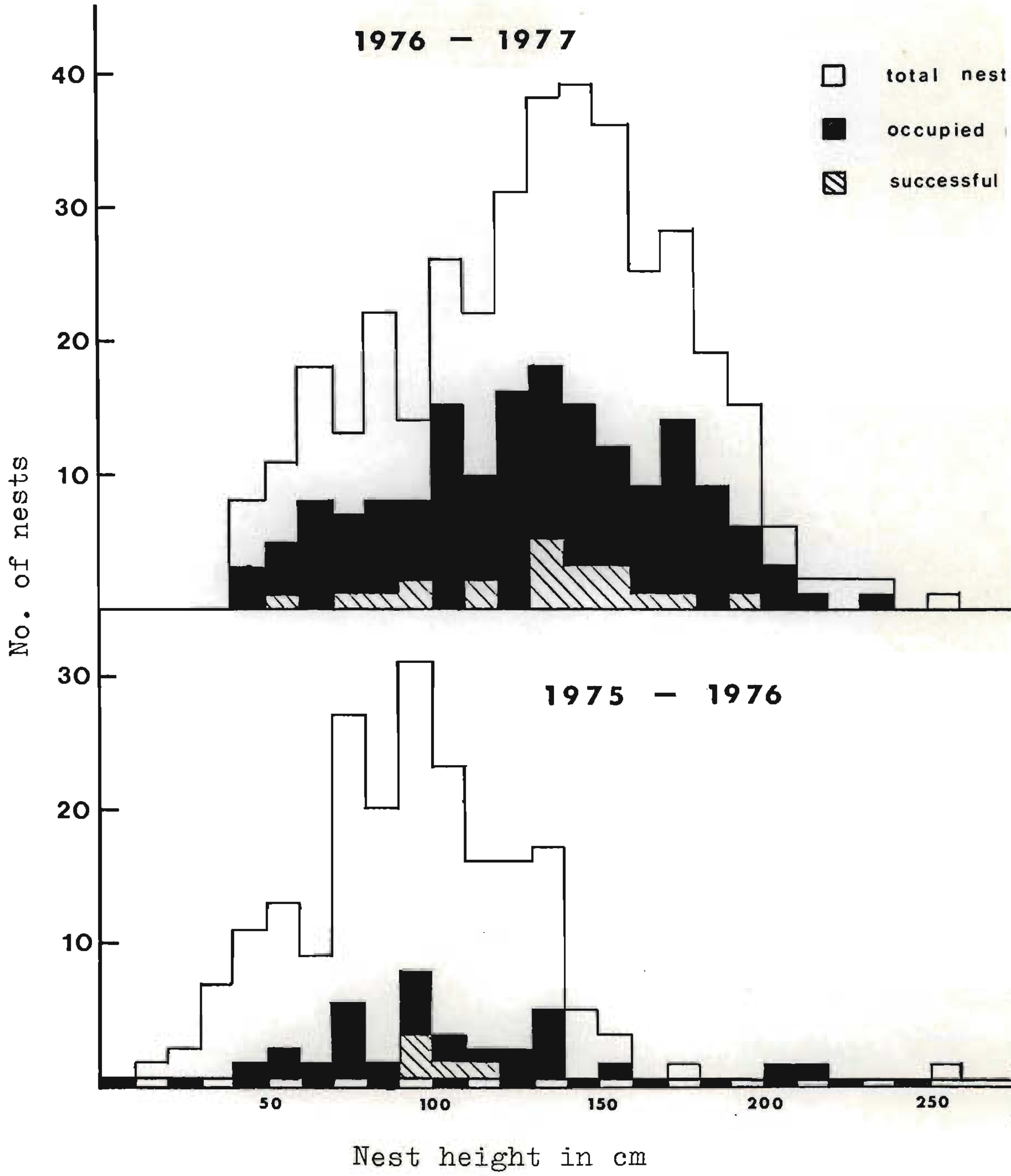


FIGURE 25

Nest heights of the Red Bishop at Malton

TABLE 33

Egg-laying by the Red Bishop at Malton in relation to the age of the nest

Season	Days since completion of the nest 0-2	3-4	5-6	6+
1975-76	10	7	7	6
1976-77	16	40	30	80
Total	26	47	37	86

TABLE 34

The clutch size of the Red Bishop at Malton

Month	c/1	c/2	c/3	c/4	Mean
November 1975	0	0	1	0	3,00
December 1975	0	1	10	1	3,00
January 1976	0	3	2	0	2,40
February 1976	0	0	9	1	3,10
March 1976	0	1	4	0	2,80
Total 1975-76	0	5	26	2	2,91
November 1976	0	6	9	3	2,83
December 1976	4	17	43	1	2,41
January 1977	4	20	28	0	2,46
February 1977	0	7	21	0	2,75
Total 1976-77	8	50	101	4	2,62

While *Phragmites* appears to be the preferred breeding habitat of the Red Bishop, this species is quite adaptable, and has been recorded as nesting in a variety of other sites, not necessarily close to water. R.K. Brooke (pers. comm.) informs me that around Salisbury in the latter half of the breeding season the tall vegetation on termite mounds forms the territory of single males, which may be widely separated from their neighbours. They have no apparent preference for nesting in particular plants, and even Khakibush *Tagetes minor* and Stinkblaar *Datura stramonium* may be used on occasion. At Barberspan Farkas (1966) records nests in the evergreen *Rhus lancea*, as well as *Ligustrum* and *Hakea*. On the site of the present Albert Falls Dam, not far from Malton, Commins (1953) found Red Bishop nests in *Datura stramonium* and *Nicandra physaloides*. Vincent (1936) found birds nesting in weedy thickets of *Indigofera*. Nests may also be built in trees (Haagner 1901; Ottow & Duve 1965; Skead 1965) and in two localities such nests were occupied (Jensen & Vernon 1970; Woodall 1971). At Malton in March 1976 I found two nests in an *Acacia* bush in open grassland, about 1 km from the study colony. They were poorly built, but one was later used by Orange-breasted Waxbills. Whybrow (1950) found the Fire-crowned Bishop *Euplectes hordeaceus* nesting in *Acacia orfata* shrubs during a drought year, when the grasses normally used for nesting failed to grow. One occupied nest was 2,7 m above the ground.

Compared to the sites mentioned above, nesting in grass or crops seems less surprising and has been recorded by numerous authors (Chapin 1954; Emlen 1957; Mackworth-Praed & Grant 1955, 1962; McLachlan & Liversidge 1958; Skead 1956, 1965; Vincent 1949). During February 1976 large flocks of Red Bishops were seen over a field of *Zea mays* (mealies or maize) across the valley from the study colony (see Fig. 2). The regularly-spaced males perched on top of the mealie plants suggested that they were holding territories there, and a search revealed over 150 nests, with both chicks and eggs present. The nests were built of strips of leaf-blade from the mealies, positioned either between two stalks, in the angle between a leaf and the stalk, or in the fronds of the heads. Following the exceptional rains, the ground was completely waterlogged, and I sank in above the ankles at each step. It proved impractical to carry out regular nest inspections in this colony, but when breeding had ended the field was searched thoroughly, every nest being pulled down and destroyed as it was checked, to avoid counting any twice. For convenience three height categories were used: below head height (1,7 m); above head height but within reach (1,7 - 2,2 m); and out of reach (above 2,2 m). A total of 267 nests was found, of which 65 were lined and had thus been occupied by a female (24,3%). Only 24 nests (9%) were below head height; 121 (45,3%) were in the range 1,7 - 2,2 m and 122 (45,6%) were above 2,2 m. Even if these nests are added to the total occupied at the study colony during 1975-76, the total is still only 99 occupied nests (21% of those built), as against 168 nests occupied (44% of those built) in 1976-77.

None of the nests in the mealie field displayed the type of damage associated with rodent predation. Four nests still contained a single egg, which had presumably failed to hatch, and one a full clutch of three eggs. In three nests there was a dead chick, in one two dead chicks and an egg, and in one a dead chick and an egg. If the 65 occupied nests had the same average clutch size as the study colony (see Table 34), they would have contained 189 eggs.

On 26 January 1977 this mealie field was again searched thoroughly. The plants were not as tall as in the previous year, and of the 24 nests found, only one was above head height. Three nests contained eggs. The ground was dry and firm underfoot, and a few days later the field was reaped for silage. Consequently there was no successful breeding at this site in 1977.

Nesting by immature males

Skead (1956) has described nest-building by immature birds, which almost reached the proportions of a "colony".

I did not observe this in the Cape (Craig 1973), but at Malton during the 1975-76 breeding season the central section of the reed-bed along the dam wall (see Fig. 20) was frequented only by brown-plumaged birds. On two occasions nest-building was observed, and 22 nests in this area which received the rating "very scruffy" were probably the work of immature males. There were also many incomplete rings, and other evidence of weaving activity.

Ringing at the breeding colonies has shown that they are frequently visited by immature males, but they are normally chased off by the territory holders before they have the opportunity to settle for any length of time. Because of the small number of colour-marked males, no accurate count of the breeding population was possible, but in 1975-76 the maximum number of territory-holding males at any visit was 12, whereas during 1976-77 more than 20 males were often seen on the colony, and the number of territory-holders was estimated at 25 on the dam, with a further five along the stream as far as the waterfall (see Fig. 20). Since some of the colour-marked birds were known to have disappeared during the season, and their territories been taken over by unmarked birds, these must be minimum estimates of the number of resident males during the entire period.

Thus when a colony is not occupied to full capacity, the immature birds have the opportunity to take up territories and build nests. The number of birds holding territories in the mealie field during 1975-76 was estimated at 30, and it seems likely that some of these birds bred at the study colony in the following season. Brenner (1966) found that the number of territorial Red-winged Blackbirds *Agelaius phoeniceus* in his breeding population varied between 17 and 21 during a five-year study, but the number of females nesting in the colony varied from seven to 42. It is perhaps significant that in the Red-winged Blackbird the female builds the nest, not the male as is the case in the Red Bishop. Immature birds are more likely to attempt nesting where conditions are not ideal.

Egg-laying and the nesting period

The eggs of the Red Bishop are a plain pale blue colour, but rarely eggs with fine black spots are found (Winterbottom 1971; Woodall 1971). Several other *Euplectes* species have blue eggs, occasionally spotted: *E. hordeaceus* (Winterbottom 1971), *E. gierowii* (Mackworth-Praed & Grant 1973) and *E. nigroventris* (Mackworth-Praed & Grant 1955). For *E. franciscanus* only unmarked blue eggs have been recorded (Mackworth-Praed & Grant 1973). In addition the Golden Bishop *E. afer* has dull white eggs with small dark spots (Winterbottom 1971), while for *E. diadematus* Nørgaard-Olesen (1970) has described plain blue eggs, but Cunningham-Van Someren (1971) and Williams (1962) state that the eggs are pale blue, lightly blotched and spotted with black and grey. It is possible that in this little-known species there may also be individual variation. There is thus a close similarity between the eggs of all the typical *Euplectes* species, whereas the members of the sub-genus *Coliuspasser* have much more heavily-marked eggs with considerable variations in pattern and colour.

An abnormal first egg, almost round and measuring 12 mm x 10,5 mm was laid in one nest. On the following two days, two normal eggs measuring 20 mm x 14,5 mm were laid, and these both hatched. Priest (1936) also found an undersized egg 10 mm x 12 mm, and he states that it contained no yolk.

The eggs were normally laid on successive days, as was the case in the studies of Skead (1956), Schmidt (1968) and Woodall (1971). Woodall (1971) records one case of four eggs being found in two days, and suggests that this was due to two females laying in the same nest - Schmidt (1968) has also suggested that this may occur in some cases. I found one nest in which three eggs were laid in two days, but since the inspections were not at the same time on each day, this need not have been an exception to the normal rate of laying. Skead (1956) found a few other irregularities: in one instance an interval of three days between the second and third eggs, and in two instances an interval of two days between the second and third eggs. My records show one nest with the second egg two days after the first; two nests with the fourth egg two days after the third; and seven nests with the third egg two days after the second.

With only a single daily nest inspection, it is difficult to determine a precise incubation period. Previous records range from 11 to 14 days, generally about 13 days (Schmidt 1968; Skead 1956; Woodall 1971). From my records it appears that the minimum interval from the laying of the last egg to the hatching of the last chick is 11 days and the maximum interval 14 days. However, in most cases it seemed likely that incubation had started before the clutch was complete, as suggested by Schmidt (1968). Maclean (1973) found this to be the rule in the Sociable Weaver Philetairus socius, and Newton (1972) states that incubation starts with the second last egg in European finches. Consequently I calculated the time from the laying of the second egg until the hatching of the first chick: 11 days in two nests; 12 days in 30 nests; 13 days in 42 nests; and 14 days in three nests. The normal incubation period is evidently 12-13 days.

Schmidt (1968) found that the chicks hatched on two or three successive days, but Skead (1956) recorded even more irregular hatching, with one nest where the third chick emerged three days after the others. My records are much more regular, with the chicks in 22 nests hatching on the same day, over two successive days in 41 nests, and over three successive days in only nine nests. In most small passerines hatching of the clutch is well synchronized (Lack 1968), but in several Arctic passerines Hussell (1972) found asynchronous hatching to be the rule, with periods of up to four days in some species. This may represent an adaptation to extreme environmental conditions.

The nestling period of the Red Bishop is given as 14-16 days (Delacour & Edmond-Blanc 1933; McLachlan & Liversidge 1958; Schmidt 1968; Skead 1956). This is even more difficult to determine, since from the age of ten days the chicks are liable to flutter out of the nest if disturbed. For this reason I ringed the chicks at eight to nine days old, and thereafter disturbed them as little as possible. In one instance the chicks flew from the nest at 11 days, although they continued to return to the nest for three or four days afterwards. Seventeen nests in which premature fledging could be excluded gave a range of 12-16 days in the nest, on average 13,5 days. For these nests, the total time from the laying of the first egg until the fledging of the last chick was 27-31 days, with a mean of 28,3 days. I do not know how long the female continues to feed the chicks after they finally leave the nest, but it is probably five or six days. A hand-reared bird began to feed for itself at 14 days, although it continued begging up to the time of its release at the age of 40 days (Mrs. H. Laycock, pers. comm.). If one assumes that the female accepts and begins lining the nest about three days before laying the first egg, a successful breeding attempt will occupy five to six weeks.

Clutch size

The normal clutch of the Red Bishop is 2-4 eggs, most commonly three (Winterbottom 1971), although up to seven have been recorded in one nest (McLachlan & Liversidge 1958). I have never found more than four eggs in a nest. The clutches recorded in the study colony are shown in Table 34. Three eggs was the commonest clutch size in both years, but one- and two-egg clutches were much more frequent in 1976-77 than in the previous season.

Figure 23 shows two very distinct peaks in egg-laying in both years. Breeding in 1975-76 can be conveniently divided into the periods November to January, and February to March, while in 1976-77 November to December and January to February constitute the two halves of the season. They are compared in Table 36.

There is no consistent pattern, but neither the mean clutch size nor the number of clutches is significantly different between the two periods. The peaks in egg-laying during 1976-77 lie six weeks apart, for 1975-76 seven to eight weeks apart. Thus if the duration of a successful nesting attempt is taken to be six weeks, it is possible

TABLE 35

The breeding success of the Red Bishop at Klawervlei

	No.	% eggs laid
Eggs laid	91	100
Robbed	12	13,2
Survived to hatching	79	86,8
Failed to hatch	45	49,4
Chicks hatched	34	37,4
Abandoned	2	2,2
Chicks fledged	32	35,2
Total losses	59	64,8

TABLE 36

The clutch size of the Red Bishop during the first and second breeding periods at Malton

Period	c/1	c/2	c/3	c/4	Total no.	Mean size
1975-76						
A	0	4	13	1	18	2,83
B	0	1	13	1	15	3,00
1976-77						
A	4	23	52	4	83	2,67
B	4	27	49	0	80	2,56

that the same birds could be laying another clutch in the second half of the season. Since very few clutches were in fact successful, there is a strong likelihood of replacement clutches in the second part of the breeding season. Unfortunately no colour-marked females were seen at any stage. However, in two nests which were robbed before completion of the clutch, a second clutch was laid later in the same nest, and there is a strong possibility that the same females were responsible. The second clutches comprised three eggs and two eggs, and the intervals since the first clutches were 14 and 17 days respectively.

Breeding success

A detailed breakdown of the breeding success of the study colony is given in Table 37. In January 1976 I was absent for seven days, during which time the eight eggs listed as "hatching unknown" were due to hatch. On my return these nests had been robbed; these eggs are excluded from the total known to have survived until hatching, and some of the percentages adjusted to a total of 90 eggs.

During the 1975-76 breeding season, predation and the heavy rains were equally important sources of mortality, while in the following season predation alone was the chief cause of nest failure. If the percentages "robbed" and "drowned" are combined, they account for 74,4% and 76,4% of the losses in the respective seasons. The eggs which failed to hatch included two full clutches of three eggs in 1975-76, and two two-egg clutches and a three-egg clutch in 1976-77; these were presumed deserted. It appears that there were more infertile eggs in 1975-76. Seel (1968) found that 12% of the surviving eggs of the House Sparrow <u>Passer domesticus</u> and 7% of those of the Tree Sparrow <u>P. montanus</u> failed to hatch, while in Ulbricht's (1975) study of the Reed Bunting <u>Emberiza schoeniclus</u> 14,5% of the eggs were infertile. Here the percentages for the two breeding seasons were 23,7% and 11,4% - the former figure does seem rather high.

TABLE 37

The breeding success of the Red Bishop at Malton

	1975-1976		1976-1977	
	No.	% eggs laid	No.	% eggs laid
Eggs laid	98	100	438	100
Robbed	16	17,8	158	36,1
Cuckoos	0	0	3	0,7
Floods	15	15,3	0	0
Other causes	0	0	14	3,2
Hatching unknown	8	8,2	0	C
Survived to hatching	59	65,5	263	60
Failed to hatch	14	23,7	30	11,4
Chicks hatched	45	50	233	53,2
Robbed	12	13,3	176	40,2
Evicted by cuckoo	0	0	3	0,7
Rains	22	22,4	1	0,2
Other causes	1	1	13	3,0
Chicks fledged	10	10,2	40	9,1
Total robbed	36	36,7	334	76,2
Total drowned	37	37,7	1	0,2
Total losses	88	89,8	398	90,9

The eggs lost to other causes were those which fell out of the nest due to movement of the supporting reeds, and those which disappeared at the time of hatching. Since the birds leave unhatched eggs in the nest, these probably represent chicks which failed to survive the hatch and were removed by the female - Seel (1968) has observed House Sparrows removing the dead bodies of such chicks, and incompletely hatched eggs. In one nest three successive eggs fell through the bottom within a day of laying - the female concerned had not chosen well! Chicks lost through other causes include those which survived the hatch, but presumably died and were removed later, and those found dead in the nest from unknown causes. On one occasion a female was seen carrying insects and repeatedly approaching the nest; the dead young had full crops, so they had not starved. As described above the eggs often hatched on successive days, and in two nests the smallest in a brood of three was found dead in the bottom of the nest after the others had fledged. Skead (1956) also recorded the death of nestlings without any apparent cause.

Apart from flooding, rain sometimes caused the death of nestlings through exposure when the nests were soaked through, even though the chicks were still being fed. Only one case was recorded in 1976-77, but in the previous season after three days of steady rain during March, 14 of the 18 chicks died. The survivors were the only ones which were fully feathered. Woodall (1971) found three dead chicks with full stomachs after a night of driving rain.

Less detailed records are available for the Western Cape colony on the farm "Klawervlei", since the nests were only checked at intervals of about three days (Craig 1973). The data are summarised in Table 35.

At Klawervlei the only chick casualties were those left in the nest when the birds abruptly abandoned the colony. The eggs which failed to hatch represented the major source of mortality. Only three were in clutches where the other eggs hatched; 11 clutches of three eggs, two of two eggs, and one each of four eggs and one egg were apparently deserted. Reed (1968) states that the Red Bishop is liable to desert if the nest contents are checked too often, but there was no indication of this at Malton. However, at Klawervlei I often used mist-nets at the breeding colony during the day, in an effort to colour-mark the birds for behavioural observations. This might have been responsible for the number of deserted clutches at this colony; at Malton no netting was done while there were occupied nests in the colony. Schmidt (1968) has recorded a colony in which "many nests, even some containing three eggs, were deserted". There was no evidence of human disturbance and his visits were infrequent, so it is possible that unaccountable large-scale desertion of clutches may occur in the Red Bishop.

Lack (1966) has discussed the relationship between breeding success and clutch size, suggesting that the commonest clutch should be that which on average produces the greatest number of surviving young. Haukioja (1970) showed that in the Reed Bunting the most efficient brood size was five, which was also the most common. Productivity of clutches was directly related to their frequency of occurrence in this species. By contrast Maclean (1973) found that the fledging success of the Sociable Weaver increased with increasing clutch size. The figures for the Red Bishop are shown in Table 38. In the first season at Malton, when conditions were assumed to be poor, two-egg clutches were much more successful than three-egg clutches. However, in the following season three-egg clutches were hardly more successful, although the success of two-egg clutches had declined markedly. Four-egg clutches were now the most successful. In the Cape, clutches of three were marginally more successful than those of four, with clutches of two less successful than either. There is no pattern apparent here, and data over a longer period are required.

In species with a restricted breeding season, breeding success varies in the course of the season. Thus Snow (1970) has shown for the Blackbird Turdus merula that success is high for early broods, then declines, but increases for late broods. This is in part due to the age

TABLE 38

The breeding success of the Red Bishop in relation to clutch size

Clutch size	Eggs laid	No. hatched	%	No. fledged	%
Malton 1975-76					
2	10	6	60	4	40
3	78	32	41	6	7,7
4	8	7	87,5	0	0
Malton 1976-77					
1	8	1	12,5	0	0
2	100	47	47	10	10
3	303	180	59,4	26	8,6
4	16	5	31,2	4	25
Cape 1972					
1	2	0	0	0	0
2	12	5	41,7	3	25
3	69	26	37,7	26	37,7
4	8	3	37,5	3	37,5

TABLE 39

The date of egg-laying in relation to the success of Red Bishop clutches at Malton

Month	% successful clutches 1975-1976	1976-1977
November	0,0	35,0
December	8,3	21,2
January	16,6	5,5
February	20,0	3,1
March	20,0	

of the birds breeding at different stages of the season, and in part to increasing predation in the first half of the breeding season. In other species such as the Great Tit Parus major (Lack 1966) and the Brewer's Blackbird Euphagus cyanocephalus (Furrer 1975) early broods are most successful, and thereafter breeding success declines. The Hairy Hermit Glaucis hirsuta illustrates a third possibility, with late nests significantly more successful (Snow & Snow 1973). In the two breeding seasons of the Red Bishop at Malton the results were reversed, as shown in Table 39. This can be explained by the effects of heavy rains and predation being more severe early in the 1975-76 season, whereas in the following year predation was very much heavier later in the season.

The nests destroyed by flooding were those along the stream and in the immediate vicinity of the inflow into the dam; those along the wall were unaffected by floods (see Fig. 20). However, there is no indication that any particular nest was more likely to escape predation due to its location in the colony. The male at the waterfall had successful nests in both years, but this was primarily due to early breeding rather than to a favourable position. The territories along the stream are perhaps suboptimal, but otherwise there is no apparent advantage in a male occupying a particular territory.

Parasitism by the Didric Cuckoo Chrysococcyx caprius

The Didric Cuckoo is perhaps the best-known of the South African cuckoos, and the Red Bishop is one of its major hosts. Roberts (1909) claimed to have found eggs of the Emerald Cuckoo Chrysococcyx cupreus in Red Bishop nests, but Jensen & Jensen (1969) reject all records of weaver hosts for this species.

At Malton Didrics were heard calling from October onwards, and the last birds were seen during March. As noted by Jensen & Vernon (1970), juvenile birds appear to remain for some weeks after the adults have left. During both breeding seasons male Didrics were heard and seen in the vicinity of the study colony, and in February 1976 a female was seen on the colony inspecting a Red Bishop nest. There was no evidence of parasitism during the first season, but there may have been Didric eggs in clutches which were lost. In the 1976-77 breeding season three Didric chicks were found. In one nest the Didric had hatched two days after the host chicks, and failed to evict them. At seven days old the Red Bishop chicks were already well-feathered while the Didric was still naked and blind, but unfortunately this nest was robbed. The other two Didric chicks evicted the Red Bishop chicks on the second and third day respectively. Reed (1968) has also recorded cases in which Didrics failed to evict the hosts; this response is apparently not shown after the fourth day. He found that eggs are also evicted, but Jensen & Vernon (1970) suggest that Didrics find eggs more difficult to evict, while Brosset (1976), experimenting in tropical Africa, found that Emerald Cuckoo chicks failed to evict eggs of the host, whereas chicks of the Red-chested Cuckoo Cuculus solitarius evicted eggs.

In the Transvaal, Reed (1968) found 7-50% of the nests in Red Bishop colonies parasitized; in the vicinity of Pietermaritzburg Jensen & Vernon (1970) found up to 42% of Red Bishop nests parasitized. They suggest a peak in breeding during January in Natal. The three Didirc chicks recorded at Malton must have hatched from eggs laid in the second week of December, allowing about 12 days for incubation (Reed 1968). For the two chicks which fledged the nestling periods were 17 days and 21 days, which are close to Reed's (1968) estimate of 19-20 days.

Field experiments with models of the Brown-headed Cowbird Molothrus ater, a parasitic icterid, showed a direct relation between the aggressive responses of their host species and the intensity of parasitism on the species concerned (Robertson & Norman 1976). These workers suggest that it may be a learned response, but it is not necessarily successful in preventing parasitism - egg removal is a much better defence. However, in colonial species with group defence, such as the Red-winged Blackbird, attacking cowbirds may prove effective. There is a close parallel to the situation in the Red Bishop, since males of this species will defend the colony area against strange conspecifics (Craig 1974), and will attack Didrics perched anywhere near the colony. In an active colony where some males are present throughout the day, this may be quite effective against parasitism. Verheyen (1953) has seen male Fire-crowned Bishops attack a Didric Cuckoo, so this response may be quite common in the genus Euplectes. Egg removal is unlikely to occur, since the Red Bishop gens of the Didric lays blue eggs virtually indistinguishable from those of the host (Jensen & Vernon 1970; Reed 1968). Ottow & Duve (1965) have recorded differently marked eggs from Red Bishop nests on two occasions, but it is not known whether these would have been accepted.

The incidence of parasitism appears to vary considerably, but in the present study it was not a significant cause of mortality in the Red Bishop clutches. Even though this species is an important host for the Didric Cuckoo in many areas, this probably has little impact on its breeding success.

Predation

The importance of nest predation at the study colony is shown by Table 37. During the course of my regular visits, I made enough observations to be reasonably sure of the identity of the major predators; reptiles, birds and mammals.

Unidentified snakes were seen on the farm twice, but never near the study colony. Small rodents appeared to be uncommon in this area, so that potential prey was scarce (although Reed Frogs Hyperolius marmoratus were abundant).

The only reptilian predator was the Nile Monitor Varanus niloticus, a notorius egg-robber (Pitman 1958). At least two specimens longer than 1 m and a small individual of about 50 cm were seen at the dam regularly. They often entered the reed beds, and on one occasion a large specimen was observed climbing up to a height of over 1,5 m and evidently investigating a Red Bishop nest, which I knew contained a single egg. It repeated the procedure at two other nests, but all three were left undamaged, and the egg had not been removed. However, later several nests containing chicks were found ripped open from the bottom, and two nests had actually been torn loose from the reeds and were floating in the water. This type of damage was ascribed to the Nile Monitor, since its head would be too large to insert through the nest entrance and remove the contents. The nest is probably first investigated with the tongue, then ripped open with the strong claws so that the contents fall into the water. Nests with chicks showed this form of damage much more frequently than those with eggs, and it is probable that the single egg mentioned above was overlooked.

At Malton the only potential avian nest predators were the cuckoos, coucals and egrets. Friedmann (1956) quotes an observation of Red Bishop males chasing a Jacobin Cuckoo Clamator jacobinus, which had evidently been robbing their nests, but no interactions between the two species were seen in the present study, though Jacobin Cuckoos often called from the thorn trees near the colony. The female Didric Cuckoo usually removes one of the host eggs (Ottow & Duve 1965), and since the dates of hatching of the chicks indicated that the Didric eggs had been added to completed clutches, this is assumed to have occurred here (see Table 37). At least two pairs of Burchell's Coucal Centropus superciliosus were resident at Malton, and aggressive reactions by other Euplectes to this coucal have been recorded (Fuggles-Couchman 1943; Lack 1935). However, coucals were seen at the study colony only twice, after the Red Bishops had finished breeding.

During December 1976 when cattle were grazing in this field accompanied by over 100 Cattle Egrets Ardeola ibis, several nests showed a new type of damage, with numerous holes where the weaving had apparently been forced apart without being broken, and the sides of the nests had been pushed in. This appeared to be the work of a pointed object, such as a Cattle Egret's bill. Van Ee (1973) has described their behaviour in a colony of Red-billed Quelea Quelea quelea. The cattle were moved within a week and the egrets left with them - there were no other records of avian predation.

Human interference could be excluded, leaving rodents and small carnivores as the only mammalian predators. Slender Mongoose Herpestes sanguineus were active in the grassland area, but it is unlikely that they would enter the water. A Clawless Otter Aonyx capensis was seen once at the main dam, but there were no signs of otters or Water Mongoose Atilax paludinosus around the study colony. Most of the nests robbed showed a small hole torn in the side, suggesting rodents as the culprits. Climbing Mice Dendromus mesomelas were found using abandoned Red Bishop nests on three occasions, but they are unlikely to take eggs. In the Cape, Schmidt (1968) found this species occupying Red Bishop nests which still contained deserted eggs.

In March 1977, as soon as breeding ended K.B. Willan set 40 small mammal traps around the fringes of the dam, and in the reed clumps. The traps were baited on the evening of 22 March, checked next morning and afternoon, and removed on the morning of 24 March. The catch was two shrews, Crocidura flavescens and C. mariquensis, one Otomys angoniensis and three Praomys natalensis. Of these species, only Praomys would be likely to eat eggs or chicks, but its very poor climbing ability (K. Willan, pers. comm.) makes this improbable. There was no evidence of the presence of the Striped Field Mouse Rhabdomys pumilio, which has been recorded as robbing the nests of several species in the Cape (Craig 1973; Elliott 1973; Rowan & Broekhuysen 1962). K. Willan suggests that rodents did not recolonize this area to any extent because of regular burning.

The negative results of the trapping suggested that the main predator during the 1976-77 season, and probably the most important predator overall, was the Brown Rat Rattus rattus. During one of my nest inspections, a very large rat was seen perched at the very tip of a reed, some 3 m above the water. When I attempted to dislodge it, it clung on very tightly, but finally dived into the water and swam off. Two days later, as I stuck my hand into a nest, a rat burst out through the back and disappeared into the reeds. The nest, which contained three chicks the previous day, was now empty. In the clump of reeds where the other rat had been seen, a clutch of three eggs had vanished from an undamaged nest.

C.B. Frith (1976) states that rats almost always entered a nest by bursting through the underside or the back of the chamber, which was the type of damage usually found at Malton. However, it is clear that rats are also sufficiently agile to enter and leave the nest by the entrance, so that undamaged nests were probably also robbed by them. K. Willan (pers. comm.) informs me that his trapping records show that rats tend to forage far into the field during the summer, returning to winter around human habitation. The incidence of predation at Malton is certainly consistent with the idea of a few animals visiting the colony periodically, as shown in Table 40 & 41.

Heavy rains were also an important source of mortality in 1975-76; Grimes (1977) records storm damage as the major cause of nest failure in the Red-headed Quelea *Quelea erythrops*. These tables show that in both years predation reached a high level only several weeks after breeding had started; thus early broods have the best chance of escaping predation. However, there is no evidence of a seasonal trend of increasing predation as has been found elsewhere (Robertson 1973), nor of decreasing predation, as Newton (1972, appendix 10) has described for British finches. Table 42 shows that, according to the evidence, rodents were by far the most important predators in both years.

Breeding success of individual males

The behaviour of the male Red Bishop was the subject of an earlier study (Craig 1973), and a descriptive account of the displays and vocalisations has been published (Craig 1974). The same terminology will be used here. Due to the lack of success in colour-ringing birds at the study colony, comparative observations on the behaviour of several males on neighbouring territories were first possible during the 1976-77 season.

TABLE 40

The weekly losses of Red Bishop clutches at Malton during the 1975-76 season

Week		Clutches present	No. robbed	%	No. lost to rains	%	Total % lost
Nov	4	1					
Dec	1	2					
Dec	2	7					
Dec	3	10	1	10	5	50	60
Dec	4	8					
Jan	1	12	2	16,7	2	16,7	33,4
Jan	2	7	6	85,7			85,7
Jan	3	3					
Jan	4	2					
Feb	1	3			1	33,3	33,3
Feb	2	4					
Feb	3	3	1	33,3			33,3
Feb	4	10					
Mar	1	12			1	8,3	8,3
Mar	2	11	1	9,1			9,1
Mar	3	10	2	20,0	4	40,0	60
Mar	4	3					
Apr	1	1					
Total		34	13	38,2	13	38,2	76,4

TABLE 41

The weekly losses of Red Bishop clutches at Malton during the 1976-77 season

Week	Clutches present	No. robbed	%
Nov 4	20	1	5,0
Dec 1	56	9	16,1
Dec 2	64	16	25,0
Dec 3	57	2	3,5
Dec 4	55	17	30,9
Jan 1	24	14	58,3
Jan 2	18	2	11,1
Jan 3	42	2	4,8
Jan 4	49	5	10,2
Feb 1	51	17	33,3
Feb 2	39	20	51,3
Feb 3	27	9	33,3
Feb 4	24	1	4,2
Mar 1	22	17	77,3
Mar 2	3	1	33,3
Total	172	133	77,3

TABLE 42

The proportions of Red Bishop clutches taken by different predators at Malton

Predator	1975-1976		1976-1977		Total	
	No.	%	No.	%	No.	%
Rodent	12	92,3	91	68,4	103	70,5
Monitor	1	7,7	35	26,3	36	24,7
Egret	0	0	7	5,3	7	4,8

Table 43 compares the behaviour and breeding success of three males for December 1976. The time observed reflects only the time which a male spent on the territory during the observation periods. Since I had a definite impression that activity varied during the course of the day (being maximal in the evening), only those observation periods which are directly comparable with respect to time of day are included in Table 43.

It is clear that vocalization occupies more time than any other displays in all three males. Birds 343 and 517 were neighbours, so that most of the time which they spent threatening was directed at each other; 106 was much less active in territorial defence. 517 was an exceptionally active male, who spent more time in display than any Red Bishop male I have monitored. He acquired more mates than the other two males, but during this month was less successful in terms of chicks fledged.

During January 1977 both 343 and 106 disappeared from the colony. They were sighted on subsequent occasions, but no longer occupied territories and took no further part in breeding activity. Male 517 initially took over 343's territory in addition to his own, but later a strange, unmarked male established himself in 343's territory. However, 517 retained a nest built by 343 - he improved it, and it was subsequently occupied.

Male 517 is compared with 521 in Table 44; once again vocalization was their major activity, but 517 was much more active in display. Nest-building is not included in these tables, since it is an irregular activity, which may however occupy long periods of time, if one is observing a male on a day on which he starts a new nest.

The breeding success of these four males, as well as two other colour-ringed birds, which were too far away for regular observation, is shown in Table 45. Territory size affects the number of potential nest sites, but territory quality hardly differed, since all the territories were in clumps of <u>Phragmites</u> in water of the same depth and at the same distance from the shore. All losses other than failure to hatch were due to predation. As discussed earlier, nest

TABLE 43

The behaviour and breeding success of male Red Bishops

Male	343	517	106
Minutes observed	135	160	155
% time sizzling	2,5	9,5	4,9
% time rattling	10,9	19,8	6,1
% time swivelling	1,4	4,0	1,7
% time bumblefly	0,2	0,4	0,3
% time display	15,0	33,7	13,0
% time pursuits	0,5	1,3	0,1
% time threats	2,2	2,4	0,5
% time defence	2,7	3,7	0,6
No. nests	4	6	3
No. ♀♀	3	5	3
Eggs laid	9	12	9
Chicks hatched	4	6	8
Chicks fledged	1	0	3

TABLE 44

The behaviour of two male Red Bishops

Male	521	517
Minutes observed	232	196
% time sizzling	2,1	4,1
% time rattling	7,0	14,0
% time swivelling	3,2	4,9
% time bumblefly	0,3	0,6
% time display	12,6	23,6
% time pursuit	0,5	5,3
% time threat	1,4	0,8
% time defence	1,9	6,1

TABLE 45

The breeding success of male Red Bishops

Male	Territory size (m^2)	No. nests	Mean ht.	No. ♀♀	No. eggs	No. eggs infertile	No. chicks	Chicks fledged
521	9	13	1,45	7	17	3	9	2
517	9	10	1,08	8	19	0	14	0
272	8	12	1,35	7	17	2	10	1
757	12	4	1,00	3	11	0	8	1
106	2	3	0,75	3	9	1	8	3
343	3	5	0,91	3	9	1	4	1
All		47		31	82	7	53	8

height is not correlated with nesting success; here the male with the lowest nests was the most successful, while 521 had one nest 2 m up robbed.

Male 517 was the most successful in terms of mates acquired and chicks hatched, but the only male to leave no offspring. In terms of the number of chicks fledged, male 106 was the most successful. The number of females is significantly correlated with the number of nests, which is hardly surprising, but there are no other significant correlations between any of the factors listed in Table 45. It would seem that successful mate attraction is no guarantee of male reproductive success.

Discussion

The breeding season

Since the survival of a species depends on its reproductive success, the breeding season must be adapted to the environmental conditions of its habitat. Baker (1938) was the first to review breeding seasons from an evolutionary viewpoint, and he introduced the terms "proximate cause" and "ultimate cause". These have come into general use in the form "proximate factor" and "ultimate factor". Immelmann (1972) defines them as follows: ultimate factors are environmental factors which have led, through natural selection, to the temporal or spatial restriction of a particular biological process; proximate factors are those external stimuli which initiate or maintain biological processes. The term "Zeitgeber", however, should be used only where endogenous rhythms are synchronized with environmental changes through external stimuli.

Food availability is the most important ultimate factor determining avian breeding seasons. Variations in the preferred food supply correlate well with differences in the breeding seasons of sympatric species (Newton 1972; Snow & Snow 1964). Quantitative data on the feeding of the Red Bishop during the year are lacking, but the work of Ward (1965a) supports the idea that food is the ultimate factor in the breeding of granivorous Ploceidae.

Immelmann (1971) considers avian reproduction under two headings: species which breed throughout the year, and those with a restricted breeding season. Even in species with continuous breeding seasons, individual birds show cycles of breeding activity, so that only a part of the population is breeding at any one time. The only species in which apparently continuous breeding has been recorded for one individual is the Moorhen Gallinula chloropus (Siegfried & Frost 1975).

The breeding season of the Red Bishop throughout its range was summarized in Table 30. This species has a sharply defined breeding season falling during the summer months, except in the Western Cape. The sexual activity of the males ends with the post-nuptial moult (see Chapter 2), and no out-of-season breeding has been recorded.

The existence of an internal rhythm of reproduction in birds was evidently first postulated by W. Rowan (in litt.) in 1926. It was taken up by other workers, and Baker & Ranson (1938) cited examples of tropical birds, including a species of Ploceus, which initially came into nuptial plumage during November in England, but in subsequent years moulted during the English summer.

Experimental studies depend on demonstrating that rhythms are maintained under constant conditions, and that the cycles then deviate to some degree from an exact 12-month period. Berthold et al. (1972b) showed that migratory warblers had a circannual testicular cycle, and more recently Gwinner & Eriksson (1977) have found both circadian and circannual rhythms interacting in the sexual cycles of male and female European Starlings Sturnus vulgaris. The present state of work in this field has been reviewed by Gwinner (1975). Lofts (1964) found evidence for seasonal changes in the testes of Red-billed Quelea under constant conditions, but to date this has been the only critical study of a ploceid. The possibility of an endogenous rhythm of moult and gonad development in Euplectes requires investigation.

Proximate factors

Several environmental factors are implicated in the control of avian breeding seasons. These will be reviewed briefly, and their significance in the Red Bishop evaluated.

1. Photoperiod

The discovery that exposure to artificially increased daylengths stimulated gonad development in a number of northern hemisphere birds led to photostimulation studies being conducted on a variety of species. The early work has been reviewed by Farner (1959), and more recent studies by Lofts & Murton (1968).

Since the first experimental studies took place in the northern hemisphere at relatively high latitudes, this led to a considerable over-emphasis of the biological significance of this response. Marshall (1960) criticised this attitude, and stated his belief that numerous species were uninfluenced by photoperiodicity. Farner (1967) has proposed three categories of avian photoperiodism: (1) primary photoperiodic species or populations, in which field and laboratory investigations have demonstrated that daylength is the major environmental factor controlling the time of reproduction; (2) secondary photoperiodic species, where daylength has a less significant role; and (3) species with permissive photoperiodic responses, which respond to experimentally altered daylengths, but do not use changes in daylength in their normal environment. He assigned the Indian Weaver <u>Ploceus philippinus</u> to category 2, and the Red-billed Quelea to category 3.

Of the Ploceidae, the Indian Weaver has been the subject of numerous photoperiod experiments. Thapliyal & Saxena (1964) claimed that males of this species could be maintained in full breeding condition throughout the year by artificially subjecting them to 15-hour days, but their data do not support this. Both Payne (1969) and Lofts & Murton (1968) consider that these results demonstrate a refractory period in the Indian Weaver. Earlier Lofts (1962) had shown that Red-billed Queleas responded to photostimulation, but had a clearly defined refractory period, during which the gonads regressed despite continued long photoperiods. The Orange Bishop Euplectes franciscanus has been shown to retain its nuptial plumage at all seasons if kept under long photoperiods in the laboratory (Brown & Rollo 1940; Rollo & Domm 1943). The gonad cycle was not investigated, and no mention was made of bill colour, a useful indicator of testicular activity (see Chapter 2). It was found that a photoperiod of 13-14 hours was optimal for inducing males to moult into nuptial plumage; if the photoperiod was reduced to 9-10 hours, the birds moulted into eclipse plumage.

The annual variations in daylength at the Cedara Meteorological Station are shown in Table 46. A comparison with the records of pre-nuptial and post-nuptial moult of the Euplectes species in the area (Tables 19 & 20) shows that most birds start the pre-nuptial moult in October. The first birds in full plumage were caught in November, when the daylength exceeded 13 hours. By March daylength was less than 13 hours, and all birds had started their post-nuptial moult by the end of this month. Thus it seems possible that the populations studied may have been responding to changes in daylength. In the Western Cape, however, breeding has been recorded early in July (N. Myburgh, pers. comm.) while the shortest day is 23 June. These birds must therefore have commenced their pre-nuptial moult while daylength was still decreasing. Moreover the range of the Red Bishop extends to the equator in East Africa (Fig. 1), and most Euplectes species have populations north and south of the equator. In European finches variations in the response to photoperiod correlated with the latitude of the breeding grounds of particular populations have been demonstrated (Newton 1972), but it is clear that few Euplectes populations would have the opportunity to use photoperiod as an environmental cue.

It is also noteworthy that, whereas stimulation by long photoperiods can induce a full cycle of gonadal development in male birds, females respond to only a very limited degree in all species which have been studied (Immelmann 1971). Here other stimuli are necessary before

TABLE 46

The annual variation in daylength at Cedara

Date	Sunrise	Sunset	Daylength
1 January	0505	1903	13h 58
1 February	0531	1857	13h 26
1 March	0551	1833	12h 42
1 April	0611	1757	11h 46
1 May	0628	1726	10h 58
1 June	0645	1710	10h 25
22 June	0654	1710	10h 16
1 July	0654	1713	10h 19
1 August	0643	1729	10h 46
1 September	0615	1746	11h 31
1 October	0540	1800	12h 20
1 November	0506	1820	13h 14
1 December	0454	1845	13h 51
22 December	0458	1859	14h 01

TABLE 47

The mean monthly temperatures at Cedara

Month °C	Mean maximum	Mean minimum	Mean daily
January	25,0	14,6	19,8
February	24,9	14,5	19,7
March	24,2	13,5	18,9
April	22,5	10,5	16,5
May	20,6	6,7	13,7
June	18,9	3,8	11,3
July	19,1	3,7	11,4
August	20,9	5,8	13,3
September	22,4	8,5	15,5
October	22,7	10,6	16,7
November	23,5	12,1	17,8
December	24,6	13,6	19,1

full breeding condition is reached.

Immelmann (1963) notes that light of different wavelengths may have markedly different effects on the development of the gonads in photoperiodic experiments. Thus variations in the intensity of the illumination could be important. There appears to be little information on this point from field studies. The sunshine records from Cedara show a mean daily value of 7,9 hours (S.D. = 0,1) for the winter months of June to August, with a marked decrease in spring to a value of 6,3 hours (S.D. = 0,6) for September to November. The value for summer is very similar; 6,2 hours (S.D. = 0,3) for December to February. It would seem that this could provide only a timing mechanism for species breeding during the winter dry season.

2. Temperature

Temperature, in contrast to daylength, is subject to wide and irregular fluctuations in all areas. Consequently it does not constitute a useful indicator of the change of season, and even in Europe plays a minor role in determining the time of breeding.

Newton (1972) shows that the egg-laying pattern of the Chaffinch Fringilla coelebs is correlated with fluctuations in temperature, but also records the breeding of Scandinavian Redpolls Carduelis flammea while the ground was still snow-covered and temperatures dropped to $-20^{\circ}C$. Kluyver (1952) found that temperature was only one of many factors which could stimulate or retard gonad development in the Great Tit to some degree. Elliott (1973) has suggested that rising temperatures are a contributory factor in early breeding of the Cape Weaver in the Western Cape, where both the Red Bishop and the Cape Weaver start breeding during the winter. Lofts & Murton (1966) concluded that for pigeons in Britain sudden changes in temperature may be more important than absolute temperatures, while for some species the effect of temperature may be indirect, operating through its influence on the food supply, in particular insects (Brenner 1967). Most workers would agree with Marshall (1960), and assign temperature a role among the accelerators and inhibitors of the reproductive cycle.

The monthly temperature records for Cedara are shown in Table 47. No data are available for Malton, but summer temperatures may be higher, and frost in winter is exceptional - at Cedara frost may occur from May to August. It is clear that at no time of the year can temperature be considered a limiting factor for homoiothermic vertebrates in this region, and its influence on the breeding cycle of the Euplectes species is regarded as negligible.

3. Rainfall

In many tropical and subtropical environments the annual alternation of wet and dry seasons represents the major periodic change in the environment. In the arid regions of Australia Immelmann (1963) has shown that there is no regular breeding season for the birds, but breeding may take place at any time if there is an adequate fall of rain. Similarly Maclean (1970) noted the influence of rainfall on the breeding of birds in the Kalahari. However, Immelmann (1967, 1970) found that the effect of rainfall was less dramatic than in Australia, and the African arid-zone species appeared to show a more obvious internal rhythm of reproduction.

Even in less arid areas, rainfall exerts a considerable influence. Snow (1976), reviewing the annual cycles of the Neotropical Cotingidae, found a close correlation with the rainfall regime throughout their range. Amongst non-passerines Kemp (1976) has demonstrated that rain is a factor determining the breeding season of many African hornbills. The contrast between north temperate and subtropical species is well illustrated by studies of the sexual cycles of pigeons in Britain and Australia. Lofts & Murton (1966) could find no evidence for rainfall effects on the breeding of the Woodpigeon Columba palumbus, but Frith et al. (1976) concluded that rain had a significant influence in three of the four species investigated.

There have been suggestions that certain desert birds can respond to the sight of rain (reviewed by Immelmann 1963, 1971), but in most cases the effects of rain operate through its influence on the vegetation and on other forms of life such as the insects. Maclean (1973) concluded that rain itself may not be a direct proximate factor for the Sociable Weaver in the Kalahari, although breeding is invariably preceded by rain. Nevertheless Payne (1969) was able to stimulate ovarian development in female Tricoloured Blackbirds Agelaius tricolor in autumn by simulated rainfall alone. Males did not respond, nor did the closely related Red-winged Blackbird, so that this seems to be a special case. The experiment of Marshall & Disney (1957), who provided caged Red-billed Quelea with fresh grass, artificial rainfall and insect food, demonstrates a behavioural response to the availability of nesting material rather than the induction of the breeding season as claimed.

The Ploceidae are certainly dependent on the availability of fresh, pliable material for weaving their nests. In Uganda Whybrow (1950) recorded a delay of three weeks in the start of nesting of the Fire-crowned Bishop during a drought, primarily due to the lack of suitable grass for nesting. Skead (1975) also regards rainfall as important in providing new growth of nesting material for waxbills, and he saw Masked Weavers Ploceus velatus start building within a week of the appearance of suitable green grass. Many Icteridae build their nests in a similar manner, and Wagner (1960) observed sporadic nest-building extending over two months in some Mexican species, when the rains were interrupted by dry spells.

Moreau (1950) cites a most unusual response to rainfall in Euplectes nigroventris in Tanzania during 1937. There had been a normal breeding season in April of that year, but when abnormally heavy rains fell in November, males came into plumage and began to build nests. However, the rains ceased and egg-laying did not occur. In 1938 eggs were laid early in May, following rain in April. Stark (1900) stated that the Golden Bishop appeared to migrate in Natal, and several authors have commented on this species' irregular arrival at breeding areas, suggesting a response to erratic rainfall (Brooke 1966; Haagner 1901;

Lynes 1924; Skead 1965). My only personal experience with the Golden Bishop was on the farm "Hopefield", 30 km north of Bloemfontein. During December 1972 males in full breeding dress and accompanied by females were caught in feeding flocks with Red Bishops and Red-billed Quèleas. There was no sign of nesting activity. Then in March 1973 heavy rains fell in the area, flooding some shallow pans near the house, where the birds bred successfully and then disappeared. They were not seen during the drought of the following year, but nested at the same site in April 1975. It seems that in this species the period of actual egg-laying may represent only a small part of the time during which the males are in nuptial plumage.

For the Western Cape, Rowan (1953) records early breeding in the Cape Weaver at the beginning of June instead of during July, and suggests a connection with the exceptionally heavy rains of April of that year. Elliott (1973) proposes that dry weather in June may stimulate early breeding in this species, following good rains earlier. The early breeding of the Red Bishop in the Cape mentioned above occurred in a year when July was an unusually dry and warm month. However, quantitative data for this region are lacking.

Haagner (1901) noted that the Red Bishop normally began breeding in the Transvaal during September-October, but that in one year the start of breeding was delayed until November, following a very dry winter. Both Woodall (1971) for the Red Bishop and Hornby (1970) for the White-winged Widow Euplectes albonotatus have recorded late breeding following a dry period.

It is likely that rainfall has both long-term and short-term effects on the breeding of the Red Bishop. Favourable conditions during the year, due to good rains, will result in more intensive breeding activity in the following summer, while the rains in the spring immediately preceding breeding will determine the period of peak activity, and further influence the overall intensity of breeding. Brooke (1966) rightly drew attention to the existence of such a relationship, though I do not agree with his interpretations. Since breeding in Rhodesia reaches a significant level in the second half of December, rainfall in November is probably too late to exert the influence which he claims, and records for the earlier part of the year should be examined. The data of Hornby (1970) support the idea of a cumulative effect of the rainfall over several months preceding breeding. It is also important that rainfall and breeding data for the same locality should be compared, as Brooke (1966) cites instances of considerable local variation in the timing of breeding Red Bishop, yet he has lumped data for the whole of Rhodesia in his paper. My records for only two seasons are inadequate to show how rainfall affects the date of breeding, but there is evidence for the ecologically similar Red-winged Blackbird that drought does not affect the time of nesting (Brenner 1966).

4. Food

The role of food as an ultimate factor in the evolution of breeding seasons has already been mentioned. However, there is evidence that for many species food may also be the main proximate factor controlling breeding.

Even in the humid tropics close to the equator, where seasonal climatic changes are minimal, it has now been shown that most bird species have a clearly defined breeding season (Brosset 1971; Fogden 1972; Ruwet 1964a; Snow & Snow 1964; Ward 1969a; Ward & Poh 1968). All these workers have found indications that there are seasonal variations in food supply, particularly in the abundance of insects. In South African savannah, Kemp (1976) has demonstrated that arthropod biomass is closely linked to rainfall, so that breeding in the local hornbill species depends on food as the main proximate factor. In his study of the Sociable Weaver Maclean (1973) found that arthropods made up the major part of the diet, and he also suggested that food and not rainfall was the real proximate factor in stimulating breeding. Frith <u>et al</u>. (1976) concluded that, although the gonad cycles of the pigeon species studied were mainly controlled by changes in photoperiod, the abundance of food and the effects of rainfall on it were important in modifying the cycles. Some pigeon species may have extended or even continuous breeding seasons (Immelmann 1963; Lofts & Murton 1966; Snow & Snow 1964; Wagner 1960), and it has been proposed that this is related to the method of feeding the young on "crop milk", which makes them less dependent on environmental food supplies at this time, while the small clutch of one or two eggs places less strain on the female (Goodwin 1967). Finally, in a recent study of African rodents, Taylor & Green (1976) found that the food supply of granivorous species changes during the rainy season, and breeding was marked by a change in diet as shown by stomach contents.

Payne (1969) was able to induce ovarian development in female Tricoloured Blackbirds in autumn by supplementing their diet with insects, but found no response in female Red-winged Blackbirds, or in males of either species. An experimental study of free-living Carrion Crows Corvus corone in Scotland (Yom-Tov 1974) showed that excess food affected the date of breeding, although it had no influence on breeding density or clutch size. He concluded that the pattern of food distribution was the ultimate factor affecting breeding success in this species.

Perrins (1970) has stressed the importance of food availability for the female birds prior to egg-laying, and both Fogden (1972) and Ward (1969a) have suggested that the protein condition of individual birds is the critical factor determining when they will breed. This aspect has now been investigated in detail in the Red-billed Quelea by Jones & Ward (1976). Comparison of the pre-breeding changes in protein and fat reserves showed that female Red-billed Quelea increased their protein reserves by 80% prior to a breeding attempt, while fat reserves increased only slightly. Insects appear to provide most of their protein requirements at this time. Jones & Ward suggest that proximate control of breeding is provided by the individual's own physical condition, particularly the state of the protein reserves. Thus no environmental releasers are required. Jones (1976) has also observed female Red-billed Quelea ingesting large amounts of calcareous grit prior to laying eggs, and proposes that this is the main source of the calcium required for egg-shell formation, with calcium storage in the skeleton making little contribution. This is in direct contrast to the views of Burkholder (1974), who studied serum calcium levels in female Red-winged Blackbirds. He considered that diet had little or no direct effect, with the calcium being derived from a reserve in medullary bone.

The work on the Red-billed Quelea is obviously highly relevant for the closely-related Euplectes species. There is no reason to assume that rainfall has any direct effect on these savannah species, and its influence must be through its effects on the vegetation and the food supply. Until there is further information on the feeding of the Red Bishop, in particular on the role of insects in its diet, no simple comparisons are possible, but I shall provisionally regard Jones & Ward's (1976) hypothesis of proximate control by individual protein condition as applying to the Red Bishop and related species. The question of calcium metabolism in passerines evidently requires more detailed investigation, perhaps using labelling with radioactive isotopes. The tremendous increase in breeding at Malton following the favourable period of 1975-1976 seems to support the hypothesis that the better physical condition of the females was a critical factor, and it is notable that the start of breeding in 1976-77 was much better synchronized than in the previous season (Fig 23).

Clutch size

This topic has received considerable attention, because of its relevance to the two major theories of bird population control: adjusted reproduction, and adjusted mortality. At present there is no satisfactory general theory of avian populations, but Cody (1966) has attempted to produce a general theory of clutch size, based on the time and energy allocations of reproduction. He assumes that clutch size is a hereditary phenotypic characteristic, that is to some extent dependent on environmental conditions. The factors known to influence clutch size will be considered below, in so far as they may be applicable to the Euplectes species. Lack (1966, 1968) discusses variations in clutch size in many species, while Klomp (1970) has also reviewed the subject in detail.

1. Genetic determination

In studies where the same individuals have been observed in successive breeding seasons, many authors have noted that the clutch size of individual females is less variable than the range found in the population (e.g. Haukioja 1970). This suggests at least partial genetic determination, but the only critical study appears to be that of Perrins & Jones (1974) on the Great Tit. This species has been studied in the vicinity of Oxford for many years (reviewed by Lack 1966), so that it was possible to make allowances for all the known environmental and age effects on clutch size before comparing the findings on over 200 birds. It was found that the remaining variations showed high heritability. Perrins & Jones (1974) emphasize that the female Great Tit does not inherit the tendency to lay a clutch of a particular size, but rather to lay a clutch of a certain size in relation to the mean clutch size of the population at that time. Some birds may, for instance, consistently lay a clutch about 15% smaller than the mean clutch size of that year.

2. Geographical variation

Moreau (1944) was amongst the first workers to examine this question. He found that in 38% of the species investigated, the clutches in Equatorial Africa were smaller than in South Africa, this trend being most marked in the passerines. However, he also noted that the clutch size of British birds exceeded that of closely-related African species by a much greater extent than the intra-African differences. A more recent comparative table is given by Lack (1968, p. 167). Haukioja (1970) recorded clutch sizes for the Reed Bunting in central Finland over several years, and showed that they were significantly larger than in Switzerland, but smaller than in Swedish Lapland. Hussell (1972) records a general increase in clutch size with increasing latitude in Arctic passerines, but finds irregularities suggesting that other factors are involved. Rowan (1966), with a more limited sample, showed that clutch size in the Cape Sparrow *Passer melanurus* was significantly larger in the Cape than in the Transvaal.

The most extensive records of clutch sizes for the Red Bishop are those of Benson *et al*. (1964), Brooke (1966) and Dean (1971). Unfortunately these are all based on nest record cards, where in many cases the nest was visited only once. Since this introduces considerable error, these records cannot be used for comparative purposes, and only studies in which nests were checked frequently are included in Table 48.

Since Skead (1956) does not give the numbers of c/1 and c/2 separately, one cannot calculate a mean clutch size from his data. It must be emphasized that only the present study and that of Schmidt (1968) include data from more than one breeding season, and Woodall (1971) suggested that the number of c/2 in his study might be higher than in an average year. If the Cape data are combined, giving a mean clutch of 2,6 and compared with the Natal mean of 2,7 there is no significant difference between the two areas. While there is some indication that clutches larger than four eggs may be commoner in the Cape than elsewhere, the present data provide no evidence for geographical variation in clutch size in the Red Bishop. Lack (1968) also lists differences in the clutch size of African passerine families in forest and savannah habitats. However, the work of Fogden (1972) and Ward (1969a) does not support his assumption that evergreen forest provides uniform food supply throughout the year, and at present there is no adequate explanation for any of the observed types of geographical variation in clutch size.

TABLE 48

The clutch size of the Red Bishop in Southern Africa

Clutch size	No. of clutches recorded				
	Rhodesia 17° 51'S	Natal 29° 30'S	E. Cape 32° 50'S	Cape (a) 33° 40'S	Cape (b) 34° 05'S
1	10	4	30	14	6
2	50	28		26	18
3	35	65	60	50	69
4	5	3	7	8	6
5-6	0	0	3	2	0
Mean	2,4	2,7		2,6	2,8

Note: Rhodesian data from Woodall (1971), Natal data from this study, E. Cape data from Skead (1956), Cape (a) data from Schmidt (1968), Cape (b) data from Craig (1973).

3. Age of the female

Several studies of long-lived seabirds such as the Kittiwake Rissa tridactyla (in Lack 1966) and the Arctic Tern Sterna paradisaea (Coulson & Horobin 1976) have shown that the clutch size tends to increase with increasing age in the females, finally decreasing again in old birds. Significant differences in the mean clutch sizes of first-year and older females have been demonstrated for some passerines such as the Blackbird and the Great Tit (Lack 1966), and the Reed Bunting (Haukioja 1970). However, in his study of the White Wagtail Motacilla alba Leinonen (1973b) found no differences in the reproductive performance of first-year birds and older females. This indicates that the effects of age may vary in different species, or may be masked by other factors in some years.

In captive populations of the Spotted-backed Weaver Ploceus cucullatus, females laid significantly smaller clutches in their first breeding season than in subsequent years (Victoria & Collias 1973). There are no data for the Euplectes species, but a similar effect of age may occur.

4. Population density

Lack (1966) has shown that there is an inverse relationship between population density and clutch size in the Great Tit in study areas in England and Holland. No such relationship was apparent for first clutches in Finland, but second clutches in all three areas were related to the size of the breeding population (von Haartman 1971). Löhrl (1974) was unable to confirm Lack's (1966) findings on the Coal Tit Parus ater, and he suggested that a number of other factors, whose importance may vary regionally, are involved in the relationship between population density and clutch size. Tompa (1967) in a study of the Pied Flycatcher Ficedula hypoleuca found increased breeding density decreased the frequency of feeding by the male, and may thus affect fledging success, but he concluded that breeding success was primarily dependent on environmental conditions.

It is interesting to note that in the 1976-77 breeding season, when there were more breeding birds at the study colony, the mean clutch size of the Red Bishops was significantly smaller: 2,62 as opposed to 2,91 ($t = 3,15$ d.f. $= 194$ $p < 0,01$). Annual variations in clutch size may be caused by a variety of factors, however, including the age composition of the population (see above) and the mean laying date of the population (Klomp 1970). In this case the age-composition of the breeding population was unknown. Figure 23 shows that laying was on average earlier than in the previous year - early laying results in an increased clutch size in many European passerines (Lack 1966, but *cf*. Haukioja 1970) - but factors other than population density may have been responsible for the smaller clutches.

5. Food supply

There is good evidence that in years of superabundant food some species may increase their clutch-size. This is particularly marked in species whose prey is subject to periodic fluctuations in numbers, such as the Tawny Owl *Strix aluco*, a rodent predator (Lack 1966), and the Bay-breasted Warbler *Dendroica castanea*, which preys on the spruce budworm (Cody 1966). For granivorous species, the effects of rainfall on the food supply have been discussed earlier, and several authors have shown that increased clutch sizes may follow good rains in ploceids (Maclean 1973; Moreau 1944). Brooke's (1966) data are unreliable because the clutch size records include an uncertain number of incomplete clutches, and the indiscriminate lumping of both rainfall and breeding data for a large area obscures many possible sources of local variation.

In their study of the protein reserves of the Red-billed Quelea, Jones & Ward (1976) showed that individual females producing c/2, c/3 and c/4 differed in the rate at which their reserves fell during egg formation. Most females initially produced one yolk more than the number of eggs actually laid, this yolk being resorbed subsequently. After presenting four possible models for the determination of clutch size in this species, they conclude that the actual clutch size produced on any occasion is the largest which the female can produce before the body reserves reach dangerously low levels.

The clutch size of the Red Bishops at Malton, however, was smaller in the 1976-77 season, when conditions appeared more favourable and many more clutches were laid. If the scheme derived for the Red-billed Quelea applies to this species, other influences must be operating to explain this apparent anomaly. These might include:

(a) a larger number of "first-breeders" at the study colony during 1976-77, with these birds laying smaller clutches;
(b) fewer insects, especially termites, during the drier summer of 1976-77 (Jones & Ward *op. cit.* regard insect food as most important in building up adequate protein reserves);
(c) increased breeding density reducing the clutch size.

It is misleading to regard the observed clutch size as a direct result of any single environmental factor, and we are still far from understanding the determination of clutch size in the Red Bishop.

6. Variations during the breeding season

In all passerine species which have been studied, the mean clutch size changes during the course of the breeding season. Two main patterns are found: either the clutch size is largest at the start of breeding, declining during the rest of the season; or the clutch size reaches a peak in the middle of the breeding period, being lower at both the start and the end of the season.

A decreasing clutch size during the breeding season is illustrated by species such as the Reed Bunting (Haukioja 1970), Great and Blue Tits *Parus major* and *P. caeruleus* (Lack 1966), the Coal Tit (Löhrl 1974), Pied and Collared Flycatchers *Ficedula hypoleuca* and *F. collaris* (Lack 1966), the Bullfinch *Pyrrhula pyrrhula* (Newton 1972), and the Sociable Weaver (Maclean 1973). Both hole-nesting and open-nesting species and both insectivores and seed-eaters are included in this category.

A peak in clutch size at the height of the breeding season is found in the Blackbird (Lack 1966), the Great Reed Warbler _Acrocephalus arundinaceus_ (Saitou 1976), the Greenfinch _Carduelis chloris_ and the Linnet _Acanthis cannabina_ (Newton 1972), the House Sparrow and the Tree Sparrow (Seel 1968), the Cape Sparrow (Siegfried 1972), and the Cape Weaver (Elliott 1973). This list again includes both hole-nesting and open-nesting species, but seed-eaters predominate. Two other African species do not conform to either pattern. Rowan & Broekhuysen (1962) found clutches of the Karroo Prinia _Prinia maculosa_ to be larger in the first and last months of breeding than in the intervening period. Morel (1969) showed that while the clutch size of the Red-billed Firefinch _Lagonosticta senegala_ varied little between different years, there were considerable variations in the course of the year "d'une interprétation difficile".

The monthly clutch sizes for the Red Bishop at Malton are shown in Table 34. They do not resemble either of the patterns described, but are very like the records for the Karroo Prinia. If the sparrows are not ploceid (see Sibley 1970), the only species for comparison within the family are the Sociable Weaver and the Cape Weaver. The former represents a special case both in habitat and social structure, but the Cape Weaver and the Red Bishop are often to be found breeding in the same reed-bed, and may exploit very similar food sources. The difference may be that the Cape Weaver was studied in a winter rainfall area, while the present study was conducted in a summer rainfall area.

7. Second clutches

Seasonal variations in clutches size will be influenced by individual birds laying more than once, since second or replacement clutches are generally smaller than first clutches. Lack (1966) notes that the type of seasonal change in clutch size found in the Blackbird is typical of birds which normally have several broods during the season; up to five broods have been recorded in this species. Haukioja (1970) found that second or replacement clutches in the Reed Bunting were either the same size or smaller than first clutches of the same birds, but Balát (1974) found that second clutches of the House Sparrow in central Czechoslovakia were significantly larger than the first clutches. This appears to be the only recorded exception to the "general rule".

Brooke (1966) regards the single peak in breeding activity of the Red Bishop in Rhodesia as indicating that few if any females are double-brooded. However, his presentation of the data has been criticised above, and no firm conclusions can be drawn from it. Mackworth-Praed & Grant (1962) state that this species is often double-brooded, and in captivity several broods have been recorded (Delacour & Edmond-Blanc 1933; Neunzig 1921). A captive pair of Orange Bishops produced three successive clutches, c/3, c/3 and c/2 (Eckleben 1974). Previous field studies of the Red Bishop provide no information on this point. In the present study there was some evidence that the birds might be double-brooded, but there was no indication that second or replacement clutches were significantly smaller than first clutches.

Breeding success

For any understanding of the population processes of a species the relationship between birth-rate and mortality must be determined. While the study of mortality is extremely difficult in free-living animals, their breeding is more easily observed. Birds have been especially well studied in this respect, but the distribution of the ornithologists has largely determined the species which have been studied over any length of time. Nevertheless, comparison with other work is valuable in suggesting what factors may be responsible for the observed differences.

Nice (1957) reviewed the nesting success of altricial birds on the basis of studies in the North Temperate zone. Summarising the available data, she found that 38-77% of the nests fledged at least one chick, the mean nest success being 49%. Of almost 22 000 eggs, 46% produced fledged chicks, with a range of 22-70%. Species with partly enclosed nests had a slightly higher rate of success, while hole-nesting species had an average fledging success of 66%. More recently Ricklefs (1969) has reviewed the subject of nesting mortality, basing his conclusions chiefly on American studies. He concluded that among temperate zone passerines, field and marsh-nesting species have the highest mortality rates. Tree- and especially hole-nesters enjoy higher success. Starvation of the young is commonest in field and marsh habitats. Generally arctic species have lower mortality rates than temperate species, and tropical species higher rates, because of the greater variety of predators. He notes that in the tropical environment, water- and marsh-dwelling non-passerines are more successful than passerines in the same habitats.

A selection of studies recording breeding success, calculated on the basis of the percentage of eggs laid which hatch and fledge, is shown in Table 49. No hole-nesting species are included, because under the artificial conditions of many studies based on populations using nest-boxes, fledging successes of over 90% are often recorded (Johansson 1972; Löhrl 1974). The list includes open-nesting palaearctic species (some of which inhabit reed-beds), open- and closed-nesting African species, Ploceidae and Icteridae. Of particular interest are the variations in success in different studies of the same species. Frequent reference will be made to this table in the following discussion.

Catchpole (1974) points out that the conventional method of calculating success as a percentage of the eggs laid can be misleading, since this assumes that each egg represents an independent observation. This is in fact not so, since factors such as predation normally affect the whole clutch. Consequently it is better to use the clutch (the nest) as the unit, a successful nest being one from which at least one chick fledges. Some authors use only one method of presentation, so that Table 50 omits some of the species in Table 49, and includes others. The overall coverage of nesting habitats remains the same, except for the addition of two tropical American species,

TABLE 49

The breeding success of some passerine birds

Species	Locality	% eggs hatched	% eggs fledged	Author
Alauda arvensis	England	68	46	Delius 1965
Motacilla alba	Finland	72,5	55,8	Leinonen 1973a
Melospiza melodia	U.S.A.	59,7	35,8	Nice 1937
Sylvia atricapilla	England	75,6	60,4	Mason 1976
Prinia maculosa	Cape	51	28	Rowan & Broekhuysen 1962
Acrocephalus arundinaceus	Japan	84,0	73,2	Saitou 1976
Acrocephalus scirpaceus	England	56,2	42,1	Catchpole 1974
Emberiza schoeniclus	Finland	-	48	Haukioja 1970
Emberiza schoeniclus	East Germany	60,2	20,4	Ulbricht 1975
Andropodus latirostris	Gabon	33,7	23,5	Brosset 1971
Pycnonotus barbatus	Gabon	30,8	15,4	Brosset 1971
Passer domesticus	Czech.	82,5	65,0	Balát 1974
Passer melanurus	Cape	72,8	59,5	Rowan 1966
Passer melanurus	Cape	64	25	Siegfried 1972
Passer luteus	Senegal	86,2	52,5	Morel & Morel 1973
Agelaius phoeniceus	U.S.A.	72,2	59,2	Smith 1943
Agelaius phoeniceus	U.S.A.	-	28	Holm 1973
Euphagus cyanocephalus	U.S.A.	77,2	39,3	La Rivers 1944
Spiza americana	U.S.A.	47,4	47,4	Harmeson 1974

TABLE 49 (continued)

The breeding success of some passerine birds

Species	Locality	% eggs hatched	% eggs fledged	Author
Quiscalus mexicanus	U.S.A.	69,7	60,3	Kok 1972a
Xanthocephalus xanthocephalus	U.S.A.	70,9	22,0	Fautin (in litt.)
Lagonosticta senegala	Senegal	45,9	28,8	Morel 1969
Uraeginthus angolensis	Transvaal	58	33	Skead 1975
Philetairus socius	Kalahari	41,8	13,1	Maclean 1973
Ploceus capensis	Cape	-	35	Elliott 1973
Foudia eminentissima	Aldabra	17,2	8,2	Frith 1976
Quelea quelea	Nigeria	95	83	Ward 1965b
Quelea erythrops	Ghana	76	53,5	Grimes 1977
Euplectes macrourus	Ivory Coast	-	38,5	Thiollay 1974
Euplectes orix	Cape	65,9	45,4	Schmidt 1968
Euplectes orix	Cape	37,4	35,2	Craig 1973
Euplectes orix	Natal	52,6	9,3	this study

Note: in some cases these percentages have been calculated from the figures given by the authors in the papers cited.

the White-bearded Manakin Manacus manacus and the Hairy Hermit. Where the figures quoted are averages based on several years of records, this will be discussed below.

The accuracy of published figures on nesting success has often been questioned, but these tables can be regarded as representative of the range of possible situations. Mayfield (1975) has described a useful method of calculating nest success, which permits the inclusion of incomplete data. In many field studies the nests are not found when started, nor followed to the conclusion. This results in observed loss rates being lower than the actual rates. To overcome this source of error he suggests measuring the exposure to possible loss in nest-days, and calculating the mortality and survival rates in these units at each stage of the nesting cycle. Rowan & Broekhuysen (1962) applied his methods (as described in an earlier paper), but they found that the success rates obtained for their study were very similar to those derived from conventional methods. In the present study inspections were sufficiently frequent for no corrections to be necessary.

From Table 49 it can be seen that while the hatching success of the Red Bishop falls well within the general range, the fledging success recorded in the present study is exceptionally low. The only comparable figures come from the studies of Brosset (1971), C.B. Frith (1976) and Maclean (1973). In the Cape fledging success was much higher, evidently due to a lower mortality at the chick stage.

During her six years of observations at the same locality, Nice (1937) found that breeding success in the Song Sparrow Melospiza melodia was very much higher for the first three years than for the last three years: 41,5% fledging success as against 23,4%. She ascribed the heavy losses of the second period to human interference, severe parasitism by the Brown-headed Cowbird and extreme weather conditions. Siegfried (1972) suggested that the marked differences between his results for the Cape Sparrow and those of Rowan (1966) could be explained by the fact that his study was conducted on birds breeding in farmland,

TABLE 50

The nesting success of some passerine birds and a humming-bird (Apodiformes)

Species	Locality	% nests successful	Author
Glaucis hirsuta	Trinidad	9,2	Snow & Snow 1973
Acrocephalus arundinaceus	Japan	86,7	Saitou 1976
Acrocephalus scirpaceus	England	50	Catchpole 1974
Fringilla coelebs	England	38	Newton 1972
Melospiza melodia	U.S.A.	47,4	Nice 1937
Motacilla alba	Finland	79,2	Leinonen 1973a
Turdus merula	England	38	Snow 1970
Turdus merula	East Germany	18,8	Stein 1974
Turdus philomelos	East Germany	18,5	Stein 1974
Sylvia atricapilla	East Germany	44,8	Stein 1974
Sylvia atricapilla	England	62	Mason 1976
Manacus manacus	Trinidad	19	Snow 1962
Passer melanurus	Cape	43	Siegfried 1972
Agelaius phoeniceus	U.S.A.	48,4	Francis 1971
Agelaius phoeniceus	U.S.A.	48,9	Holm 1973
Agelaius phoeniceus	U.S.A.	39,8	Payne 1969
Agelaius phoeniceus	U.S.A.	34,6	Blakley 1976

TABLE 50 (continued)

The nesting success of some passerine birds and a humming-bird (Apodiformes)

Species	Locality	% nests successful	Author
Agelaius phoeniceus	Costa Rica	21,5	Orians 1973
Euphagus cyanocephalus	U.S.A.	50,4	Furrer 1975
Spiza americana	U.S.A.	51,5	Harmeson 1974
Quelea quelea	Nigeria	93,7	Ward 1965b
Quelea erythrops	Ghana	67,2	Grimes 1977
Euplectes albonotatus	Rhodesia	33	Hornby 1967
Euplectes macrourus	Ivory Coast	46	Thiollay 1974
Euplectes orix	Cape	45	Schmidt 1968
Euplectes orix	Cape	36,4	Craig 1973
Euplectes orix	Natal	12,9	this study

Note: in some cases these percentages have been calculated from the figures given by the authors.

whereas Rowan's records were from suburban populations. Siegfried (1972) showed that most nests came to grief through being blown out by high winds; it is likely that in a garden habitat more sheltered sites would be available.

The nesting success of the Red Bishop in Natal is also much lower than most of the species represented in Table 50. The only similar results are those of Stein (1974) for the two thrushes, Snow & Snow (1973), Snow (1962) and Orians (1973). Snow's (1970) data for the Blackbird are compiled over a number of years, and in his paper he compares nests in urban and rural habitats, showing that success in the latter is lower; Stein's (1974) study area was in relatively undisturbed forest. In addition to the work of Nice (1937) discussed above, three other studies include records derived from several breeding seasons: Newton (1972) found a range of 18-60% success in the Chaffinch; Snow (1962) from 10-41% success in the White-bearded Manakin; and the data collected by Francis (1971) show a nesting success of 27-69% in the Red-winged Blackbird. Orians (1973) found an appreciably lower success rate for this species in a tropical marsh.

Predation

The role of predation in natural ecosystems is still being debated, and the best approach is to limit oneself to the particular situation being studied. In the case of breeding success in birds, the intensity of predation may vary considerably in different areas, but there is ample evidence for its importance from many studies.

Although predation is not generally regarded as heavy in the north temperate zone, several authors in Tables 49 & 50 mention predation as a major source of mortality. Delius (1965) states that in the ground-nesting Skylark Alauda arvensis, 90% of the losses are due to predation, although breeding success is still high. In Ulbricht's (1975) study 69% of the Reed Bunting's eggs were taken by predators at some stage of the breeding cycle, and Stein (1974) recorded a variety of potential predators, which were evidently responsible for the high nest losses of the thrushes.

Though he considered the Blackcaps Sylvia atricapilla to be less vulnerable to predators, their success was markedly lower than in England (cf. Mason 1976).

Lack (1966, 1968) has discussed nest losses in the tropical areas, and the very high rate of nest predation in tropical forest is stressed by Brosset (1971, 1974), Fogden (1972), Snow (1962) and Snow & Snow (1973). Orians (1973) compared the success of Red-winged Blackbirds in a tropical marsh with studies in temperate areas, and proposed that predation was an important limiting factor in the tropical environment.

Of the other studies showing low breeding success, Maclean (1973) remarks that most losses of chicks in the Sociable Weaver were due to predation, and the Aldabran Fody Foudia eminentissima lost 81% of the eggs laid and 48% of the chicks hatched to predators (C.B. Frith 1976). Only Siegfried (1972) found that predation was unimportant for the Cape Sparrow in his study area.

None of the previous studies of the Red Bishop give any information on predation, but Reed (1968) remarks that all the host species of the Didric Cuckoo in the Transvaal "suffer a fairly high degree of nest predation". As can be seen from Table 37, predation was very important for the colony at Malton.

Ward (1965b) considered that predation had no effect on the breeding populations of the Red-billed Quelea, and this was certainly the case at the colony where he made his observations. However, Thiollay (1975) records a very different situation at nine Red-billed Quelea colonies in Mali. Large numbers of avian predators; raptors, storks, herons, ibises, hornbills and crows in particular, assembled to feed on the nestlings. At one colony of 28 000 nests, 763 predators were counted, many of them being migrants which are especially abundant at that latitude in September. Thiollay estimated that 32% of the nests were destroyed between laying and hatching, and a further 25% of the nestlings were taken, and concluded that predation may considerably reduce reproductive success in this species. Van Ee (1973) and Pienaar (in litt.) give instances of

Red-billed Quelea colonies which failed completely because of intense predation.

1. The identity of the predators

Since one seldom sees a nest being robbed, the predator has to be tentatively identified from the traces which it leaves. For instance, in European woodlands broken eggshells left in the nest indicate that the Jay *Garrulus glandarius* was responsible (Stein 1974). Unfortunately most nests are simply found empty, as noted by numerous authors (e.g. Hornby 1967; Rowan & Broekhuysen 1962; Ulbricht 1975).

In relatively undisturbed areas, snakes are probably important throughout the tropical and subtropical zone. Maclean (1973) found that the Cape Cobra *Naja nivea* was responsible for heavy losses in the Sociable Weaver nests in the Kalahari Gemsbok National Park. Pitman (1958) has reviewed snake predation on birds in Africa, and it is clear from the accounts which he quotes, and from chance observations such as that of Pike (1974) that arboreal snakes have little difficulty in reaching weaver nests of any type. The main culprit is the Boomslang *Dispholidus typus*. Snakes are also good swimmers, and Orians (1973) observed snake predation on marsh-nesting Red-winged Blackbirds. Nevertheless I do not think that snakes were responsible for predation at Malton, even in the case of undamaged nests. The Nile Monitor definitely robbed some nests, and this species must be a major threat to all birds nesting close to water. The Dabchicks *Podiceps ruficollis* always swam behind a monitor in the water, calling shrilly, and they often drew my attention to its presence.

Avian predators of Red-billed Quelea nestlings have been mentioned above; Hall (1970a) records the complete destruction of a colony of Vieillot's Black Weavers *Ploceus nigerrimus* by a party of Casqued Hornbills *Bycanistes subcylindricus*, and also saw Pied Crows *Corvus albus* robbing weaver nests. On Aldabra C.B. Frith (1976) describes Pied Crows taking both eggs and nestlings of the Aldabran Fody. In the Pietermaritzburg area the Little Sparrowhawk

Accipiter minullus has been seen robbing the nests of the Spotted-backed Weaver (D. Campbell, pers. comm.). At Klawervlei in the Cape, the Purple Gallinule *Porphyrio porphyrio* was suspected of robbing some nests which were found ripped open from below (Craig 1973). This species has not been recorded at Malton. Moorhens, which Elliott (1973) saw robbing Cape Weaver nests, were restricted to the main dam. Except for the brief appearance of the Cattle Egrets, potential bird predators appeared to be absent from this colony.

In an environment modified by human activity, mammalian predators tend to be scarce. Rodents are least affected, and the present distribution of rats, both *Rattus rattus* and *R. norvegicus*, is in large measure due to man. Ship-borne rats have become established on most islands; C.B. Frith (1976) found rats to be the main nest-predators of the Aldabran Fody, and Drummond (1960) cites observations from seabird colonies on the German islands of Norderoog and Scharhoern, where control measures became necessary as rats not only robbed the nests, but also killed and ate adult birds. The intensity of rat predation recorded in this study suggests that rats may also have an important effect on birds breeding in agricultural land.

2. Behaviour towards predators

The effectiveness of attacks on predators by the breeding birds has been demonstrated for seabird colonies by Kruuk (1964). Experimental results have also shown that Lapwings *Vanellus vanellus* defending their territories against predators reduce predation on nests other than their own (Göransson *et al*. 1975). Nest defence significantly reduces predation in species such as gulls and crows, in which conspecifics may be important predators of chicks (Hunt & Hunt 1976; Yom-Tov 1974).

The Red Bishop will respond aggressively to many other species, and several birds can certainly drive off cuckoos or coucals. Red Bishops were seen threatening Cattle Egrets and Nile Monitors, but against such predators they are helpless. It is unlikely that they could deter rats either, so that active defence of their nests is impractical. Elgood & Ward (1963) suggest that by reducing the time a colony is occupied, the percentage of young lost is minimised, so that synchronous breeding in weavers forms a passive defence against nest predators. This is the method used by the Red-billed Quelea, often with great success, as the colony studied by Ward (1965b) illustrates. Similarly a comparison of the breeding success of Red-winged Blackbirds in marshes and upland habitats led Robertson (1972, 1973) to propose that large colony size and synchronous nesting was advantageous since it reduced the predation rate on a percentage basis. Darling (1938) had originally put forward this idea to explain synchrony in seabird colonies, but these granivorous species provide even better examples of its effectiveness.

In the Red Bishop colony at Malton, breeding appeared to be more closely synchronized in 1976-77, when more birds were breeding and predation was heavier. Breeding early in the season was more successful (see Table 39); this accords with the predictions of Robertson (1973) and suggests that the Red Bishop also employs synchrony as an anti-predator strategy. However, the colony is occupied for a relatively long period compared to species such as the Red-billed Quelea.

3. Nest site and predation

Brosset (1974) has compared the form and location of the nests of various forest birds, and has shown that camouflage is much less effective against predation than siting the nest in a relatively inaccessible position. Over 70% of the nests in the undergrowth were destroyed, but only 35% of those on branches overhanging water. Several authors have recorded the success of nests in different sites for the same species, and it is clear that there is no optimal type of nest site for all conditions. Furrer (1975) found that the Brewer's Blackbird was not able to use nest site flexibility as an anti-predator strategy as might have been expected. In the Red-winged Blackbird Holm (1973) found that egg predation was lower for cattail nests than for nests in bulrushes, but the reverse was true of chick predation. However, for this species egg predation was the chief source of mortality, and cattails were the preferred nesting habitat.

Although the name of the Reed Warbler *Acrocephalus scirpaceus* suggests specialisations for nesting in reeds, Catchpole (1974) demonstrated that nests in *Phragmites* were markedly less successful than in other vegetation, and breeding in other habitats was commoner than expected. Saitou (1976) found that Great Reed Warbler nests in *Rottboelia* were much less successful than those in *Phragmites*, due to predation and parasitism by the European Cuckoo *Cuculus canorus*.

At the study colony, all the successful Red Bishop nests were in *Phragmites*. However, there is some indication that breeding success might have been higher in the mealie field during 1975-76. The occasional use of such breeding sites by the Red Bishop may contribute appreciably to its success.

With ground-based predators it seems logical that success will increase with increasing nest height. Rowan (1966) showed that this applied to the Cape Sparrow, as did La Rivers (1944) for the Brewer's Blackbird and Catchpole (1974) for the Reed Warbler. Francis (1971) re-examined the claims of such a relationship for the Red-winged Blackbird, and found that none of the figures cited were statistically significant. There was also no correlation between depth of water below the nest and predation. However, Holm (1973) did find that breeding success increased with nest height in her colony of Red-winged Blackbirds. For the Red Bishop there is no correlation between nest height and success (Fig. 25), and even the highest nests did not escape predators.

In his study of the Reed Warbler, Catchpole (1974) found that adult birds tended to return to a specific area where they had bred successfully in previous years. There was, however, little direct relationship between the habitat in which the birds had been reared and that selected for their first breeding attempt. Since the post-fledging period was often spent away from the nesting area, he suggests that this may be a critical period for any form of "habitat imprinting". The Red Bishop tends to roost in Phragmites reed-beds, so that fledglings may spend most of their time in this area after leaving the nest, but a large number of individual records over a long period are required.

Berndt & Winkel (1975) have investigated this question in the Pied Flycatcher. They showed that most birds return to breed in the area where they hatched. Of those which settled elsewhere, most selected deciduous woods, regardless of whether they had been reared in deciduous forests or evergreen forests. Thus species-specific preferences may play a dominant role. Furrer (1975) found no correspondence between the type of nest in which Brewer's Blackbirds were reared, and the type which they subsequently used for breeding, but he did not examine their post-fledging distribution.

Breeding success of individual males

In a polygynous system some males will prove more successful in attracting mates than others, and it is predicted that it will be advantageous for males to acquire as many mates as possible. In the Cape Weaver (Elliott 1973), the Red-winged Blackbird (Holm 1973) and the Bobolink Dolichonyx oryzivorus (Martin 1974) it has been shown that polygynous males produce more surviving offspring than monogynous males and the breeding success of the male increases with the number of mates.

Similar results were obtained for the breeding success of males at the Klawervlei colony in the Cape, but I now realise that these figures cannot be regarded as reliable. Not all the males were colour-ringed, and in view of the changes in territory ownership noted during the present study, the success of territories rather than of individual birds was recorded. The data from the colony at Malton indicate that the most polygynous Red Bishop male is not necessarily the most successful breeder. The sample is small and may represent an exceptional case. However, it does suggest that heavy, random predation may negate the apparent advantages scored in the competition for mates. It remains puzzling why birds should abandon their territories early in the season, yet remain in the area in full breeding condition - the most successful male (106) spent only five weeks on his territory, while his neighbour retained his territory for four months.

Kok (1972b) in a study of the polygynous Boat-tailed Grackle Quiscalus mexicanus, found the following factors to be correlated with the number of young fledged: territory size, number of nests, average number of flight displays per hour, median number of terminal phrases per song, and the overall level of the male's behavioural performance. It appeared that the most successful breeders were those males with an optimal balance of these factors. It is likely that in the Red Bishop a simple correlation with harem size is also inadequate, and factors such as early occupation of a territory may be more important than any aspects of courtship behaviour.

Summary

Both in respect of nests built and of eggs laid, there was much more breeding activity in 1976-77 than in the previous year. This appeared to be related to the rainfall during the year preceding breeding. Food supply may prove to be both the ultimate and the proximate factor determining the breeding season of the Red Bishop, with the availability of nest-building material also important. These two factors are affected by rainfall.

Variations in clutch size were irregular, and their influence on breeding success was not clear. Heavy rains accounted for about half the observed losses in the first year, while in the following year almost all losses were due to predation. Nest height was not a factor in avoiding either predation or flooding, but certain areas of the colony were very vulnerable to floods. Breeding success was extremely low in both years, primarily due to heavy predation by marauding rats. It is possible that breeding at other sites would be more successful, and flexibility in nest site selection in this species is considered highly adaptive. When predation was the major source of nest mortality, early nests were the most successful, and synchronized breeding may be advantageous.

CHAPTER FOUR

The evolution of polygyny in the genus Euplectes

Introduction

Reviewing the literature on the pair-bond in birds, Lack (1968) found that about 2% of the species are polygynous, 0,4% polyandrous, and 6% promiscuous (assuming that all hummingbirds are promiscuous). Thus polygyny is a rare mating system in the birds, and has been selected for only under special conditions. Due to the attraction of the exotic, there is a considerable literature on polygynous mating systems, and in recent years a number of authors have produced theoretical arguments to account for the evolution of polygyny (e.g. Verner 1964; Selander 1965; Orians 1969; Bartholomew 1970; Downhower & Armitage 1971; Wiley 1974; Wittenberger 1976). These models have generally been based on studies of particular groups, and it is clear that any theory claiming to be generally applicable must be tested on all species for which adequate information is available.

Although nine Euplectes species had been described by 1800, and all the currently recognised species by 1900 (see Table 51), there was little information on their breeding biology. Darwin (1871) had suggested that E. progne and E. axillaris were polygynous on the basis of Gurney's (1860, 1861) observations in Natal, but this was only speculation. Lynes (1924) first recorded non-breeding individuals in the flocks of sparrowy-plumaged birds present throughout the breeding season, yet he dismissed the possibility that the birds might be polygynous. However, Bowen (1926) reported observations suggesting polygyny in E. franciscanus, and Baily (1926) stated that these species were generally polygynous in captivity. Polygyny in E. nigroventris was mooted by Vaughan (1930), and in their monograph on the genus in 1933 Delacour & Edmond-Blanc cited observations by J. Vincent in South Africa which suggested polygyny in E. ardens, axillaris, capensis, hordeaceus and progne. Delacour & Edmond-Blanc (1933) concluded that polygyny was probably general in the genus. The final proof was provided by Lack's (1935) observations on E. hordeaceus, when "it was only after several days of intensive watching that I proved that (to my surprise) the bird was polygamous". It is now generally held that all the species are polygynous, except for E. jacksoni, which is promiscuous (Crook 1964), but data are still lacking for aureus, diadematus, gierowii and hartlaubi.

The mating systems of the Ploceidae have been reviewed by Crook (1964) in his pioneering monograph. However, his own research was chiefly on the genus Ploceus; the Euplectes species were treated in much less detail. The present study provides the first data on the population structure of any members of the genus, as well as providing more information on breeding biology and behaviour. In this chapter I shall summarise the available information on the behaviour of all the Euplectes species, and then consider their biology and evolution in the light of studies of other groups showing comparable adaptations. The sixteen species in the genus Euplectes as recognised by Hall & Moreau (1970) are listed in Table 51; the scientific names will be used throughout this chapter, since there are no standardised English names for some species.

Methods

All the relevant information on the Euplectes species has been extracted from the literature, including information from captive birds. In addition to a previous study of the behaviour of E. orix (Craig 1974), I have observed the following species in the field: E. afer, albonotatus, ardens, axillaris, capensis, progne. These observations are still inadequate for detailed comparisons, but provide confirmation of the published descriptions. However, written descriptions of vocalizations are useless for comparative purposes. Field recordings of the vocalizations of E. orix were made on an Uher 4400 Report tape recorder, and the sonograms were prepared by Mr. A. Channing on a Kay Spectrograph model

TABLE 51

The genus _Euplectes_ Swainson 1829

Euplectes afer (Gmelin), 1789: Africa = Senegal.
Golden Bishop.

Euplectes albonotatus (Cassin), 1848: Port Natal.
White-winged Widow.

Euplectes ardens (Boddaert), 1789: Cape of Good Hope.
Red-collared Widow.

Euplectes aureus (Gmelin), 1789: Bonguella.
Golden-backed Bishop.

Euplectes axillaris (A. Smith), 1838: Caffreland = Eastern Cape.
Red-shouldered Widow.

Euplectes capensis (Linnaeus), 1766: Cape of Good Hope.
Cape Bishop.

Euplectes diadematus Fischer & Reichenow, 1878: Malindi.
Fire-fronted Bishop.

Euplectes franciscanus (Isert), 1789: Accra.
Orange Bishop.

Euplectes gierowii Cabanis, 1880: South West Africa = Malanje, Angola. Black-winged Red Bishop.

Euplectes hartlaubi (Bocage), 1878: Caconda, Angola.
Marsh Widow.

Euplectes hordeaceus (Linnaeus), 1758: "in Indiis" = Senegal.
Fire-crowned Bishop.

Euplectes jacksoni (Sharpe), 1891: Masailand.
Jackson's Widow.

Euplectes macrourus (Gmelin), 1789: Whidah, Dahomey.
Yellow-backed Widow.

Euplectes nigroventris Cassin, 1848: Zanzibar.
Black-fronted Bishop.

Euplectes orix (Linnaeus), 1758: Africa = Angola.
Red Bishop.

Euplectes progne (Boddaert), 1783: Cape of Good Hope.
Sakabula. (Long-tailed Widow).

Note: the species listed by Crook (1964) as _Euplectes anomala_ has since been assigned to the genus _Quelea_ (Hall & Moreau 1970).

7029A. These are compared with records of captive birds already published - the methods used there are described in the attached paper (Craig 1976).

Results

Territorial behaviour

In all species the males defend a territory during the breeding season. The size of the area defended is quite variable: for E. hordeaceus different authors give figures ranging from 100 m^2 (Ruwet 1965) to 1000 m^2 (Lack 1935). The smallest territories are those of E. orix in Phragmites (see Table 45), but for this species Woodall (1971) has recorded territories of around 300 m^2 in mixed vegetation. Territory size is dependent primarily on the type of vegetation, and the population density. It is not necessarily related to body size, as E. progne, the largest species, does not defend an especially large area (pers. obs.), and E. jacksoni defends a "dancing ground" covering no more than 10 m^2 (Van Someren 1945). In no case is the territory related to food supply, and the males will join the flocks to feed elsewhere throughout the breeding season. Females disregard the boundaries of the territories, but will defend the immediate vicinity of the nest against other birds.

The commonest form of territorial defence is by means of aerial pursuits - the "supplant chases" of Crook (1964). This has been recorded for all species which have been observed in the field. The territory holder flies at the intruder, which either veers off before landing, or takes flight again immediately. I have never seen an intruder attempt to resist the resident, but in one case at Malton, by sheer persistence a strange male E. orix managed to establish himself on a recently-vacated territory, which was being defended by a neighbour in addition to his own territory. The pursuit flight is fast and direct, in marked contrast to the flight displays associated with courtship. The body plumage is not markedly erected, and in the long-tailed species the tail is held straight out behind - in E. progne a male pursuing another presents quite a different spectacle from the courtship display, when the tail is spread and bent down in a curve. Generally there is no physical contact during the pursuit, but on occasion, especially in the case of neighbouring males, they may actually collide in the air and grapple briefly before separating. I have seen this happen in E. axillaris, and Lack (1935) writes "Often the pursuing male received a severe buffet ..." when a male E. hordeaceus pursued an intruder into his neighbour's territory.

At the territory boundary "threatening matches" have now been recorded for several species (Table 52). Crook (1964) does not mention this display as occurring in the genus Euplectes, but it would fall under his category of "aggressive dance without song bows or stretches". None of the other authors mention any calls during the threat displays, and I have always found the birds to be silent while threatening. The two opposing males alternately hop towards and away from each other in specific threat postures, usually fluffing some of the body plumage, in particular the head feathers. The bill is always pointed at the opponent, and the tail is spread - this is especially marked in species with longer tails in nuptial plumage, such as E. albonotatus and axillaris. Often the birds will break off without fighting, but sometimes they will suddenly close and grapple with beak and claw. E. orix males may fall into the water in their struggles, but I have never seen any physical damage result.

Of particular interest is the fact that numerous instances of interspecific territorial defence have been recorded, as summarized in Table 54. Although the species do show ecological separation with regard to the preferred nesting habitat (Emlen 1957; Skead 1965), ten species have been recorded as occupying mutually exclusive territories in the presence of at least one other member of the genus. Overlapping territories with apparent mutual tolerance have also been noted in the field (see Table 54), but in none of these cases were observations made at the beginning of the breeding season when the territories were being established. Lack (1935) found that resident males of

TABLE 52

Euplectes species with territory boundary displays

Species	Authors
albonotatus	Emlen 1957, pers. obs.
ardens	Emlen 1957
axillaris	Emlen 1957, Skead 1959, pers. obs.
capensis	Emlen 1957, Lack 1935, pers. obs.
hordeaceus	Lack 1935
macrourus	Emlen 1957
nigroventris	Moreau & Moreau 1938
orix	Craig 1974, Emlen 1957

TABLE 53

Interspecific hybrids in the genus *Euplectes*

Species			Author
♂ *albonotatus*	X	♀ *orix*	Gray 1958
♂ *ardens*	X	♀ *macrourus*	Gray 1958
♂ *axillaris*	X	♀ *macrourus*	Hopkinson 1938
axillaris	X	*capensis*	Delacour & Edmond-Blanc 1933
♂ *hordeaceus*	X	♀ *ardens*	Baily 1916b

TABLE 54

Interspecific territorial behaviour in Euplectes species

Species	Authors
ardens - albonotatus	Brooke pers. comm., Emlen 1957, Fuggles-Couchman 1943
ardens - hordeaceus	Lack 1935, Reichenow 1904
ardens - capensis	Mouritz 1913, Newton 1937, pers. obs.
ardens - orix	Brooke pers. comm., Emlen 1957, Woodall 1971
axillaris - macrourus	Ruwet 1964b, 1965
axillaris - orix	pers. obs.
axillaris - progne	Priest 1936, Reichenow 1904, pers. obs.
capensis - hordeaceus	Lack 1935
capensis - macrourus	Emlen 1957
hordeaceus - albonotatus	Winterbottom 1936
hordeaceus - nigroventris	Fuggles-Couchman 1943
orix - afer	Farkas 1966
orix - albonotatus	Brooke pers. comm.
orix - macrourus	Emlen 1957
Overlapping territories, but no aggression observed	
capensis - albonotatus capensis - ardens	Hornby 1970
franciscanus - hordeaceus	Bannerman 1949
nigroventris - axillaris nigroventris - albonotatus	Fuggles-Couchman 1943
orix - hordeaceus	Brooke pers. comm.

E. capensis and *hordeaceus* tolerated each other, but both excluded intruders of either species. As described above, the displays used in territorial defence are similar throughout the genus, and can apparently serve for both intra- and interspecific communication. Even though the threat display of *E. axillaris* emphasises the epaulets characteristic of this species (Emlen 1957, pers. obs.), I observed regular boundary displays between a colour-ringed male *axillaris* and male *orix* 517 at the edge of the dam, where their territories adjoined. On one occasion, as the male *axillaris* flew over, male 517 flew up to strike him in mid-air, and they grappled until they dropped into the reeds, when they separated and began a boundary display.

Aggressive behaviour of *E. orix* towards other species was reviewed by Craig (1974). At Malton Cape Weavers *Ploceus capensis* and Lesser Masked Weavers *Ploceus intermedius* were seen in the colony, and the latter bred successfully. Only immature male Cape Weavers were present, and because of their larger size they were able to dominate the Red Bishops, which nevertheless always threatened them. A male Lesser Masked Weaver built his nest on a very tall reed in the area of my hide, and was regularly chased by the resident Red Bishops, which generally managed to restrict the weaver to the immediate vicinity of his nest. The weaver seldom returned their threats, and remained subordinate to them, though later tolerated to a considerable extent. *E. orix* is the only *Euplectes* likely to encounter extensive competition with the *Ploceus* weavers, since both prefer reed-beds for nesting.

In captivity the *Euplectes* species are noted for their intolerance of each other while in breeding plumage, and they will also harass a variety of other species (Neunzig 1921; Rutgers 1973). This is no doubt a consequence of the small size of the aviary in comparison with the territories occupied by any of the species under natural conditions.

Courtship and mate selection

The courtship displays of the genus have long attracted the attention of observers, since it is during these displays that the special features of the nuptial plumage are most obviously displayed. Despite the modifications due to these species-specific features, the general pattern of courtship is the same throughout the genus: on the arrival of a female, the male approaches in a conspicuous flight display, lands nearby and performs a perched display, terminated by a copulation approach if the female remains in the territory. If she flies off, she is often followed in another flight display, and the whole sequence may be repeated several times. Compared to normal flight, the approach flight of a courting male appears to be slower, generally with slower wing-beats than usual. In the species which I have observed, the vocalizations in flight differ from those accompanying perched courtship; this is discussed in the next section.

The form of the displays in individual species is closely related to the major features of the nuptial plumage, as summarised in Table 55. Short-tailed species with coloured plumes on the back erect these to resemble puffed-out balls of feathers during the "bumble-flights" (Craig 1974) typical of E. afer (Lynes 1924 and others; pers. obs.) orix (Stark 1900 and many others; Craig 1974), the three similar red-and-black species hordeaceus, nigroventris and franciscanus (Delacour & Edmond-Blanc 1933), and capensis (Mouritz 1913 and others; pers. obs.). The yellow epaulets of capensis do not seem to be displayed specially, but in albonotatus, axillaris and progne the epaulets are very conspicuous in flight, with the wing movements enhancing their visual effect. Only macrourus combines a long tail with coloured plumes on the mantle and epaulets; here again the epaulets are not emphasized as much as the other features. The flight is reported to be jerky and ungainly, with the body held almost vertically, the mantle feathers erected, and the tail wagged and flared (Chapin 1954; Emlen 1957; Reichenow 1904). This species shares with capensis the unusual characteristic of a white streak down the centre of the chest, which may play some role in perched displays (Chapin 1954; Emlen 1957).

In the other long-tailed species, the rectrices are

TABLE 55

Colours in the nuptial plumage of male *Euplectes*

Species	Bill	Wing	Tail	Epaulet	Back
afer	black	brown	short, brown	-	yellow
albonotatus	blue-grey	black	medium, black	yellow & white	black
ardens	black	black	long, black	-	black
aureus	black	brown	short, brown	-	orange
axillaris	blue-grey	black	medium, black	red & buff	black
capensis	black	brown	short, black	yellow	yellow
diadematus	black	brown	short, brown	-	yellow
franciscanus	black	brown	short, brown	-	red
gierowii	black	black	short, black	-	orange
hartlaubi	blue-grey	black	long, black	yellow & buff	black
hordeaceus	black	black	short, black	-	red
jacksoni	blue-grey	brown	long, black	black	black
macrourus	black	black	long, black	yellow	yellow
nigroventris	black	brown	short, brown	-	red
orix	black	brown	short, brown	-	red
progne	blue-grey	black	long, black	red & white	black

Note: in all species the body plumage is predominantly black. The colours given are those of the nominate races; there are variations in some populations.

held in specific positions during the flight, so that the visual effect of the large tail is increased. The flight display of ardens is typically a long glide, with the central rectrices depressed to produce a deep keel, expanding the tail in the vertical plane like a rudder (Emlen 1957; pers. obs.). The huge tail of progne is expanded in a similar way, but it hangs below the body like an inverted question-mark, while the slow, deliberate wing-beats display the epaulets (Teschemaker 1910 and many others; pers. obs.). It does often appear that the male uses the wind to maintain station, as suggested by Reichenow (1904). Stark (1900) first reported that male progne were unable to fly in wet weather and could then be caught by hand, and Haagner (1910) stated that Basotho had been seen to catch the birds in the Eastern Free State during heavy rain. However, both Davies (1910) and Teschemaker (1910) deny this on the basis of field and aviary observations - Teschemaker writes "The popular fallacy that a male Giant Whydah in breeding plumage cannot fly in a high wind is an amusing one .... The suggestion that the bird cannot fly in heavy rain is equally fictitious". I have certainly seen them displaying on blustery days with intermittent rain, without suffering any apparent inconvenience. The courtship of hartlaubi has yet to be described, but it is evidently closely related to progne (Hall & Moreau 1970).

The concept of "undirected flight displays" in the genus Euplectes as proposed by Emlen (1957) and Crook (1964) has been criticised elsewhere (Craig 1974); it is a misleading term which does not aid in our understanding of these displays. It is clear that aerial display may be more important in some species than others; male orix seldom spend more than 2% of their time in aerial display, but preliminary observations of axillaris indicate that the male may spend 10% or more of his time flying over the territory. More quantitative data on species specialising in this type of display are urgently required.

The remarkable courtship of E. jacksoni merits a more detailed description. This species is restricted to the highlands of East Africa, where the males establish "dancing grounds" in suitable grassland areas. The dancing ring of each male commences as an ill-defined circle about 1 m across, which becomes a smoothly-beaten track through the male nipping off and treading down the grass. A single tuft of grass is left in the centre, in which the male forms two cup-shaped recesses on opposite sides, by making short runs at the tuft with lowered head. When displaying, the male faces this tuft with the head thrown back and the long feathers of the nape ruffled, the tail plumes arched forwards, almost touching the head, except for the outermost ones on either side which hang sideways and downwards. In this posture he performs high jumps of almost 1 m and low jumps in various rhythms, calling in the air with quivering wings. The male commences dancing immediately on the appearance of females, but stops if they land in the ring and then makes short rushes towards the hen, accompanied by a different call. This summary is based chiefly on the descriptions of Jackson (1938), Van Someren (1945) and Van Someren (1956) - in addition Baily (1916a) has an account of breeding in captivity. Particularly interesting is Van Someren's (1945) finding that removing the tuft from a ring did not stop the male displaying, but this ring was no longer visited by females.

Perched courtship is evidently most active in species breeding in reeds, where displays like the swivelling of E. orix have been described for afer (Delacour & Edmond-Blanc 1933), capensis (Emlen 1957), franciscanus (von Boetticher 1952), hordeaceus (Verheyen 1953) and nigroventris (von Boetticher 1952). In the grassland species perched courtship seems to involve a more static posture, with both wings and tail spread, and the body plumage generally ruffled, while the head is bowed and the bird calls constantly. Spreading of the wings and drooping them slightly serves to display the epaulets in axillaris (Skead 1959; pers. obs.), albonotatus (Mitchell 1966), macrourus (Jackson 1938), and progne (pers. obs.), but the wings are also spread in ardens (Mitchell 1966). Pumping the body up and down as the male approaches the female probably derives from an intention movement of mounting, and has been reported for several species as immediately preceding copulation: albonotatus (Mitchell 1966; Hornby 1967), ardens (Mitchell 1966), axillaris (Mitchell 1966), macrourus (Emlen 1957), orix (Craig 1974), and progne (Norris 1968).

Wing-quivering while the male hangs below the nest is typical of the Ploceus species (Crook 1964), but appears to be rare in Euplectes. I have observed it in E. orix only in Natal; it was performed regularly in the colony at Malton. Mitchell (1966) records a similar display by captive male albonotatus. Crook (1964) reports that in Uganda male orix sometimes postured in front of females with slowly undulating wings, and Vincent (1936) describes a male hordeaceus perched by a female slowly flapping its wings below the breast "like a duck drying its wings", but in neither case was the male displaying at the nest.

Male Euplectes appear to display to all eclipse plumaged birds that enter their territories, though they are not quite as undiscriminating as the Viduinae observed by Nicolai (1969). I have seen male orix and axillaris court immature males of their own species and browns of other species, while Emlen (1957) and Vincent (1949) also saw courtship directed at other species. It thus seems the responsibility of the female to select a mate of the correct species. Under natural conditions the strikingly different nuptial plumages of most sympatric species and their vocalizations (see below) should ensure species isolation.

In captivity hybrids have been recorded (Table 53), and may in fact be commoner than the records indicate, since females of many species are rarely imported and difficult to identify without experience, while the dealer will always assure his customer that this is the right bird! Gray (1958) does include other records, but I have accepted only the more reliable accounts from this uncritical compilation. In the case of an albonotatus-orix cross, a male hybrid was produced with mixed plumage characters; it lived some six years and tried to mate with a female franciscanus without result - unfortunately no details of its courtship displays are given. The occurrence of hybrids emphasizes the close relationship between the members of the genus.

Copulation is preceded by soliciting by the female in the typical passerine manner, quivering the wings and tail. It has to date been described for albonotatus (Mitchell 1966), diadematus (Cunningham-Van Someren 1971), hordeaceus (Lack 1935) and orix (Woodall 1971; pers. obs.). If a male orix tries to mount without the female soliciting him, she adopts an aggressive head-forward posture and will repulse him with vigorous pecks - this appears to be the one time the female can dominate the male.

Z. Tierpsychol., 41, 191—201 (1976)

ISSN 0044-3573 / ASTM-Coden: ZETIAG

Aus dem Lehrstuhl für Verhaltensphysiologie der Universität Bielefeld

Vocalizations of Male *Euplectes* in Captivity[1])

By A. J. F. K. Craig

With 9 figures

Received: 30. 6. 1975

Revised: 4. 9. 1975

Abstract

The dramatic visual displays of the *Euplectes*-♂♂ have led to their vocalizations being neglected. 6 ♂♂ of *Euplectes franciscanus* and *E. afer*, and 2 *E. hordeaceus*-♂♂ were kept in aviaries in sound-proof rooms, where vocalizations were recorded during observations of their behaviour, and later analysed on a sound spectrograph.

The calls described and illustrated do not represent the complete repertoire of these species. However, the distinctive songs of *E. afer* and *E. franciscanus* indicate that detailed field studies of vocalization in this genus are required.

Introduction

Since the sound spectrograph has made objective visual analysis possible, birdsong has been the subject of intensive study (see reviews in Thorpe 1961, Armstrong 1963, Thielcke 1970a). Other "calls" have received less attention, although it is recognized that calls may perform many, if not all of the functions commonly attributed to "song" (Thielcke 1970b).

The only analyses of the vocalizations of the Ploceidae are by Collias (1963) and Crook (1969). In the genus *Euplectes* Crook (1969) describes "a series of machine-like repetitive sounds, buzzes or whirrs that accompany the visual display", and adds that "these undistinguished cries have received little attention".

A field study of the Red Bishop *Euplectes orix* (Craig 1974) suggested that vocalizations may be important in the breeding biology of these species. This paper presents a preliminary description of the calls of male *Euplectes afer, E. franciscanus* and *E. hordeaceus* (taxonomy as in Hall and Moreau 1970), recorded in the laboratories of the Lehrstuhl für Verhaltensphysiologie der Universität Bielefeld.

[1]) Based on data presented in a paper entitled "Isolationsmechanismen bei einigen Arten der Webervogelgattung *Euplectes*" at the 86th annual meeting of the German Ornithological Society on 8 November, 1974.

Materials and Methods

The birds used in this study were obtained from dealers in Germany; as far as is known, the groups used for the recordings came from the same shipments. The Golden Bishops *Euplectes afer* belonged to the northern race *E. a. afer* (Gmelin), showing the complete gold collar across the chest.

6 male *E. franciscanus* and 6 male *E. afer* were placed in aviaries measuring 2 × 2 × 1 m in separate sound-proof rooms in the institute, with a 14 : 10 h light-dark rhythm. Under these conditions they retained full breeding plumage throughout 8 months of observation (cf. ROLLO and DOMM 1943). Only 2 *E. hordeaceus*-♂♂ were available; they were kept under the same conditions, but with 2 *E. franciscanus*-♀♀.

Recordings were made with an Uher 4400 Report tape recorder and M 815 directional microphone, at a tape speed of 19 cm/sec. During recordings the birds were observed through small glass panels in the doors, so that the calls could be correlated with their behaviour. Additional observations were made on *E. franciscanus*-♂♂ and -♀♀ in indoor aviaries.

Sonograms were prepared on a Vibralyzer 7030A Sound Spectrograph of the Kay Elemetrics Co., at normal speed and with the wide filter setting. For all calls, settings from both 0.08—8 kHz and 0.16—16 kHz were used; the latter are illustrated only where there are significant amounts of energy above 8 kHz.

Description of the calls

As emphasized by THIELCKE (1970b), there are few calls which occur only in a single situation, and many transitional types may be found. BRÉMOND (1971) defines communication as occurring when one bird modifies its behaviour in response to the call of another, but the significance of the calls to conspecifics is often difficult to establish. Thus detailed field observations are still required to determine the behavioural contexts of the calls recorded here.

E. afer

(1) A bird held in the hand may utter a series of strident squawks, with the bill held wide open. They cover a broad band of frequencies between 2 kHz and 12 kHz, but most energy is concentrated around 7 kHz. Each squawk lasts about 0.2 sec (Fig. 1a, call 1).

(2) In disputes, such as when several ♂♂ tried to bathe at the same time, a rapid "ka-ka-ka-ka" is given, accompanied by vigorous pecking bouts. With a range of 4—10 kHz and the dominant frequency at 6—7 kHz, this call resembles (1) but is shorter and given in rapid bursts (Fig. 1a, call 2).

(3) During normal activity, a series of "chuk" calls are given at short intervals. The frequency range is limited to 3.5—6 kHz, and the duration of the call is 0.1 sec. Apparently identical calls are given in alarm; even when the birds are undisturbed, the intensity and interval between calls is variable (Fig. 1b, call 2).

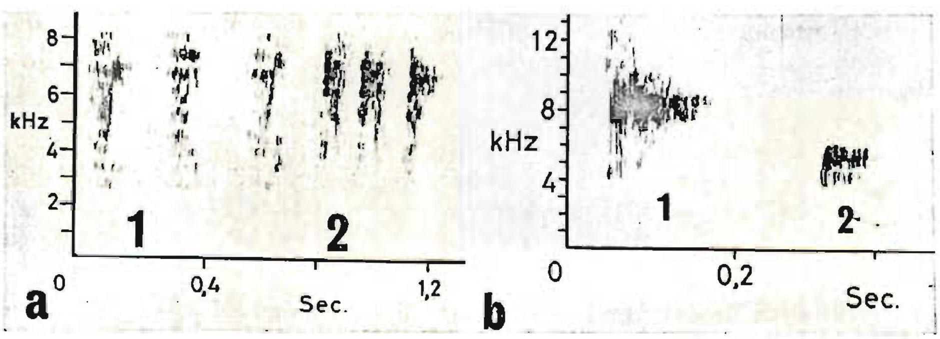


Fig. 1: E. afer. (a) calls 1 and 2; (b) calls 3 and 4

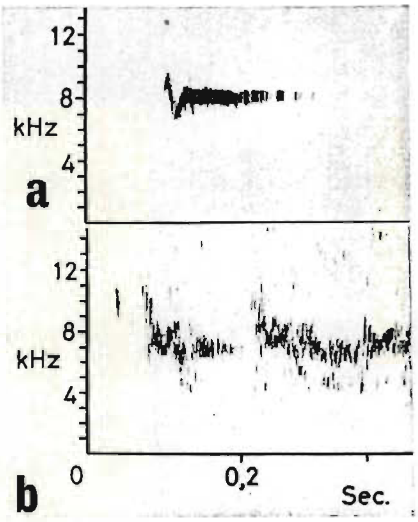


Fig. 2: E. afer. (a) call 5; (b) call 6

(4) A harsh "seep" call is given in aggressive encounters as one ♂ displaces another. Lasting 0.2 sec the sonogram shows an intense band between 7 kHz and 9 kHz with some spreading into higher and lower frequencies. The call appears to be given singly, often breaking into a sequence of "chut" notes (Fig. 1b, call 1).

(5) A plaintive piping call was heard occasionally, evidently from subordinate birds which had just been displaced. It shows an extremely narrow frequency band around 8 kHz, and may be repeated at intervals of several sec (Fig. 2a).

(6) A loud rattle, often lasting 1 or 2 sec with the individual elements no longer separable, was heard either while the calling bird flew, or when other birds flew past him. Its frequency range is not clearly defined (Fig. 2b).

(7) One vocalization could from its structure and context be termed a song. It was given by ♂♂ perched in the aviary and associated with a particular body posture (Fig. 3), and also during fluffed flights directed at birds in non-breeding dress, after the ♂♂ had been returned to communal aviaries.

The song consists basically of three sections; an introductory "gargle" lasting 0.4—1 sec, followed by a series of "tirr-tirr" trilling notes for 0.6—2 sec and terminated by one or more loud "rik" calls, each lasting 0.2 sec. Thus the full song may vary in length from 1.3 sec to more than 4 sec.

Often only the introductory gargle is given, in a short phrase lasting 0.8—1.3 sec. Here 4 elements A/B/C/D can be distinguished (Fig. 4a). Element A contains two parts, the second of which includes lower frequencies, whereas in C and D the second part contains more high frequencies. In the full song (Fig. 4b) some or all of these elements are followed by the trill E and the rik F, which bears a close resemblance to call (6).

The quantitative data are still insufficient for an analysis of the various forms of song. However, the following qualitative statements can be made: (a) Both types of song were given by all ♂♂. There was no evidence of individual constancy in form or duration. (b) Full song always started with some of the elements A—D followed by E and F, in that order. (c) The order A/B/C/D was maintained except in one instance where the gargle comprised A/D/B. Element C was rare, the commonest form of

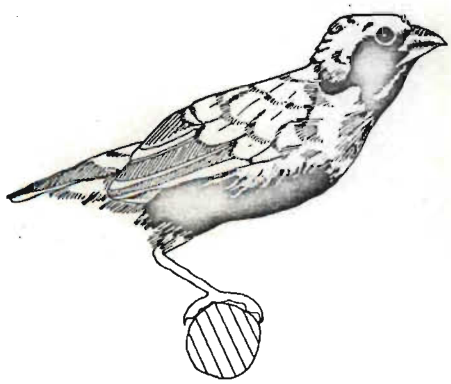


Fig. 3: Body posture of ♂ *E. afer* singing (from a photograph, drawn by L. Cowan)

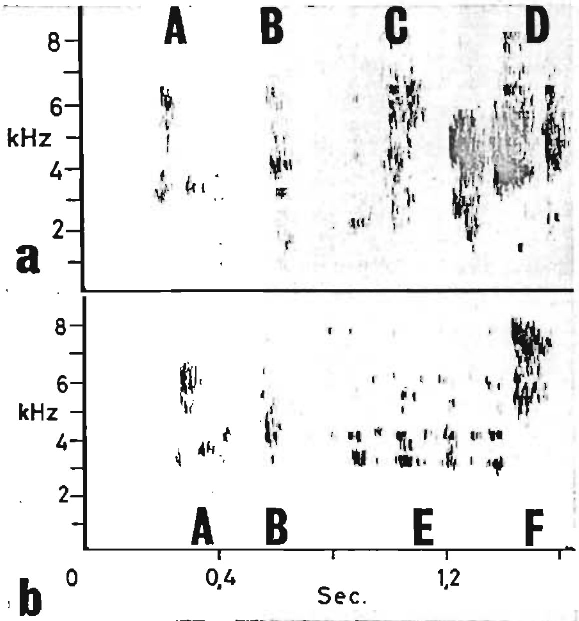


Fig. 4: *E. afer.* (a) introductory "gargle" of the song; (b) full song, including only two elements of the "gargle"

the gargle being A/D only, with A/B also occurring.

A short sizzling or buzzing song in flight is mentioned by Neunzig (1921), von Boetticher (1952), and McLachlan and Liversidge (1958). Neunzig's description of the song as a wonderful mixture of chipping, hissing and chattering sounds is probably the best, while "a noise like rustling grass" (Cheeseman and Sclater 1936) typifies the often misleading comparisons found in the literature.

E. franciscanus

(1) As in the case of *E. afer,* birds held in the hand may utter loud squawks. These last about 0.3 sec with the predominant frequency at 2 to 4 kHz, and are given at longer intervals than in *E. afer* (cf. call 2 in Figs. 5 a and 1a). Squawks were also heard from *E. orix*-♂♂ when handled for ringing (Woodall 1971, Craig 1974).

(2) The aggressive "chak" given by one bird displacing another resembles (1) in frequency range (call 1, Fig. 5 a). This call was also heard from ♀♀, toward other ♀♀.

(3) A shrill chipping note is used as a contact call in this species (Neunzig 1921). It is given by both ♂♂ and ♀♀ and also serves as the alarm call. The individual "chip" notes last only 0.05 sec covering the range 2—9 kHz (Fig. 5b, call 1). The interval between successive chips is very variable. In *E. orix* Haagner (1901) recorded a grating chirp rendered "tchwirt tchwirt"; the chipping call of this species (Craig 1974) is heard in similar contexts to that of *E. franciscanus.*

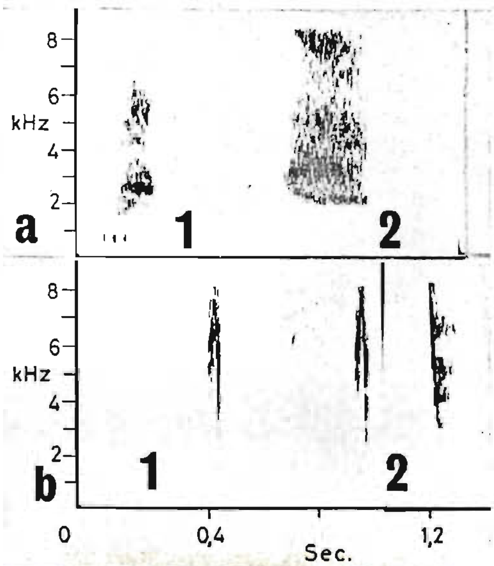
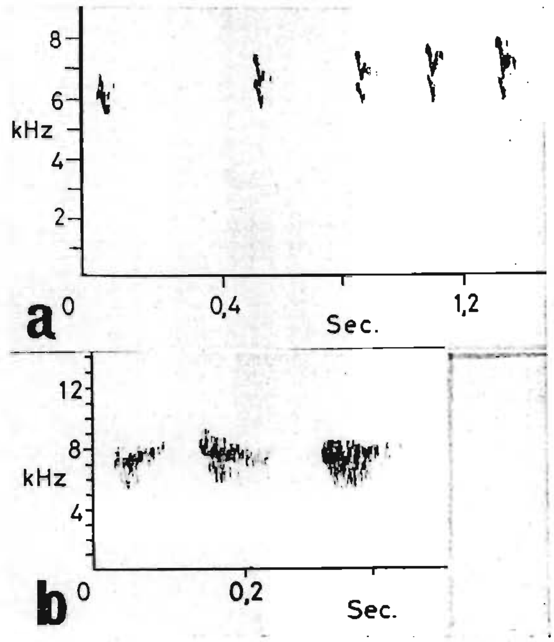


Fig. 5: *E. franciscanus.* (a) calls 1 and 2; (b) call 3

Fig. 6: E. franciscanus. (a) call 4; (b) call 5



Before a ♂ starts a bout of aggressive chasing, the chipping call changes to a harsher "chup" with emphasis on the frequencies 4—6 kHz (Fig. 5b, call 2). Transitional types are often found. While giving this call the ♂ leans forward on the perch, flicking the wings, and after a few sec flies at another bird to displace it. Where a clear ranking order exists within the caged group, the threat-notes and wing-flicking may be sufficient to cause a subordinate to leave its perch or the food bowl.

(4) A high piping call composed of two frequency bands between 6 kHz and 8 kHz is heard rarely (Fig. 6 a). The significance of this call is unclear; a similar sounding call in *E. orix* was given in contexts where "rattling" was expected (Craig 1974), and some instances were noted for *E. franciscanus*. It also constitutes some of the introductory elements to the song — see below.

(5) When making a short flight or as other birds flew over, the ♂ commonly gave a short "rattling" call, comprising a series of elements with a frequency range of 5—9 kHz and a duration of 0.1—0.2 sec (Fig. 6 b). This call may prove to be homologous with the rattling of *E. orix* (Craig 1974) and with call 6 of *E. afer*.

(6) The simple sizzling song (von Boetticher 1952) closely resembles that of *E. orix*. It is not a sparrow-like chirping as stated by Neunzig (1921), but in addition to the sizzling tones may include interludes with a variety of complex notes, sounding like the twittering of a swallow as Duncan (1906) writes of *E. orix*. Some examples of such sequences are shown in Figs. 7 a, b and c. Frequently a few introductory notes will precede a "burst" of sizzling lasting 1 sec or more, then a brief "tick" will be followed by another sizzle (Fig. 7 d). Some of the introductory notes resemble those of call 4.

The sizzling part of the song shows a very even coverage of the range 1—8 kHz. The other notes vary in duration from 0.1—0.8 sec and are very variable in form, though most often lying between 2 kHz and 3 kHz.

Bannerman (1949) writes that song may be given from a perch or in flight, but in the aviaries it was never heard from flying birds. Sizzling in flight was also rare for *E. orix* (Craig 1974). When sizzling on a perch, *E. franciscanus*-♂♂ adopted a characteristic posture (Fig. 8). This call was also heard in copulation approaches to ♀♀.

E. hordeaceus

(1) A call best rendered by the sound "tut-tut", covering the range 4—8 kHz and lasting about 0.1 sec (Fig. 9 a), given by a ♂ resting on a perch.

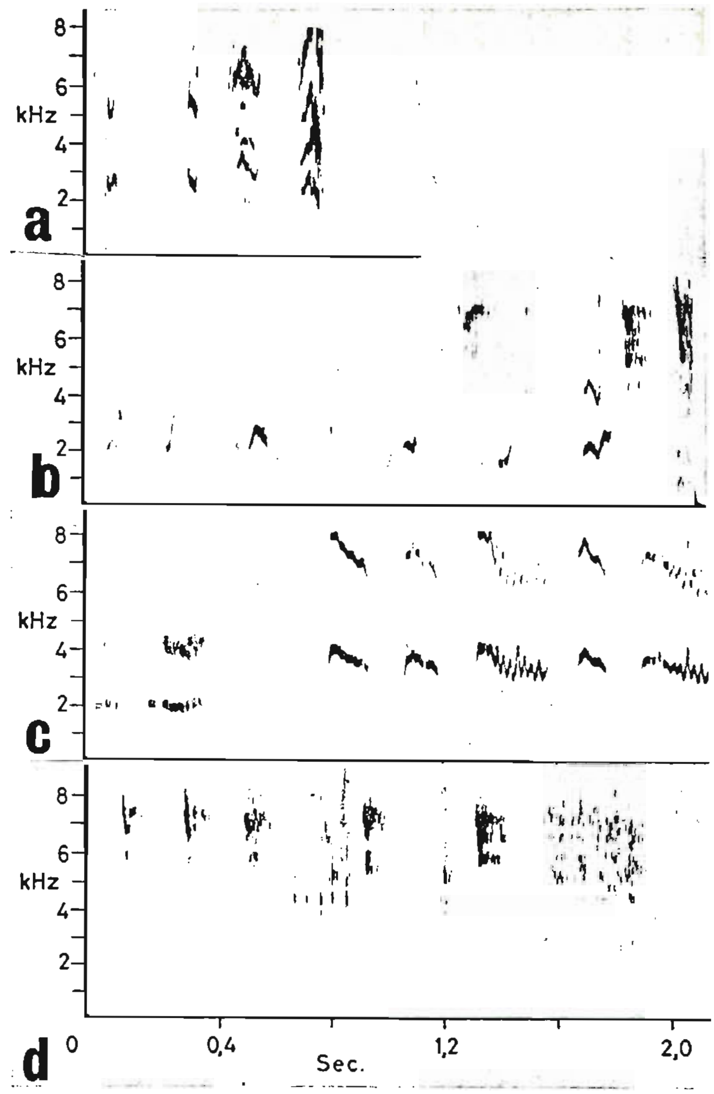


Fig. 7: E. franciscanus. (a), (b), (c) introductory notes of the song; (d) the sizzle

It was often associated with comfort movements such as feather ruffling and yawning, and there was no evidence of "communication".

(2) A piping call, sounding very like call 5 of *E. afer* and call 4 of *E. franciscanus*, but rather different in structure (Fig. 9 b). It lasts 0.2 sec with loud portions at 5—6 kHz and 8—9 kHz. It was only heard from the subordinate ♂ after he had been displaced from a perch by his companion.

(3) An aggressive "chak" was heard during agonistic behaviour, and appeared identical to the corresponding call of *E. franciscanus*. The recordings were not suitable for reproduction due to extraneous noises.

(4) A rapid "trirt" which might be repeated several times, each call lasting 0.2—0.3 sec and showing rapid changes in frequency around the basic level of 7 kHz (Fig. 9 c). It was always given by a ♂ as he flew off, either to feed or to another perch, and may be comparable to call 6 of *E. afer* and call 5 of

Fig. 8: Body posture of *E. franciscanus* singing (from a photograph, drawn by L. COWAN)

E. franciscanus.

A sizzling song is mentioned by some authors (NEUNZIG 1921, VON BOETTICHER 1952, MACKWORTH-PRAED and GRANT 1962), while a weak metallic song in flight is described by LACK (1935) and CHAPIN (1954). It is not clear what call these descriptions refer to, and call 4 cannot be regarded as the "song" of *E. hordeaceus* until recordings of birds under natural conditions are available.

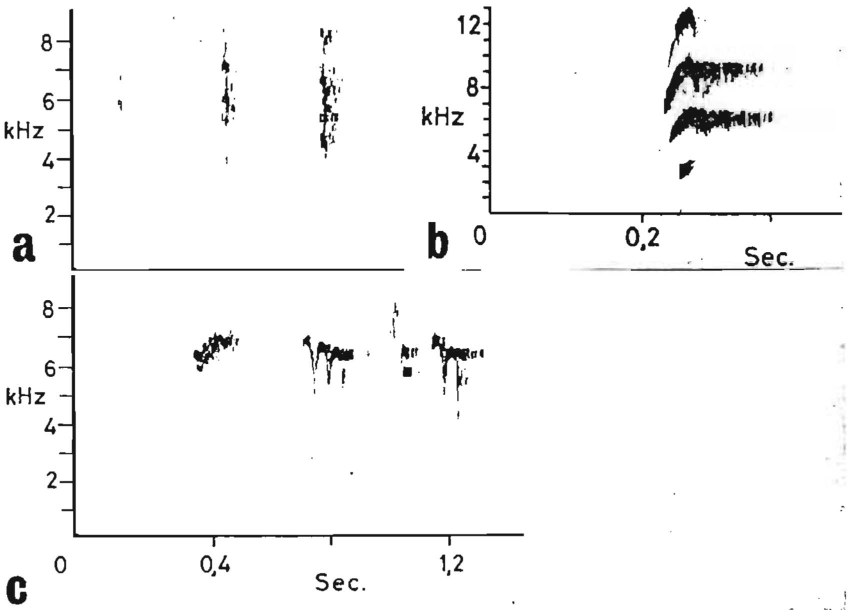


Fig. 9: E. hordeaceus. (a) call 1; (b) call 2; (c) call 4

Discussion

(a) *Vocal repertoire.* — The vocal repertoire of some songbirds may encompass some 20 calls while the domestic fowl has about 26 distinct vocalisations (THIELCKE 1970 a). Although this study does not cover the complete repertoire of the *Euplectes* species, it bears comparison with studies of other passerines. CONRADS (1971) describes 8 calls in *Emberiza hortulana*, ANDREW (1957) found 10 in *Emberiza calandra*, and COLLIAS (1963) describes 15 calls in the Village Weaver *Ploceus cucullatus*. Some of the latter, however, appear to be minor variations, not meriting separate listing. CROOK (1969) did not record two of these calls in the field, and listed 12 vocalizations for the Ploceidae, of which no more than 7 were found in any one species (e. g. *Quelea quelea* CROOK 1960).

Since only adult ♂♂ were concerned in this study, calls such as the begging call and location call of nestlings, and the solicitation call of ♀♀ may be found in the wild.

(b) *Physical characteristics of the calls.* — In all three species, there are few calls containing frequencies below 3 kHz or above 10 kHz, while most energy is concentrated between 4 kHz and 8 kHz. It is tempting to suggest that this is the range in which optimum reception takes place. SCHWARTZKOPFF (1973) reviewing the scanty data on hearing range in birds, shows that while species such as *Pyrrhula pyrrhula* may have an upper limit of hearing at 21 kHz, the greatest sensitivity is around 3.2 kHz for this species, and of the same order in other passerines such as *Serinus serinus.*

CODY (1969) notes that marsh-dwelling members of three American passerine families include a "buzzy passage" of wide frequency range in their repertoire, which may be adapted to communication in this environment. The influence of the surrounding vegetation on the form of the vocalizations has been demonstrated (e. g. CHAPPUIS 1971), but the social context of the calls may be the primary factor: GÜTTINGER and NICOLAI (1973) found little correlation between habitat and call-type in the Estrildidae, where close-range signals are likely to be more important than in the groups cited as examples by CHAPPUIS (1971). In the case of the *Euplectes* species, the calls of wide frequency range will provide for good localisation (MARLER 1955), which may be their chief function when the ♂ is perched out of sight in reeds or other tall vegetation.

(c) *Specificity of the calls.* — The agonistic "chaks" of the three species are indistinguishable to the human ear, and show close similarities in their sonograms. Their general form also resembles the illustrations of CROOK (1969).

MARLER (1957) writes that aggressive calls often appear to be mutually understood by different species, and suggests that the similarities may be advantageous where there is interspecific competition — the idea of selection for such resemblance is expanded by CODY (1969). The extent of competition between these *Euplectes* species in the wild is unknown, but they are sympatric over wide areas (HALL and MOREAU 1970), and interspecific territorial behaviour has been recorded for some members of the genus (see references in CRAIG 1974).

Call 3 of *E. afer* and *E. franciscanus* has a similar sound, despite the differences in the sonograms. GÜTTINGER and NICOLAI (1973) also found species-specific differences in structure of similar-sounding contact calls, but while their estrildids only answered the calls of conspecifics, the *Euplectes* spp. would often reply to the calls of other species. The remaining calls described above are easily distinguished by ear or on the sonograms.

NICOLAI (1964, 1973) has drawn attention to resemblances between the *Euplectes* species-group and the parasitic Viduinae. Of the viduine vocalizations, he cites the "Schäckerstrophe" as sounding typically euplectine. However, comparison of the sonograms does not show any special likeness to the *Euplectes* calls described here, while the Schäckerstrophe looks very like the "chatter" of the icterid *Quiscalus mexicanus* (KOK 1971). It would seem that the calls of the Viduinae will not provide convincing evidence of their relationships.

(d)Song in *Euplectes.* — The vocalizations of *E. afer* and *E. franciscanus* described as song, fit CROOK's (1969) definition of "short song": "a relatively brief phrase containing preliminary chattering or warbling sounds and usually ending in a harsh and sometimes prolonged wheeze".

BRÉMOND (1971) describes a typical territorial song as covering a large range of frequencies, broken up into phrases and repetitive; THORPE and LADE (1961) use similar terms to describe the song of the Emberizidae, which functions primarily in territorial proclamation.

In some Ploceidae, song is used in territorial defence (CROOK 1964), but reviewing observations on *Quelea quelea,* CROOK (1969) adds that song may also occur spontaneously when ♂♂ are alone in their territories, and also in aviaries during periods of inactivity. In both *E. afer* and *E. franciscanus* and in wild *E. orix* song has been heard in situations recalling the "solitary song" (ungerichteter Gesang) of the Estrildidae (see HALL 1962, HARRISON 1962, IMMELMANN 1968). Song in this group has no territorial significance (HALL 1962, IMMELMANN 1968), its main function being as an introduction to copulation.

Captive male *E. afer* and *E. franciscanus* often sang while sitting very close to other birds, but singing never provoked aggression. In one case an immature ♂ approached a sizzling adult *E. franciscanus,* leaning forward in a manner recalling the "Zuhörer" in *Lonchura punctulata* as illustrated in IMMELMANN (1968). He was allowed to remain almost touching the ♂ for several minutes before being driven off.

Although IMMELMANN (1968) records song in several estrildid species with undeveloped gonads, in most passerines there is a clear relationship between song and gonad maturation (THORPE 1961, ARMSTRONG 1963, SELANDER and HANSEN 1965, THIELCKE 1970a, KOK 1971). In the Zebra Finch *Taeniopygia guttata,* PRÖVE (1974) was able to confirm the suggestion of MORRIS (1954) that "singing is the sexual pattern with the lowest threshold", by treating castrated ♂♂ with varying doses of testosterone. Singing was induced first, but with increasing testosterone levels courtship and finally copulation reappeared. In preliminary experiments on *Euplectes franciscanus* four ♂♂ which had been singing were castrated. Although they remained in full breeding plumage (cf. WITSCHI 1961) and gave all the other calls, song was not heard in the three months following the operation. Since the ♀♀ never sang, even with testosterone injections, song in this species is probably also restricted to ♂♂ with active gonads.

Acknowledgements

Professor K. IMMELMANN and the members of his research team gave me every assistance during this study, and I am most grateful to them all. Professor G. L. MACLEAN also read the draft manuscript.

Summary

The vocalizations of ♂♂ of the three species *Euplectes afer, E. franciscanus* and *E. hordeaceus* as recorded in captivity are described, accompanied by sonograms.

The vocal repertoires of *E. afer* and *E. franciscanus* comprised 6 and 5 calls respectively. The songs of these two species are quite distinct. Only

four calls, none of which could be classified as a song, were recorded for *E. hordeaceus*. The calls are of similar type in all three species, but do show specific differences. The contact calls and the very similar aggressive "chaks" may be used in interspecific communication.

The song of *E. afer* is composed of six clearly defined elements A/B/C/D/E/F, which occur in various combinations. *E. franciscanus* has a sizzling song, but may include a variety of other notes. In both cases the song encompasses a very wide frequency range and lacks "pure" notes. Singing is probably directly related to testis development.

Zusammenfassung

Die Lautäußerungen von ♂♂ der drei Arten *Euplectes afer*, *E. franciscanus* und *E. hordeaceus* wurden in Gefangenschaft aufgenommen und mit Hilfe von Sonagrammen beschrieben.

Das Rufvokabular von *E. afer* und *E. franciscanus* enthält sechs bzw. fünf verschiedene Rufe. Die Gesänge der beiden Arten sind leicht unterscheidbar. *E. hordeaceus* äußerte nur vier Rufe, von denen man keinen als Gesang bezeichnen kann. Das Rufmuster der drei Arten ist ähnlich, aber die meisten Rufe sind deutlich artspezifisch. Infolge ihrer Ähnlichkeit könnten die Kampflaute und die Kontaktrufe auch der zwischenartlichen Kommunikation dienen.

Der Gesang von *E. afer* ist aus sechs deutlich erkennbaren Elementen A/B/C/D/E/F aufgebaut, die in verschiedenen Kombinationen vorgetragen werden können. *E. franciscanus* hat einen zischenden Gesang mit sehr variablen Elementen. In beiden Fällen zeigen die Gesänge einen sehr breiten Frequenzbereich ohne reine Töne. Es gibt Hinweise dafür, daß der Gesang vom Entwicklungszustand der Keimdrüsen abhängt.

Literature cited

Andrew, R. J. (1957): A comparative study of the calls of *Emberiza* spp. Ibis 99, 27—42 • Armstrong, E. A. (1963): A study of bird song. Oxford University Press, Oxford • Bannerman, D. A. (1949): The birds of tropical West Africa. Vol. 7. Oliver & Boyd, London • von Boetticher, H. (1952): Die Widahvögel und Witwen. Geest und Portig KG, Leipzig • Brémond, J. C. (1971:) Communications acoustiques chez les oiseaux. J. Psych. norm. path. **3**, 353—380 • Chapin, J. P. (1954): The birds of the Belgian Congo. Part 4. Bull. Am. Mus. Nat. Hist. Vol. 75B • Chappuis, C. (1971): Un exemple de l'influence du milieu sur les émissions vocales des oiseaux: l'évolution des chants en fôret équatoriale. La terre et la vie **118**, 183—202 • Cheeseman, R. E., and W. L. Sclater (1936): On a collection of birds from North-Western Abyssinia; Part 4. Ibis 13, 163—197 • Cody, M. L. (1969): Convergent characteristics in sympatric species: a possible relation to interspecific competition and aggression. Condor 71, 222—239 • Collias, N. E. (1963): A spectrographic analysis of the vocal repertoire of the African Village Weaverbird. Condor 65, 517—527 • Conrads, K. (1971): Über die Rufe des Ortolans (*Emberiza hortulana* L.). Vogelwarte 26, 169—175 • Craig, A. J. F. K. (1974): Reproductive behaviour of the male Red Bishop Bird. Ostrich **45**, 149—160 • Crook, J. H. (1960): Studies on the social behaviour of *Quelea q. quelea* (Linn.) in French West Africa. Behav. 16, 1—55 • Crook, J. H. (1964): The evolution of social organisation and visual communication in the weaver-birds (Ploceinae). Behav. Suppl. 10, 1—178 • Crook, J. H. (1969): Functional and ecological aspects of vocalization in Weaver-birds. In: Bird Vocalizations (R. A. Hinde, ed.), Cambridge University Press, Cambridge • Duncan, A. (1906): Notes on the genus *Pyromelana* (Bishop Birds). J. S. Afr. Orn. Un. **1**, 57—61 • Güttinger, H. R., and J. Nicolai (1973): Struktur und Funktion der Rufe bei Prachtfinken (Estrildidae). Z. Tierpsychol. 33, 319—334 • Haagner, A. (1901): Ornithological notes from the Transvaal. Ibis 8, 190—194 • Hall, B. P., and R. E. Moreau (1970): An atlas of speciation in African Passerine birds. Trustees of the British Museum (Natural History), London • HALL, M. F. (1962): Evolutionary aspects of Estrildid song. Symp. zool. Soc. Lond. **8**, 37—55 • HARRISON, C. J. O. (1962): Solitary song and its inhibition in some Estrildidae. J. Orn. **103**, 369—379 • IMMELMANN, K. (1968): Zur biologischen Bedeutung des Estrildidengesanges. J. Orn. 109, 284—299 • KOK, O. B. (1971): Vocal behaviour of the Great-tailed Grackle (*Quiscalus mexicanus prosopidicola*). Condor 73, 348—363 • LACK, D. (1935): Territory and polygamy in a Bishop-bird *Euplectes h. hordeacea* (Linn.). Ibis 77, 817—836 • MACKWORTH-PRAED, C. W., and C. H. B. GRANT (1962): Birds of the southern third of Africa. Vol. 2. Longmans, London • McLACHLAN, G. R., and R. LIVERSIDGE (1958): Roberts birds of South Africa. John Voelcker Bird Fund, Cape Town • MARLER, P. (1955): The characteristics of certain animal calls. Nature 176, 6—7 • MARLER, P. (1957): Specific distinctiveness in the communication signals of birds. Behav. 11, 13—39 • MORRIS, D. M. (1954): The reproductive behaviour of the Zebra Finch *Peophila guttata* with special reference to pseudo-female behaviour and displacement activities. Behav. 6, 271—321 • NEUNZIG, K. (1921): Die fremdländischen Stubenvögel. A. Asher & Co., Amsterdam (reprint 1965) • NICOLAI, J. (1964): Der Brutparasitismus der Viduinae als ethologisches Problem. Z. Tierpsychol. **21**, 129—204 • NICOLAI, J. (1973): Das Lernprogramm in der Gesangsausbildung der Strohwitwe *Tetraenura fischeri* Reichenow. Z. Tierpsychol. **32**, 113—138 • PRÖVE, E. (1974): Der Einfluß von Kastration und Testosteronsubstitution auf das Sexualverhalten männlicher Zebrafinken (*Taeniopygia guttata castanotis* Gould). J. Orn. **115**, 338—347 • ROLLO, M., and L. V. DOMM (1943): Light requirements of the Weaver Finch. Auk 60, 357—367 • SCHWARTZKOPFF, J. (1973): Mechanoreception. In: Avian biology, Vol. 3 (D. S. FARNER and J. R. KING, eds.). Academic Press, London • SELANDER, R. K., and R. J. HAUSER (1965): Gonadal and behavioural cycles in the Great-tailed Grackle. Condor **67**, 157—182 • THIELCKE, G. (1970a): Vogelstimmen. Springer-Verlag, Berlin—Heidelberg—New York • THIELCKE, G. (1970b): Die sozialen Funktionen der Vogelstimmen. Vogelwarte **25**, 204—229 • THORPE, W. H. (1961): Bird-song. Cambridge University Press, Cambridge • THORPE, W. H., and B. I. LADE (1961): The songs of some families of the Passeriformes. II. The songs of the buntings (Emberizidae). Ibis **103a**, 246—259 • WITSCHI, E. (1961): Sex and secondary sexual characters. In: Biology and comparative physiology of birds. Vol. 2 (J. A. MARSHALL, ed.), Academic Press, London • WOODALL, P. F. (1971): Notes on a Rhodesian colony of the Red Bishop. Ostrich **42**, 205—210.

Author's address: A. J. F. K. CRAIG, Dept. of Zoology, University of Natal, P.O. Box 375, Pietermaritzburg 3200, South Africa.

Vocalizations of E. orix

Recordings were obtained of the three main vocalizations described in Craig (1974), and also of the squawk given by birds handled during ringing. These were the only calls heard from E. orix in the field and in the aviary during this study.

(1) The harsh squawks are uttered with the bill held wide open, and the bird is liable to peck if given the opportunity. A.J. Manson (pers. comm.) has noted that males are more likely to squawk when handled than females, and I have also found this to be the case. The call lasts about 0,2 s and covers the entire range of frequencies from 0-8 kHz, but most energy is concentrated between 1 and 5 kHz. Successive calls follow at intervals of several seconds (Fig. 26a, call 1).

Similar harsh squawks are given during some aggressive encounters in the field, especially when the male is trying to displace a larger species such as a weaver. These calls usually accompany attacks on the Didric Cuckoo Chrysococcyx caprius. Since in other species the squawks given by birds in the hand were identical to those given during fights, this is probably also the case in E. orix.

This call is very similar to those recorded from E. franciscanus and hordeaceus in the same context, although it does appear to include more low frequencies. The corresponding call of E. afer is much more rapid and high-pitched.

(2) A chipping call is used by both sexes as an alarm call and as a contact call in the flocks. It lasts only 0,1 s and covers the range 3-8 kHz, with most of the energy around 5 kHz (Fig. 26a, call 2). When the birds are alarmed, the interval between calls is decreased.

E. franciscanus has a very similar chipping call, but the "chuk" of afer is quite distinctive. In the field I found that the flight calls of orix and axillaris could be distinguished quite easily, and it seems likely that the birds can distinguish the calls of conspecifics from those of sympatric species.

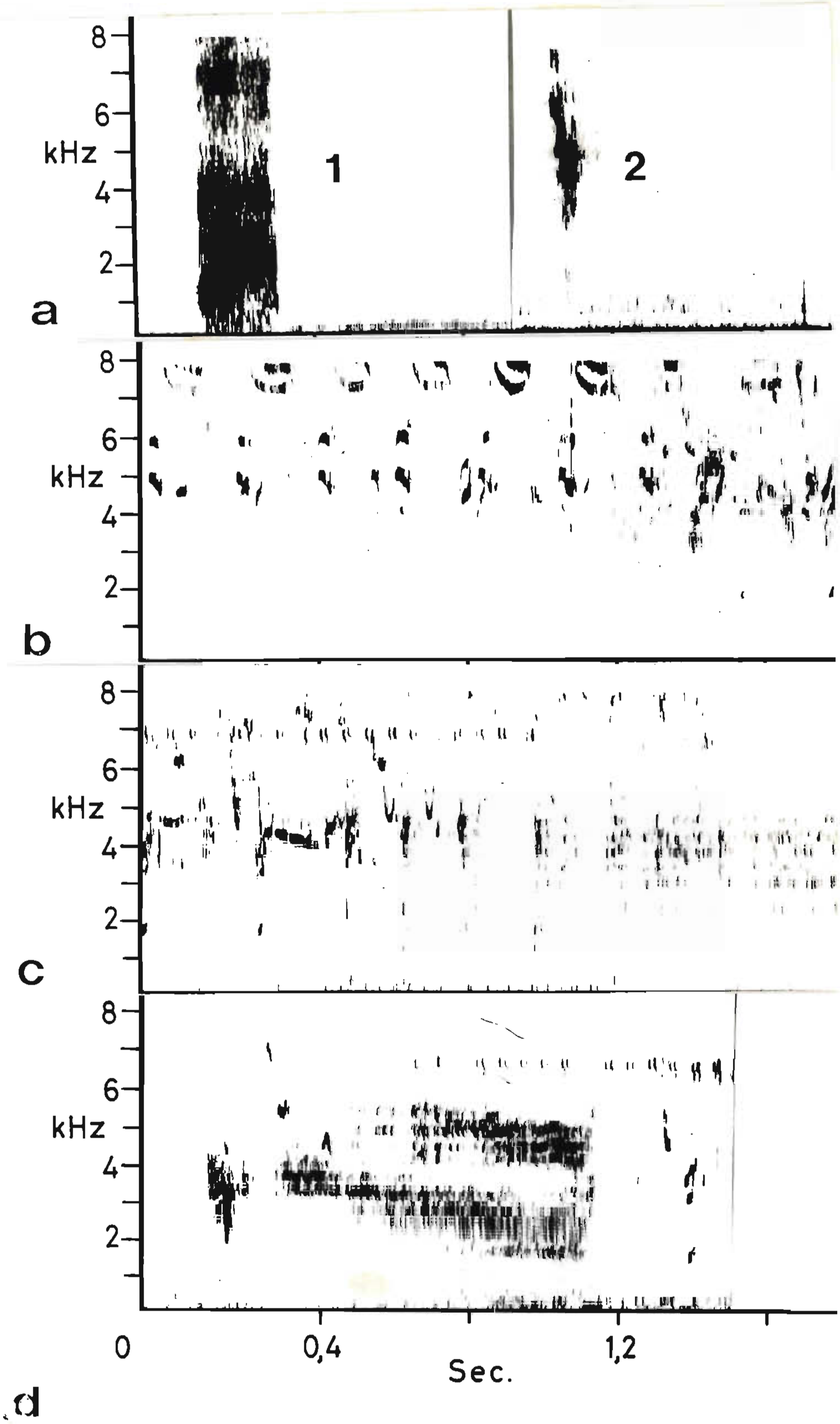


FIGURE 26

Vocalizations of Euplectes orix

(a) call 1 - the squawk; call 2 - chipping; (b) rattling; (c) sizzling; (d) terminal phrase of the sizzle.

(3) Rattling is apparently used only by males, but may be heard throughout the year. In captive birds it is always given by birds gathering around the food bowl, and may occur in aggressive interactions. During the breeding season, a male on his territory will rattle as other birds fly over, or when he flies off and on his return. Under these circumstances it usually consists of a short burst lasting 5-10 s. However, during the swivelling courtship display, the male rattles continuously and this may continue for several minutes. The successive units of the rattle each last from 0,1-0,2 s, comprising three elements at 5 kHz, one at 6 kHz and two between 7 and 8 kHz (Fig. 26b).

Although the rattle of _orix_ lies in the same general frequency range as the rattling calls of _afer_, _franciscanus_ and _hordeaceus_, it is quite different in form. Since this is the call with which males of all four species respond to the approach of another bird, it may play an important role in species recognition during the breeding season.

(4) Sizzling is the song of _E. orix_. It is given only by males in the breeding season, and is evidently correlated with gonadal activity; castrated males never sizzled, although they still rattled and showed normal threat behaviour. A male often sizzles while perched alone on his territory, and a burst of sizzling is commonly preceded by rattling. Very rarely a male may sizzle during a bumble-flight. Sizzling also accompanies the display in which the male hangs below the nest while the female inspects it, and sizzling is the only vocalization used in copulation approaches.

The introductory part of the sizzle contains varied elements, mostly between 3 and 6 kHz, and may last for 1-2 s. The main section covers the range 1-8 kHz, with no distinct elements (Fig. 26c). A single sizzle lasts 5-10 s, but several bursts of sizzling may follow one another, continuing for some minutes. They may be terminated by a loud gargling sound, which shows two broad bands between 5-6 kHz and 2-4 kHz, both tailing off towards lower frequencies (Fig 26d).

The song of _E. afer_, which I have now also heard in the field, is much more complex than the sizzling of orix and franciscanus. As would be expected, the songs of these two species are very similar, but that of E. franciscanus seems to lie mostly in the frequency range 6-8 kHz, while the song of orix is in the region below 6 kHz. However, since rattling is used in courtship, and sizzling is only directed at the female immediately prior to copulation, when she has already accepted the male, the vocalizations of these two species are probably sufficiently distinct to serve for reproductive isolation, and for the present they should be retained as separate species. More recordings of vocalizations in the field will add considerably to our understanding of the behaviour of this genus.

Nesting

All Euplectes species build a woven, domed nest from strips of green vegetation, with the entrance at the side (Collias & Collias 1964). The nest of aureus remains unknown, but it is unlikely to differ from this general pattern. As discussed by Emlen (1957), the preferred nesting areas of different species are usually ecologically separate, but nest site and height may vary considerably for the same species in different areas, as described for orix in Chapter 3.

From the published records it appears that reeds are most favoured by the short-tailed orix species-group, but at the same time these species are the most catholic in their choice of nest sites, quite often using woody shrubs as well as rank grass, standing crops and trees. Bannerman (1949) even reports single nests of E. franciscanus in Nigeria 20 m up in trees, but does not state whether or not they were occupied. Where the vegetation provides enough nesting sites within a small radius, the territories may be clumped to the extent that the birds can be termed "colonial"; this has been reported for afer (Winterbottom 1971; pers. obs.) and nigroventris (Vaughan 1930). However, no other species appears to approach the organization typical of an orix colony, and Crook's (1964) term "neighbourhoods" better describes their breeding dispersion.

The medium- and long-tailed species are typically inhabitants of open grassland with well-spaced territories. Only _axillaris_ may reach densities approaching colonies (Pinto & Lamm 1960), but Chapin (1954) refers to "small colonies" of _ardens_. The latter species appears to be the least addicted to damp areas (Ruwet 1965), and may build its nest either in tall plants or low down in a grass tuft (Winterbottom 1971). The other long-tailed species seem to have the most specific nesting requirements of the whole genus, with the most constant nest sites. The nests are built close to the ground in areas of relatively short, dense grass in _jacksoni_ (Van Someren 1945; Van Someren 1956), _hartlaubi_ (Chapin 1954), _macrourus_ (Vincent 1936) and _progne_ (Haagner 1910).

In the Ploceinae or true weavers the male weaves the nest; this is generally the case in the _Euplectes_ species. It has, however, been stated that only the female builds in some species, and in a few cases actual building has not been observed. I have watched male _albonotatus_, _axillaris_ and _capensis_ building, and the statements by Reichenow (1904) and Priest (1936) that female _axillaris_ build the nest alone can certainly be refuted, as well as Mouritz's (1913) claim that this is the case in _capensis_. It is also possible that some observations of browns building in fact refer to the activities of immature males. Cunningham-Van Someren's (1971) two days of observation on _diadematus_ do not prove that males do not build, while there is no information for _gierowii_ or _hartlaubi_. Skead (1965) states that the male _progne_ does build an outer frame, while McLachlan & Liversidge (1958) agree with Stark (1900) that only the female builds. Teschemaker (1910) observed a captive male build a well-formed nest in a bush about 1 m from the ground, but all the other nests were built by the female; Norris (1968) also saw only the female build the low, well-concealed nests. Dr. A. Kemp informs me that from his observations the male _progne_ definitely does make a start to the nest, though the female does most of the work. Only in the case of _jacksoni_, where the nesting areas are well away from the display grounds, is there good evidence that the male plays no part in the building of the nest (Van Someren 1945; Van

Someren 1956).

Lining the nest is done by the female alone in all cases, and she continues to bring material to the nest during incubation. There is definitely a trend towards increasing female participation in nest-building; Vincent (1936) notes that the inner structure of the nest of axillaris can be removed as a separate section, Hornby (1967) remarks that the female's contribution is much more than a mere lining in albonotatus, and Skead (1965) suggests that the male ardens only makes a token start to the nest, leaving most of the work to the female. Bullock (1938) observed female franciscanus building their own nests in captivity, using these in preference to those provided by the male!

Nest-demolition is practised by many Ploceus species (Collias & Collias 1964). Lack (1935) found that unoccupied nests of E. hordeaceus disappeared and suggested that they had been destroyed by the males, but he did not actually observe this happening. The only observed cases of nest demolition involve male franciscanus in captivity (Phillipps 1905; Steiner 1967); these may have been due to insufficient provision of building material. Leaf-stripping has apparently been recorded only in orix (see Chapter 3), although Van Someren (1956) noted that capensis may nip off the tips of many herbs in the immediate vicinity of the nest.

Bannerman (1949) reports a single instance of a male hordeaceus covering the eggs; otherwise all authors agree that in the wild male Euplectes neither incubate nor feed the young. I have often seen fledged orix begging from a male but they are invariably ignored. In contrast the male Cape Weaver, though also polygynous, feeds its chicks to an appreciable extent both in the nest and after fledging (Elliott 1973). Observations on captive birds, where the male has no opportunity to acquire extra mates, suggest that feeding by the males may not be completely lost in Euplectes: in both afer (Siroki 1974) and franciscanus (Kleefisch 1971) the male fed the chicks once they had left the nest. Even more surprising is the case reported by Rooke (1938), who saw a male franciscanus in eclipse plumage feeding a brood of nestling canaries over a period of 11 days, and even removing droppings from the nest. Once the birds left the nest, the male took no further interest in them, and soon afterwards commenced the pre-nuptial moult. Baily (1916b) reporting on a hybrid *hordeaceus* x *ardens*, states that the male *hordeaceus* was once seen taking a grub to the female *ardens* on the nest, but he did not feed the nestlings subsequently.

Feeding and roosting flocks

Out of the breeding season the *Euplectes* species gather in large flocks, either of only one species, or more usually of several species. The composition of some of these feeding associations is shown in Table 56. Vaughan's (1930) observations on Zanzibar are the only records of feeding associations between *Ploceus* and *Euplectes*; in my experience they tend to remain separate, even when feeding in the same general area. The Red-billed Quelea *Quelea quelea*, which is probably closely related to *Euplectes*, is often found in the flocks when the *Euplectes* species predominate, but the huge Red-billed Quelea flocks of West Africa do not usually contain any other species (Morel 1968). As was discussed in Chapter 2, the feeding ecology of *Euplectes* remains unstudied, though there is circumstantial evidence that the mixed flocks are exploiting the same food sources, and there may be interspecific competition during the dry season.

The extent to which any species is found in the mixed flocks may vary according to local conditions. Neunzig (1921) quotes family parties as the social units of *capensis*, and both Brooke (1966) and Chapin (1954) noted that this species does not readily form large flocks or join the mixed flocks of other species. Yet Van Someren (1956) found *capensis* in East Africa forming "fairly large flocks, all of their own kind or mixed with other whydahs", and in Zambia Winterbottom (1936) saw *capensis* in flocks with *macrourus* and the Pin-tailed Whydah *Vidua macroura*. The distances moved by the flocks during the dry season will also vary from year to year depending on food availability.

TABLE 56

The composition of some mixed-species flocks

Species	Authors
E. ardens, albonotatus, axillaris, orix, progne.	pers. obs.
E. ardens, axillaris, orix, progne, Vidua macroura.	Skead 1959, pers. obs.
E. ardens, albonotatus, axillaris, macrourus.	Ruwet 1964b
E. ardens, capensis.	de Bont et al. 1965 Vincent 1936, pers. obs.
E. ardens, Quelea erythrops.	Skead 1965
E. ardens, Quelea quelea.	Markus 1964
E. franciscanus, Anomalospiza imberbis.	Chapin 1954
E. franciscanus, Vidua macroura, Hypochera spp.	Bannerman 1949
E. franciscanus, Quelea quelea.	von Boetticher 1952
E. hordeaceus, capensis.	Bannerman 1949
E. hordeaceus, franciscanus.	Jackson 1938
E. hordeaceus, franciscanus, albonotatus.	Lynes 1924
E. hordeaceus, franciscanus, macrourus.	Bannerman 1949
E. hordeaceus, nigroventris, Ploceus subaureus.	Vaughan 1930
E. hordeaceus, Quelea quelea.	Reichenow 1904
E. orix, afer.	Reichenow 1904
E. orix, afer, Quelea quelea.	pers. obs.
E. orix, capensis.	pers. obs.
E. orix, Anomalospiza imberbis.	pers. obs.

There are no data for E. aureus, gierowii or hartlaubi. Only single-species flocks have been recorded for E. diadematus (Mackworth-Praed & Grant 1955) and E. jacksoni (Nicolai 1969, Van Someren 1945).

These mixed flocks also roost together in the evenings, most often in reed-beds. Here they may be associated with large numbers of other ploceids, in my experience especially Cape Weavers and Spotted-backed Weavers Ploceus cucullatus. The large numbers of birds, including males in nuptial plumage, which used the roost at Cedara throughout the breeding season, suggest that in E. ardens and axillaris only females with eggs or chicks in the nest actually spend the night on the grassland territories, while all other birds continue to use the communal roost. Hornby (1967) states that male albonotatus appear to roost with the flock, only returning to the territory on the following day. Males of both progne (Mackworth-Praed & Grant 1962) and jacksoni (Nicolai 1969) are also reported to leave the territories in the evening and roost together in large companies in reed-beds. Species like orix which breed in reeds roost on the territory, but other birds are apparently permitted to join them in the evening (pers. obs.).

Discussion

A general theory of polygyny

The earliest hypothesis to account for the occurrence of polygyny was that polygyny is an evolutionary response to unbalanced sex ratios favouring females (e.g. Ryves & Ryves 1934). However, this is contradicted by numerous recent studies, which show that the sex ratios of monogamous and polygynous birds do not differ (see Chapter 1). The availability of mates in local populations may lead to polygyny in normally monogamous species such as the Reed Bunting Emberiza schoeniclus (Bell & Hornby 1969), but it cannot serve as a general explanation.

In his comparative studies of the Ploceinae, Crook (1964) found a clear correlation between mating system and the abundance and seasonal availability of food. The insectivorous species of the forest and forest fringe experience relatively little seasonal change in food supply and are monogamous. In contrast, the savannah-dwelling granivores have a temporary surplus of food following the tremendous peak of grass and insect production after the rains, and these species are polygynous. The only exception to this scheme is the monogamous Red-billed Quelea, but Crook suggests that monogamy in this species is a secondary adaptation. It inhabits drier areas than most other species, and occurs in vast numbers; thus the food supply in the breeding area may be exhausted more quickly, entailing longer flights to forage and the participation of both sexes in feeding the young. Morel (1968) has calculated that the food requirements of even a moderate-sized colony of Red-billed Queleas far exceed the grass and insect biomass of the immediate vicinity, and he recorded birds collecting food from more than 10 km away. The persistence of sexual dimorphism in the genus *Quelea* lends weight to the argument that it is derived from polygynous stock.

Unfortunately this diet-mating system theory does not hold for other groups. If a granivorous diet alone could account for the evolution of polygyny in savannah species, the Estrildidae should also have evolved polygyny, since they are granivores in the same environment as the Ploceinae, yet all species are strictly monogamous. In the New World Icteridae polygyny is common only among frugivorous and marsh-nesting species, which include many insectivores (Orians 1972). Crook's (1964) theory also accounts for the reduction of the male's role in feeding the young, but does not explain the advantages of polygyny to the female. Under favourable conditions the female may be able to rear the young unaided, but she should still be able to raise more young with male assistance. In polygynous matings of the Great Reed Warbler *Acrocephalus arundinaceus* Dyrcz (1977) found that significantly more nestlings died of starvation in polygynous broods than in monogamous broods, although overall nestling production was marginally higher from polygynous broods.

Since the male sex cells are tiny compared to those of the female, the male's initial "investment" at the time of mating is very small, and he may maximise his chances of leaving surviving offspring by copulating with many females and abandoning them (Trivers 1972). This discrepancy in the contribution of the parents to their young can be regarded as the basis of the evolution of reproductive strategies. In polygynous species the male's investment in his offspring remains minimal; in many monogamous species with male parental care, his contribution may approach that of the female, and in the rare cases of polyandry where the male is left to care for the young on his own, he may invest more than the female. Dawkins & Carlisle (1976) point out that the evolution of maternal care in terrestrial animals is probably related to the practice of copulation, which leaves the zygote in the body of the female.

It follows that selection of the best available mate is most critical for the female, and consequently female choice becomes an important factor. On this basis, Verner (1964) proposed that in the Long-billed Marsh Wren Telmatodytes palustris, differences in the quality of male territories might be great enough for females to be more successful mating with already mated males in optimal habitat, rather than with unmated males in poor habitat, even if this meant rearing the young virtually unaided. Subsequently Orians (1969) represented this situation in a generalized graphical model (Fig. 27); this is generally referred to as the "Orians-Verner model". The model predicts that polygyny will be favoured when the success of secondary females (F_2) in optimal conditions (O) is greater than that of monogamous females (F_1) in poor conditions (P). Thus those males which offer optimal conditions will be selected as mates by unmated females.

Orians (1969) made seven predictions regarding mating systems in birds and mammals: (1) polyandry should be rare; (2) monogamy should be the predominant mating pattern in birds, but rarer in mammals; (3) polygyny should evolve more readily among precocial species; (4) polygyny is likely to occur in marsh-nesting birds with altricial young; (5) polygyny should be commoner in early successional habitats; (6) polygyny can be expected where feeding areas are widespread but nesting sites are restricted; (7) polygyny and promiscuity should occur when clutch size is controlled by factors other than the number of young the

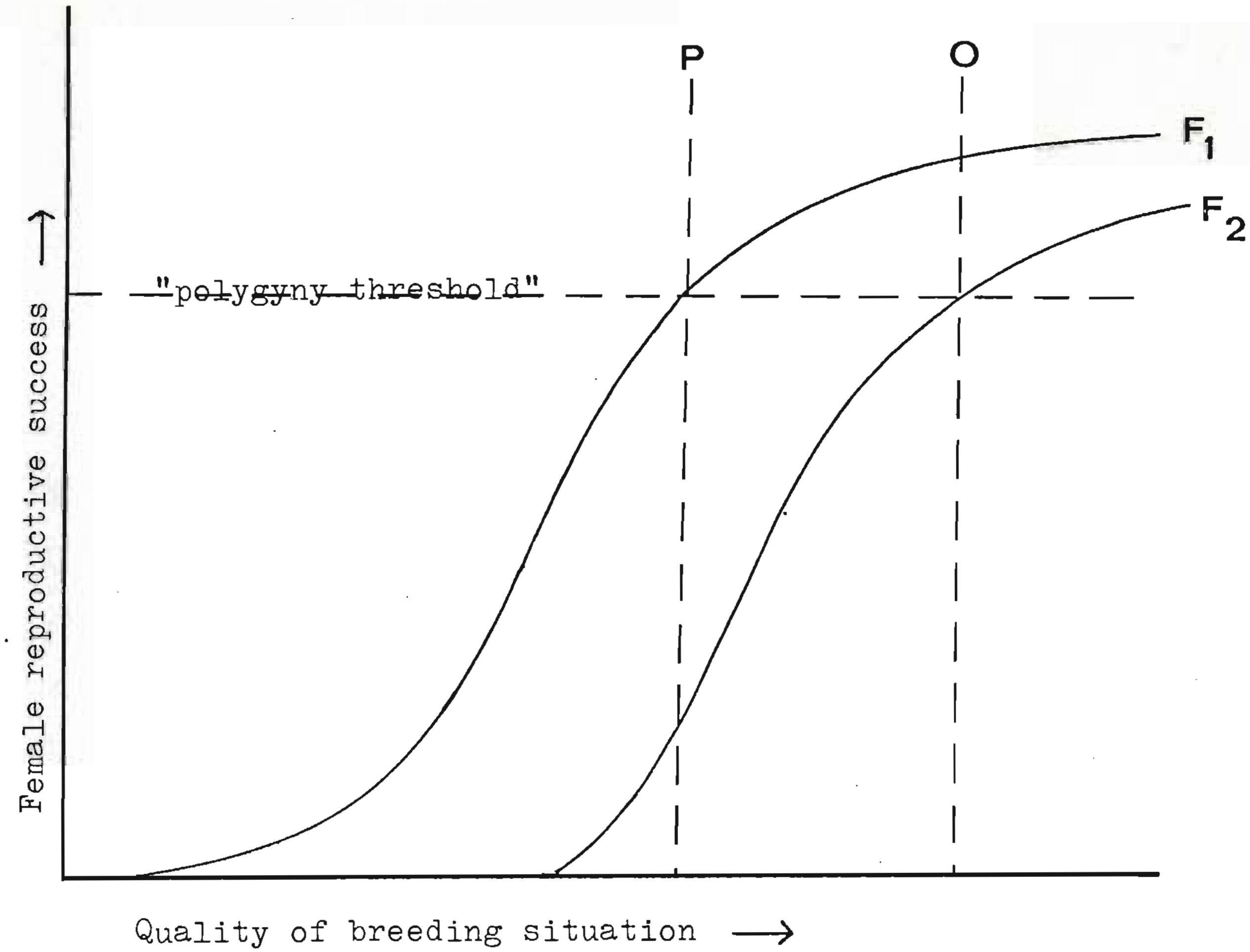


FIGURE 27

The Orians-Verner model of conditions favouring polygyny Modified from Orians (1969); see text for explanation.

parents can rear.

Of the above predictions, (1) and (2) are confirmed by Lack's (1968) data on the pair-bond in birds, but (3) is only partially fulfilled since most Anatidae are monogamous. Some examples of prediction (5) are known, such as the Dickcissel Spiza americana (Zimmerman 1966). Case (7) was an attempt to account for polygyny in the frugivorous Icteridae, where Orians (1969, 1972) suggests that the diet limits the number of eggs which the female can produce. While clutch size is dependent on the food available to the female (see Chapter 3) and food availability also affects litter size in mammals (Downhower & Armitage 1971), there is no evidence of a correlation between a small clutch and polygyny. Von Haartman (1955) considered this question, and found no evidence of a reduced clutch size in polygynous species. The clutch size of polygynous Ploceinae is not smaller than that of monogamous species (Moreau 1960). Wittenberger (1976) proposes that in the frugivorous Icteridae the use of traditional colony sites effectively restricts the availability of suitable nest sites, thus making this a case of prediction (6). Both predictions (4) and (6) are applicable to the Ploceinae, and many examples are known from other families.

Since this model provides a set of predictions which can be tested against the situations found in practice, it has formed the basis of most later treatments of the problem of polygyny. Downhower & Armitage (1971) claim that the model is too restrictive in that it places all the emphasis on advantage to the female, but their results from a study of the Yellow-bellied Marmot Marmota flaviventris clearly show that polygyny is advantageous for unmated females, as predicted by the Orians-Verner model. In this species monogamy is, however, the optimal female strategy, which implies that already mated females should defend their status against new arrivals. Wittenberger (1976) suggests that in certain mammal species polygyny may be actively prevented by female behaviour (aggression to other females) rather than selected against by environmental conditions.

Using the Orians-Verner model as a starting-point, Wittenberger (1976) derives two further predictions: (a) when polygyny has evolved in response to physiognomic differences between habitats, all territorial males will acquire mates, and there will be delayed maturation of male plumage; conversely (b) when polygyny has evolved at least partially in response to differences in the food resources between habitats, there will be unmated territorial males and no delay in male plumage maturation. These predictions are compared with the published evidence, and he concludes that there are two ways in which polygyny has evolved in altricial birds. In colonial species polygyny evolved apparently because a few males could defend the limited number of safe nesting sites available, thus obliging many females to mate with already mated males. In noncolonial species polygyny arose because a combination of differences between optimal and marginal habitats enabled second-mated females in optimal habitats to be as successful as monogamous females in marginal habitats.

A major weakness in this argument is his initial assumption that "The Orians-Verner is not applicable to species in which females cannot determine the mated status of potential mates". There is no reason to assume that this is possible for any bird species, and the model as stated does not demand it - the female chooses the optimal breeding situation available to her. If the male is courting and the nesting opportunities meet her requirements, the presence of other females in the area is irrelevant. A second flaw in Wittenberger's (1976) reasoning is the deduction that where delayed maturation of male plumage is found, all territory-holders will acquire mates. In the Red-winged Blackbird *Agelaius phoeniceus* (Holm 1973), the Long-billed Marsh Wren (Verner 1964), the Boat-tailed Grackle *Quiscalus mexicanus* (Selander & Giller 1961) and in *Euplectes orix* (pers. obs.) there are unmated males in the colonies while other birds are polygynously mated. The breeding sex ratio calculated for *E. orix* (Chapter 1) also suggests that not all adult males will acquire mates. Female choice implies that some males will be more successful than others, and some may fail to acquire mates. Finally the distinction between colonial and noncolonial modes of evolution of polygyny rests on the comparison of extant species, but there is no a priori reason to assume that colonial breeding preceded polygyny in the evolution of these species.

An aspect neglected in all these studies is the longevity of the species. Elliott (1975) in a mathematical treatment based on studies of marmots, appears to be the first to consider the relationship between longevity and polygyny. He points out that an animal species with a long expected lifespan may be able to sacrifice maximum yearly reproduction, if the probability of survival and future reproduction is increased. Fisher (1975) studying the Laysan Albatross Diomeda immutabilis, a notably long-lived species with very low mortality rates, found that postponing breeding was clearly advantageous to the individual. The young birds do not breed in significant numbers until they are eight or nine years, and in the first years of breeding raise fewer chicks than older birds. In addition birds which start breeding earlier than normal have lower survival rates. No seabird species is polygynous, but this is related to other ecological factors (Lack 1968).

Deferred maturation, which is very characteristic of highly polygynous bird species, must depend on a relatively low adult mortality rate to be selected for. The polygynous White-bearded Manakin Manacus manacus has a very low annual mortality of about 11% (Snow 1962), and there is some evidence that the adult mortality of Euplectes orix is also low (see Chapter 1). If the work of Morel (1969) on the Red-billed Firefinch Lagonosticta senegala is representative of the situation in other estrildids, their short lifespans and high mortality rates may explain why polygyny has not evolved in this group.

The Orians-Verner model represents the best explanation of avian polygyny yet devised, and is clearly applicable to the Ploceinae. For the Euplectes species, feeding areas are widespread but nesting sites are restricted by their specific requirements. The origins of marsh-nesting will be dealt with later, but the situation is not comparable with that of the polygynous marsh-nesting icterids, whose territory provides an appreciable amount of food for the young. The longevity of the birds has an important bearing on the subsequent evolution of polygyny in the group.

Sexual selection

Darwin (1871) described sexual selection as "the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction", and he recognised that sexual selection should have its greatest effect in polygynous mating systems. Here females will choose males with particular characters, and sexual dimorphism will be enhanced. This is strikingly illustrated by the plumage and displays of bird species with non-monogamous mating systems, and it is commonly accompanied by delayed maturation of the males.

Morphological features concerned with feeding may also be modified by sexual dimorphism, and this is then difficult to separate from the effects of natural selection. Selander (1972) reviews changes in the feeding apparatus of birds and concludes that only when these structures alone are modified can one assume that this is due to selection for differential niche utilisation by the two sexes; an example of this is the bill of the Huia *Heteralocha acutirostris*.

Under sexual selection, characters such as large size, conspicuous plumage and aggressive tendencies are highly adaptive in competition among males for mates, but if carried to extremes they will reduce the probability of survival of the individual. Thus a balance is established, maximising the fitness of individual males. Instead of employing increasingly conspicuous plumage, objects may be substituted for secondary sexual characters, as shown by the bower birds (Selander 1972). The term "transferalism" has been used to describe the situation where characteristics of the territory have become significant in female choice;

the role of the nest in the courtship of the Ploceinae may be another example of this.

In the pinnepeds Bartholomew (1970) regards the remarkable sexual dimorphism in size as a direct result of the polygynous mating system, but in birds many families do not show an obvious relationship between body size dimorphism and mating system (e.g. the manakins, Pipridae; Selander 1972). It is perhaps most striking in grouse, but here size dimorphism has been ascribed to pressures other than sexual selection.

Reviewing the social organisation of grouse, Wiley (1974) rejects the Orians-Verner model as an explanation of polygyny in the family, since single parental care is general in both monogamous and polygynous species, the young are precocial, and only in three monogamous species does the female restrict her choice of a nest-site to her mate's territory. Wiley proposes that ecological conditions affect the evolution of body size, and large body size and increased life expectancy could favour deferred reproduction, especially in males - polygyny is associated with the resulting imbalance in the breeding sex ratios. Thus he suggests that polygyny should be influenced by ecological conditions which reduce the advantages of dual parental care, and increase the advantages of the sexes maturing at different ages.

Size dimorphism in the Ploceinae is not extreme, and more easily explained by sexual selection than by ecological factors. Large size is less likely to be advantageous to a tropical passerine than to a ground-dwelling herbivore in the north temperate zone. Selander (1972) emphasizes that sexual selection can also occur in monogamous bird species, since female choice is a general phenomenon and there is good evidence of a surplus of males in the adult population of many passerines (see Chapter 1). Since the nuptial plumage of the Euplectes species is lost after the breeding season, one may assume that it has evolved through sexual selection. Moreau (1960) showed that there was a close correlation between the plumage characters of the Ploceinae and the mating system of the species.

The role of the territory

The Orians-Verner model was based on studies of territorial passerines. Verner (1964) originally suggested that the female Long-billed Marsh Wren selected her mate on the basis of features of the territory, and much research has since concentrated on this question. The two important resources in the territory are nest sites (or nests in species whose males build them) and food. If the birds do not actually forage in the territory, it may be located close to feeding areas.

Verner & Willson (1966) found that most records of polygyny in American passerines concerned birds breeding in high productivity habitats such as marshes and savannah. The marsh-nesting Yellow-headed Blackbird _Xanthocephalus xanthocephalus_ feeds on the territory to a large extent; the females tend to maintain exclusive sub-territories within which they forage (Willson 1966). Nesting success of the females is correlated with territory size, but they choose territories with the most suitable nest sites. However, Holm (1973) showed that harem size and breeding success in the Red-winged Blackbird were related to the type and density of vegetation on the territory and not to its size or the food supply; most of the feeding was done away from the territory. A nest site with adjoining food supply is apparently provided by polygynous males of the North American Dipper _Cinclus mexicanus_ (Price & Bock 1973). Suitable nest sites are scarce, and a male may have several nest sites in his territory, while there are none in the adjacent areas, which are consequently unoccupied and available for foraging.

The Dickcissel breeds in fields with good vegetation cover, and Zimmerman (1966) found that mated males had larger territories than bachelors, with better cover offering more nest sites. In a later study, Zimmerman (1971) correlated the volume of vegetation on the territory with the number of mates, and showed that at high male densities some individuals were forced into occupying areas of less suitable vegetation, where they failed to get mates. Harmeson (1974) could not confirm the relationship between cover and number of mates, though she also found changes in territory size with increasing male density, and evidence that some birds were forced into suboptimal habitat. In addition, she recorded differences in food availability, and suggested that foraging on the territory might be important. In similar habitat, secondary females of the Bobolink Dolichonyx oryzivorus become less selective in their choice of food and forage closer to the nest, apparently to compensate for the lack of male assistance in feeding the young (Martin 1974). Orians' (1969) model also predicted that other species in this habitat might be polygynous, and this was confirmed for the Indigo Bunting Passerina cyanea by Carey & Nolan (1975). Here too, success appeared to be related to the vegetation on the territory.

Saitou (1976) has found that the pairing success of male Great Reed Warblers was correlated with the date of their arrival in spring. Those arriving early occupied territories in Phragmites and some obtained two mates, while later arrivals were often forced to occupy the less favoured Rottboelia area, and some remained unmated. The average territory size of monogamous and bigamous males was almost identical (910 m^2 and 930 m^2 respectively), but unmated males had significantly larger territories (1350 m^2). Thus mating success was not related to territory size. Since breeding success was higher for nests in Phragmites, Saitou suggests that the quality of the territory determines the female's choice of a mate, and that it will be advantageous for a female to nest in Phragmites, even as the second mate of an already mated male.

From these studies it would seem that successful polygyny depends primarily on the availability of suitable nest sites on the male's territory. Breeding success may also be affected by the amount of food that can be collected on the territory - but this is much more difficult to assess.

In Europe von Haartman (1951, 1969) found that polygyny was relatively most frequent in hole-nesting species, or in those which built domed nests. Species such as the Pied Flycatcher *Ficedula hypoleuca* practise successive polygyny, with the male having up to six territories, moving on to the next one during the incubation period of the first female (von Haartman 1951). He suggests that the restricted number of nest sites may facilitate polygyny in hole-nesters, while in such protected nests the lower heat loss may enable the female to leave the young alone for longer periods to forage on her own.

The age of the female may determine the time when she will nest, and thus also influence her choice of a mate. This topic has scarcely been investigated, but Blakley (1976) produced evidence that younger females nest later in the Red-winged Blackbird, and then mate with already mated males. Martin (1974) also found that the secondary females of the Bobolink were younger than the primary mates. Blakley (1976) proposes that, because successful nesting of an earlier female is a good indicator of the suitability of a territory, there may be an adaptive advantage in inexperienced females selecting territories where other females are already nesting.

Observations of successive polygyny in the Ipswich Sparrow *Passerculus sandwichensis princeps* led McLaren (1972) to propose a novel explanation for the adaptive significance of territoriality in birds. He writes " .. I believe that breeding territoriality is a minimal requirement for polygyny among solitary nesters and has evolved largely or entirely to that end in many species." Welsh (1975) also holds that the possibility of polygyny is the prime reason for territory maintenance in *Passerculus sandwichensis*. Territorial behaviour is certainly shown by all polygynous species, but McLaren's (1972) arguments are unconvincing and it is naïve to expect that a single sentence will explain the phenomenon of territoriality.

Returning to the Long-billed Marsh Wren, Verner & Engelson (1970) later found that male pairing success could not be correlated with any of the territorial parameters measured. There were, however, significant differences in the nest-building proficiency of bachelor males, which appeared to account for their failure to acquire mates.

Since feeding flocks of *Euplectes* are to be seen throughout the breeding season, the territory appears to be of little importance as a source of food, even for the grassland species. Birds from the breeding colonies of *Euplectes orix* have been observed in flocks which definitely contained birds from more than one colony. As in the above-mentioned studies, the primary function of the territory is to provide a nest site. In most *Euplectes* species the male also provides the basic nest structure, and at least in the case of *E. orix* there is evidence that the quality of the nest may influence female choice (Chapter 3) as has been found in other weavers (Collias & Collias 1964). Radtke (1957) quotes field observations of *E. afer* from a correspondent who claimed to detect individual differences in the nests of the males, and suggested that the females assessed the durability of the nest, ignoring those of inexperienced males. As the male's role in nest-building becomes smaller, other factors must increase in importance for the female. In particular the situation in *E. progne*, where display site and nesting territory may be separate (A. Kemp, pers. comm.), and in *E. jacksoni* where the male does not establish a nesting territory (Van Someren 1945) requires detailed study. It is tempting to regard the central tuft on *jacksoni*'s dancing ground as a symbolic nest.

The behaviour of the male

Both visual displays and vocalizations are known to be important in the reproductive isolation of many bird species. Sexual selection in polygynous species implies that displays are also significant in determining the reproductive success of particular males. Aggressive behaviour is vital for territory maintenance, and the dramatic effects of dominance in inter-male competition are well illustrated by species such as the Elephant Seal *Mirounga angustirostris*, where fewer than one third of the males copulate at all (Le Boeuf 1974). Dominance ranking within a breeding colony may play a role in some bird species such as the Cape Weaver, in which Elliott (1973) found that some birds were regularly prevented from courting females by their more dominant neighbours, but in Euplectes orix I have never seen courtship interrupted by other males trespassing on the territory.

It is difficult to separate the effects of male behaviour on female choice from the influence of territorial (including nest) parameters. Elliott (1973) found that physical size of male Cape Weavers was unrelated to mating success, and behavioural comparisons were inconclusive; my data on E. orix are also inadequate to demonstrate any effect of behaviour on mate attraction (Chapter 3). The most interesting results come from work on the Red-winged Blackbird, which employs red epaulets (very like those of E. axillaris) and a distinctive song in its displays. Peek (1972) and Smith (1972) both demonstrated that males with blackened epaulets lost their territories, and consequently their opportunities of mating, much more often than normal males. Later in the season when territories were well established, some experimental males were able to maintain their territories, and acquired further mates (Smith 1972). Even more surprising was the finding by Smith (1976) that males producing abnormal song following sectioning of the hypoglossal nerves were able to maintain their territories and breed as successfully as control birds. This suggests that while the male's behaviour may enhance his attractiveness to some degree, it may be much less significant than generally assumed. Further experiments on other species are needed to establish how widespread this is.

Competition for a territory may also involve interspecific competition. Cody (1969) proposed that sympatric species may converge in appearance to increase interspecific territoriality, which he regards as highly adaptive. Murray (1971, 1976) has reviewed the recorded instances of interspecific aggression, and finds little evidence of convergence in the species concerned. He suggests that interspecific territoriality is generally misdirected intraspecific territoriality behaviour in areas where ecological separation of the species is incomplete, and this will occur without convergence when the exclusion of potential competitors is advantageous, regardless of their species.

Emlen et al. (1975) considered that their study of sympatric populations of the Indigo Bunting Passerina cyanea and the Lazuli Bünting P. amoena provided evidence of convergence in song type. Within the area of sympatry the two species responded aggressively to both song types, but elsewhere they responded only to the song of conspecifics. In respect of certain characters, known to play a role in male-male recognition in these species, the songs in the zone of sympatry appeared to be "intermediate". By contrast, Ferry & Deschaintre (1974) found that both sympatric and allopatric populations of the Icterine Warbler Hippolais icterina and the Melodious Warbler H. polyglotta responded to each others' songs, suggesting a spontaneous predisposition to do so. The role of learning needs to be studied further in both cases.

Verner (1975) cites another case where misdirected territorial aggression does not seem to apply. He found that Yellow-headed Blackbirds aggressively exclude Long-billed Marsh Wrens from the vicinity of their nests, and suggested that exclusion might be selected for in this case, owing to competition for newly-emerged Odonata, and the Long-billed Marsh Wren's habit of puncturing the eggs of other species nesting within its territory.

Most documented cases of interspecific competition for nesting areas occur in habitats which are optimal for only one of the species involved, and this species then excludes its less specialised competitor. The Reed Warbler Acrocephalus scirpaceus will exclude the Sedge Warbler A. schoenobaenus from reed-beds where the two species are sympatric, while in field vegetation they maintain interspecific territories (Catchpole 1973). Similarly the Yellow-headed Blackbird, which will only nest over standing water, excludes the Red-winged Blackbird from such areas (Miller 1968). Although they do not resist the aggression of Red-winged Blackbirds, Tricoloured Blackbirds Agelaius tricolor exclude Red-winged Blackbirds from their colonies by sheer weight of numbers. Orians & Collier (1963) concluded that these two species have diverged primarily through their different social systems. Diesselhorst (1971) saw a male Vieillot's Black Weaver Ploceus nigerrimus drive off a pair of Spectacled Weavers P. ocularis, which were trying to nest in the same palm tree, and noted that the Spectacled Weavers had difficulty in tearing off strips of material from the palm leaves and built much more slowly than their competitor. This was evidently not an optimal nest site for them.

Among the Euplectes species habitat separation is more common than interspecific territoriality, and the similarities in the plumage of the males rest on common descent rather than on convergence in the sense of Cody (1969). Murray's (1971) theory provides a better explanation for interspecific territorial behaviour in this group. In the red and black species such as E. orix, hordeaceus and nigroventris mis-identification of males could be expected. Colour may be a more important visual stimulus in male-male interactions than in male-female contexts; Dücker (1970) has shown that plumage colours have greater significance for male E. franciscanus than for females, and that this may in part depend on sexual hormones.

Nevertheless, all species-specific characters may have some significance for the female in selecting her mate. Though males will court any brown-plumaged birds, hybrids have yet to be recorded in the wild, showing the existence of efficient isolating mechanisms. In mixed colonies of Boat-tailed Grackles Quiscalus mexicanus and Great-tailed Grackles Q. major, Selander & Giller (1961) also found males courting females of either species, but there was complete reproductive isolation, apparently depending on the selective role of the females. Vocalizations, plumage displays and preferred nesting habitat differ between the Euplectes species, and from my observations I agree with Emlen (1957) that the female is responding to a "total nesting situation" made up of all these different elements. The most distinctive displays (e.g. jacksoni) appear in cases where the male contributes least to the siting and construction of the nest.

Although the mating system of E. jacksoni is of exceptional interest, there appears to have been no recent study of this species. However, several lek mating systems have now been analysed in some detail. Hogan-Warburg's (1966) study of the Ruff Philomachus pugnax revealed surprising differences between large and small leks, with satellite males on small leks actually performing more copulations than the resident territory-holders. Nevertheless a small proportion of the males perform most of the copulations, and females appear to favour those males with fully developed nuptial plumage. Wiley (1974) has reviewed the literature on lek-forming grouse. Their leks occupy traditional locations, and males tend to return to the same lek in successive years. Most copulations are performed near the centre of the lek by a minority of the attending males; in the Sage Grouse Centrocercus urophasianus about 10% of the males performed 75% of the copulations.

Among the passerines, only the manakins (Pipridae) have been studied intensively. In the White-bearded Manakin Manacus manacus Lill (1974) also found that most copulations were performed by a small percentage of the resident males. Female choice was evidently responsible for the non-random distribution of matings, but neither in the White-bearded Manakin nor in the Golden-headed Manakin Pipra erythrocephala was male mating success correlated with the behaviour or morphology of individual males. Female choice in both species seems to be influenced by characteristics of the territory; Lill suggests that this may be an example of "transferalism".

Selander (1972) criticised the lack of discrimination in the choice of partners implied by the term "promiscuous", and proposed the alternative term "polybrachygamy" to describe an individual mating with two or more individuals during a breeding season, with a very brief, transitory pair-bond. This term has failed to gain general acceptance, although the inaptness of the label promiscuous is widely recognized. Lill (1974) has shown that females of both the White-bearded Manakin and the Golden-headed Manakin tend to show an absolute or strong preference for a single male during one breeding season, and there is some evidence that this is also the case in grouse (Wiley 1974) and in the Ruff (Hogan-Warburg 1966). Thus the females are probably much less promiscuous than the males.

For Euplectes jacksoni, a few predictions can be made: it is likely that the differences in mating success of individual males will be more marked than in any other Euplectes species; most females probably mate with only one male each breeding season; maturation of the males may be delayed even longer than in the other species; and finally, the results of Van Someren's (1945) experimental removal of the tuft on one court imply that the territory may also determine female mate-selection in this species.

The colony and the flock

Protection from predators has often been cited as the reason why birds form large associations with members of their own or other species. Yet even prior to man's impact on the ecosystem, which has been especially detrimental to predators, it is unlikely that predation was the major source of mortality in any bird species. More recent theories have concentrated on possible advantages to the individual bird in respect of feeding and reproductive success.

Some interesting experiments on the European Starling Sturnus vulgaris showed that individual birds in large flocks spend less time in surveillance than in small groups, and respond more quickly to the appearance of a hawk model. The same effect was found in mixed groups of European Starlings and Red-winged Blackbirds, which often forage together in California (Powell 1974). From theoretical considerations, Thompson et al. (1974) conclude that risk for the individual bird decreases with increasing flock size, but small flocks are most successful in terms of feeding rate. The optimal flock size will depend on the balance between these two tendencies, but they suggest that minimising risk may be more important for small birds.

From his observations of gull colonies, Darling (1938) proposed what has since become known as the "Darling effect". He stated that in larger colonies (a) egg-laying began earlier; (b) breeding was better synchronised; and (c) breeding success was higher. More detailed studies of seabird colonies have since shown that many of the observed differences are probably a consequence of the age structure of the population, rather than the effects of social stimulation (e.g. Coulson 1968). The first investigation of the "Darling effect" in a passerine bird was carried out by Smith (1943) on the Red-winged Blackbird. While egg-laying was more closely synchronized in the largest colony, the total breeding period was also much longer than in smaller colonies. There was no evidence that breeding started earlier in the largest colony, and breeding success did not differ between the colonies studied.

Later Orians (1961) re-examined the question in the Red-winged Blackbird and the Tricoloured Blackbird. He also found that in the Red-winged Blackbird variations in timing and synchrony were related to ecological factors rather than colony size, and in the Tricoloured Blackbird time of breeding, synchrony and clutch size were independent of colony size. However, he suggested that the differences in time of breeding of colonies of Tricoloured Blackbirds in the same district might be influenced by social stimulation in the nomadic flocks prior to breeding. The timing of breeding in the Brewer's Blackbird <u>Euphagus cyanocephalus</u> is also determined by environmental factors (Horn 1970). The precopulatory display of this species appears contagious, resulting in synchronization of displays throughout the colony. Horn (1970) found that this leads to a correlation between the synchrony of nesting and the compactness of the colony.

Observations of the Ploceinae have also failed to confirm the existence of the "Darling effect", although there may be some effects due to social stimulation. Hall's (1970b) study of the Spotted-backed Weaver and Vieillot's Black Weaver in Uganda showed that breeding was correlated with rainfall, but differences in synchrony between neighbouring colonies provided some evidence for social stimulation. In aviary colonies of the Spotted-back Weaver, Victoria & Collias (1973) found that social facilitation of egg-laying occurred at the start and the close of the breeding season, and crowding the birds at these times increased egg-laying activity. During the 1976-77 season at Malton, there was some evidence of increased synchrony in egg-laying at the Euplectes orix colony which might be ascribed to social stimulation, but this appeared to be of little significance in terms of breeding success (see Chapter 3).

Snapp (1976) lists four factors which could select for colonial breeding: (1) predation; (2) food supply; (3) social stimulation; and (4) nest site availability. In the European Swallow Hirundo rustica there was no evidence that the number of pairs in the colony or the degree of synchronization affected breeding success by influencing losses due to predation and food shortage. Thus she concluded that colonies in this species represent passive aggregations of breeding pairs due to nest site availability. Food distribution may, however, be a major factor in determining nesting distribution, as Horn (1968) has convincingly demonstrated for the Brewer's Blackbird. His model predicts that colonial nesting is appropriate for a species exploiting food supplies which vary both spatially and temporally. Within the colony nest-spacing will represent a compromise between the effects of foraging efficiency and predation.

Lack (1968) still maintained that communal roosting in all birds, and flocking and colonial breeding in most species, is primarily for protection from predators. The importance of food-finding rather than predation is emphasized by the recent hypothesis of Ward & Zahavi (1973). They suggest that roosting and breeding assemblies of birds serve principally as information centres, where unsuccessful foragers can acquire information about the location of good feeding areas. This can apply to species which breed colonially and feed in flocks, as well as to species such as herons, which breed in colonies yet tend to feed solitarily, as demonstrated by the elegant study of the Great Blue Heron Ardea herodias by Krebs (1974). Recent support for Ward & Zahavi (1973) is also provided by the work of Emlen & Demong (1975) on the Sand Martin Riparia riparia. Fledging within the colony is highly synchronized, and Emlen & Demong (1975) suggest that since this species is feeding on a highly variable food supply, social foraging maximises feeding efficiency. Thus birds emerging late are deprived of the benefits of pooled information, with the flock acting as an information centre. The concept of "information centres" is a major contribution to our understanding of avian social organisations.

Ward's (1965a) work on the Red-billed Quelea gave strong support to the theory, and similar patterns of roosting and feeding dispersion are found in the Euplectes species. Aviary observations by Crook (1961) on E. afer and Red-billed Queleas showed that social tendencies are much more marked in the Red-billed Quelea. Morel (1968) also contrasts these two species, noting that E. afer is not truly colonial, and though a strong flyer, is more bound to standing water than the wide-ranging Red-billed Quelea flocks. These differences may in part explain the tremendous success of the Red-billed Quelea compared to all the other Ploceinae, and have doubtless assisted it in adapting to current agricultural practices in Africa. The Euplectes species are also successful, but perhaps more restricted by their specialised breeding habits.

Conclusion

The evolution of the Euplectes species

The Ploceinae are of African origin, and according to Crook (1964) their radiation has probably occurred entirely within the Pleistocene. During this period the climate of Africa has alternated between pluvial and relatively arid epochs, which must have had a considerable influence on the speciation of this group. From their present distribution, it seems likely that the Ploceinae evolved in the savannah, and subsequently invaded the forests. One may postulate that the original forms were seed eaters, and fairly social.

Since weaving as a nest-building technique is common to all members of the sub-family, this must have arisen early in their adaptive radiation. The requirements of nest-building may have formed the basis of territorial behaviour. However, because of the type of food exploited, aggregations were advantageous for foraging and the birds gathered to roost. These roosts also required protection from predators, and in the open grassland areas the safest place for large numbers of birds to gather is in dense waterside vegetation. In addition, areas with abundant water are likely to have the most reliable food supplies. Because of all these advantages, the roosting area would be the most suitable breeding site.

During arid periods there would be intense competition for the few suitable breeding sites - areas which were within easy reach of adequate food supplies. This would lead to increased selection for territorial behaviour, with territorial defence becoming the primary responsibility of the male. Not all males would hold territories meeting the requirements for successful breeding, so that female choice could lead to the favouring of a limited number of males, and consequently to polygyny. Nest-building, formerly shared between the sexes, now became the chief task of the male, who was obliged to spend most of his time on the territory, while sexual selection and competition between males would enhance displays serving for intraspecific communication.

This is the condition represented by the least specialised <u>Euplectes</u>, such as <u>E. orix</u>. Breeding and roosting sites are often identical. The assumption of nuptial plumage involves only moult of the body feathers, and neither wings nor tail have been modified. Sexual dimorphism is not marked in non-breeding plumage, and the size differences between males and females do not suggest any ecological separation. Thus there may be competition for food during the dry season, and a higher female mortality leading to a biased sex ratio in some populations. Nevertheless, due to deferred maturity in the males as a byproduct of the competition in the polygynous mating system, the breeding sex ratio shows more females than males.

In the other members of the genus these features are progressively modified. Breeding and roosting areas are separate, with the birds nesting in grassland, though generally in wet areas. The nuptial plumage includes specialised tail feathers, and the males retain distinctive markings in eclipse plumage. Sexual dimorphism in size is marked, and age classes can also be distinguished. In the species which have been studied, the sex ratio is closer to unity than in E. orix, but the breeding sex ratio reflects an even larger proportion of females. The most obvious changes affecting the males of the genus are shown in Figure 28 (see also Table 55); the lines joining the blocks indicate my ideas of the relationships between the species.

The two most distinctive species are E. ardens and jacksoni. The remarkable mating system of jacksoni has already been described, but the suggestion that there is a separation between the nesting area and the display territory in progne reveals a possible intermediate stage. E. ardens shows no obvious connection with any other species. Despite the very long tail of the male in nuptial plumage, the size difference between males and females is not as great as in the other species with even medium tails (see Chapter 2). The display is a rapid glide, rather than the laboured flight of progne, and the nesting area tends to be in drier country than that favoured by any other species. E. ardens also has the distinction of being the only species which is sympatric with every other member of the genus.

Man is the chief factor in the ecology of the Euplectes species to-day. These seed-eaters have all benefitted from the extensive cultivation of crops. In the changed conditions the least specialised species, E. orix and its closest relatives, have been the most successful. Irrigation and the building of dams has provided orix with nesting

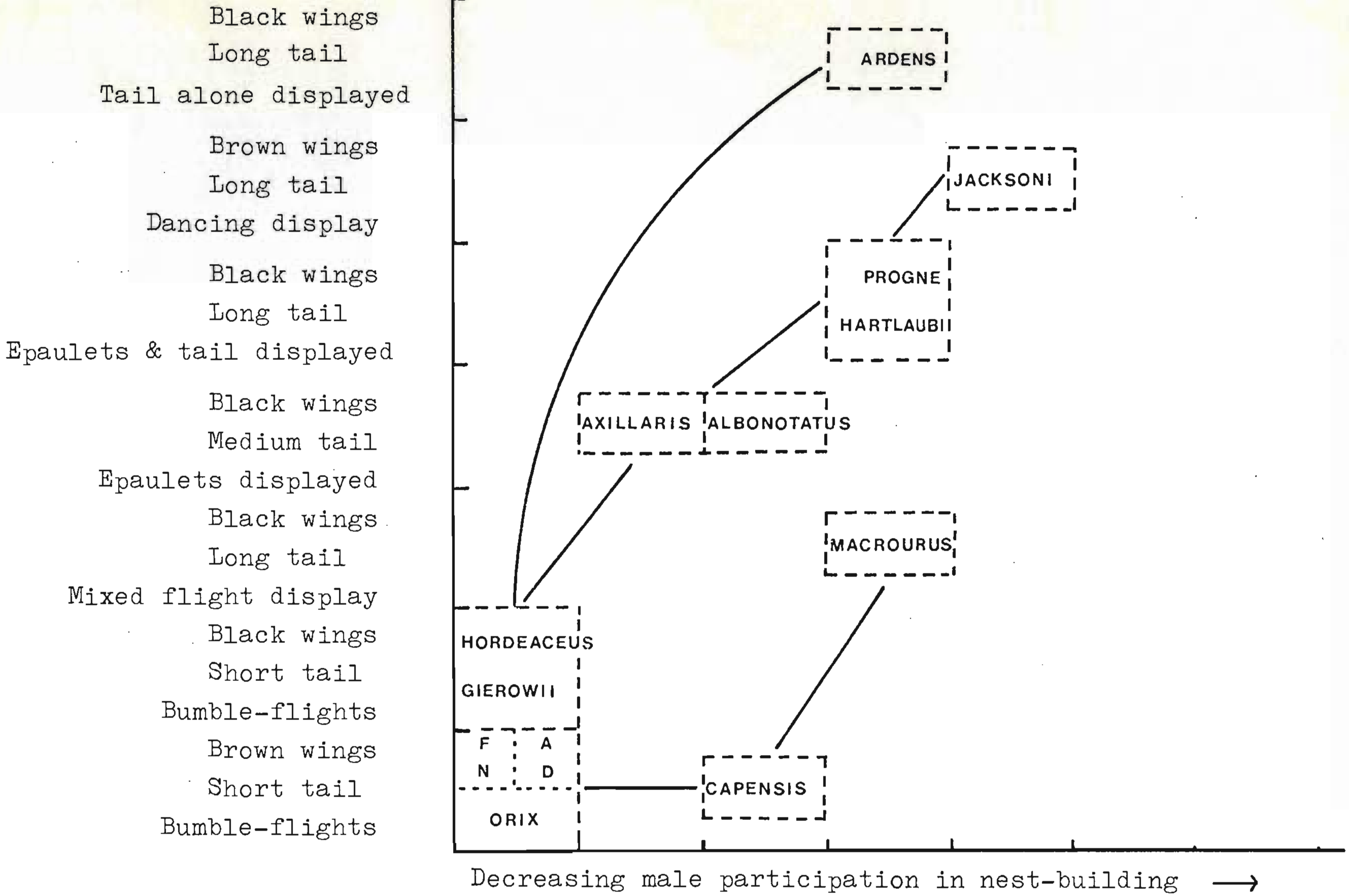


FIGURE 28

Evolutionary trends in the genus Euplectes

aureus is omitted. f = franciscanus, n = nigroventris, a = afer, d = diadematus.

sites conveniently close to the food supplies, and it is the only species to have achieved pest status in many areas. The smallest, least dimorphic species such as *orix* and *afer* seem to be capable of the most extensive movements if locally unfavourable conditions arise. The slow, bouncing flight of *progne* is obvious even in males in eclipse plumage, and this species is much more restricted in its distribution, and also in its nesting requirements. Only *jacksoni* could be directly threatened by man's activities at present, since it has a very small distribution range and the most specialised habitat requirements of any of the group.

The evolutionary steps and relationships suggested here are purely speculative, since our knowledge of many species is still fragmentary, but they may serve as a guide for future research. The interactions between man and the *Euplectes* species could play an important role in agriculture in Africa for the future, since these birds seem to be adapting very successfully to life on the farm.

SUMMARY

The breeding biology of the Red Bishop was studied at the same colony for two seasons, and the annual cycle of this species and of the Red-shouldered and Red-collared Widows was investigated by means of a regular ringing program in Natal. Additional data were provided by a ringer in Rhodesia.

1. Wing-length is a standard measurement taken on all birds caught. A technique for distinguishing the different components of the population on the basis of wing-length is described. In the Red Bishop the population can be separated into only two groups, males and females, but in the Red-shouldered and Red-collared Widows there is a third distinct group, representing subadult males.

2. The sex ratios of the different species have been determined. In both Natal and Rhodesia there is a significant excess of male Red Bishops, but the sex ratio of the Red-collared Widow appears to be balanced. The Red-shouldered Widow in Natal also has an excess of males. However, since subadult males do not breed, there is an excess of females in the breeding population. Only in certain months of the year is there a significant imbalance in the sex ratio. This may be related to seasonal movements within the population.

3. The mortality rates calculated for the Red Bishop and the Red-collared Widow are less than 50%, and there is no evidence of differential mortality of the sexes.

4. At the start of the breeding season, the adult males of all three species undergo a partial moult and acquire their distinctive nuptial plumages. This moult lasts approximately one month, and in the Red Bishop the concurrent darkening of the bill can be used as an index of testis development.

5. At the end of the breeding season, all birds including the juveniles undergo a complete moult. There are no apparent species-specific or sexual differences in the timing of this moult. In the Red Bishop the moult lasts

more than three months in individual birds. In the Red-collared Widow it may last for only nine weeks, and the moult is of intermediate duration in the Red-shouldered Widow. Females of the latter species may complete their moult more rapidly than the males.

6. The timing of the pre-nuptial and the post-nuptial moult varies little between years in the same locality.

7. The pattern of weight change is similar for all three species. Males are heaviest at the start of the breeding season, then lose weight. They increase in weight again during the moult, but reach their lowest annual weights during the dry season. The females' weight changes are in general less marked, with peaks during the period of egg-laying and during the moult.

8. Some observations on feeding are recorded, but the data are too scanty to be correlated with seasonal weight changes.

9. The amount of breeding activity at the Red Bishop colony appeared to depend on the amount of rain during the year preceding breeding, but was unaffected by rain during the breeding season.

10. Variations in the clutch size of the Red Bishop are not obviously related to environmental factors. It is suggested that the physical condition of the individual females determines the clutch size.

11. Breeding success was low, chiefly due to heavy predation by rats. Nest height did not affect breeding success. In the first year heavy rains also caused the death of many broods. When predation is the main source of mortality, nests early in the season are most successful.

12. Under the conditions of this study, the behaviour of individual males was not correlated with their breeding success, as measured by the number of chicks fledged.

13. The behaviour of the genus _Euplectes_ is reviewed, and some new data on their vocalizations are presented.

14. The current theories of polygyny are discussed. It is concluded that restricted availability of nest sites together with the need to feed in flocks may have been important in the evolution of polygyny in this genus.

REFERENCES

ABS, M. 1964 Flügelmesswerte und Gewichte wandernder Erlenzeisige (Carduelis spinus). Vogelwarte 22: 173-176

ADLERSPARRE, A. 1938 Erscheinungen des physiologischen Alterns bei Vögeln. Orn. Mber. 46: 176-177

ADLERSPARRE, A. 1939 Über das Verhalten zweier Pyromelana-Arten bei karotinoidreicher und karotinoidarmer Kost. J. Orn. 87: 24-27

ALDRICH, J.W. 1973 Disparate sex ratios in waterfowl. In D.S. Farner (ed.), Breeding biology of birds, 482-489. National Academy of Sciences, Washington D.C.

ANDREW, R.J. 1957 A comparative study of the calls of Emberiza spp. (Buntings). Ibis 99: 27-42

ARMSTRONG, E.A. 1963 A study of bird song. Oxford University Press, Oxford.

ASSENMACHER, I. 1958 La mue des oiseaux et son déterminisme endocrinien. Alauda 26: 241-289

BAILY, W.S. 1916a The breeding of Jackson's Whydahs. Bird Notes News 7: 209-214

BAILY, W.S. 1916b The breeding of a hybrid Crimson-crowned Weaver x Red-collared Whydah. Bird Notes News 7: 235-240

BAILY, W.S. 1926 Is Pyromelana franciscana polygamous? Ibis 3(12th ser.): 628

BAKER, J.R. 1938 The evolution of breeding seasons. In G.R. de Beer (ed.), Evolution; essays on aspects of evolutionary biology, 161-177. Oxford University Press, Oxford.

BAKER, J.R. & R.M. RANSON 1938 The breeding seasons of southern hemisphere birds in the northern hemisphere. Proc. zool. Soc. Lond. 108: 101-141

BALÁT, F. 1974 Gelegegrösse und Brutverluste des Haussperlings Passer domesticus (L) in Mittelmähren. Zool. Listy 23: 229-240

BALDWIN, S.P. & S.C. KENDEIGH 1938 Variations in the weight of birds. Auk 55: 416-467

BALGOOYEN, T.G. 1976 Behaviour and ecology of the American Kestrel (Falco sparverius L.) in the Sierra Nevada of California. Univ. Calif. Publs Zool. 103: 1-87

BANNERMAN, D.A. 1949 The birds of Tropical West Africa. Vol. 7 Oliver & Boyd, Edinburgh.

BARTHOLOMEW, G.A. 1970 A model for the evolution of pinniped polygyny. Evolution 24: 546-559

BATES, G.L. 1927 Notes on some birds of Cameroon and the Lake Chad region: their status and breeding-times. Ibis 4(12th ser.): 1-64

BELL, B.D. 1970 Moult in the Reed Bunting - a preliminary analysis. Bird Study 17: 269-281

BELL, B.D. & R.J. HORNBY 1969 Polygamy and nest-sharing in the Reed Bunting. Ibis 111: 402-405

BENSON, C.W., R.K. BROOKE & C.J. VERNON 1964 Bird breeding data for the Rhodesias and Nyasaland. Occ. Pap. Natn. Mus. Sth. Rhod. 27B: 30-105

BERNDT, R. & W. WINKEL 1975 Gibt es beim Trauerschnäpper Ficedula hypoleuca eine Prägung auf den Biotop des Geburtsortes? J. Orn. 116: 195-201

BERTHOLD, P., E. GWINNER & P. KLEIN 1972a Circannuale Periodik bei Grasmücken. I Periodik des Körpergewichts, der Mauser und der Nachtunruhe bei Sylvia atricapilla und S. borin unter verschiedenen konstanten Bedingungen. J. Orn. 113: 170-190

BERTHOLD, P., E. GWINNER & P. KLEIN 1972b Circannuale Periodik bei Grasmücken. II Periodik der Gonadengrösse bei Sylvia atricapilla und S. borin unter verschiedenen konstanten Bedingungen. J. Orn. 113: 407-417

BIEBACH, H. 1977 Das Winterfett der Amsel (Turdus merula). J. Orn. 118: 117-133

BLAKLEY, N.R. 1976 Successive polygyny in upland nesting Redwinged Blackbirds. Condor 78: 129-133

BLANCHARD, B.D. 1941 The White-crowned Sparrows (Zonotrichia leucophrys) of the Pacific seaboard: environment and annual cycle. Univ. Calif. Publs Zool. 46: 1-178

von BOETTICHER, H. 1952 Die Widahvögel und Witwen. Geest & Portig K-G, Leipzig.

de BONT, A.F., A. de ROO & J. DEHEEGHER 1965 Resultats du baguage d'oiseaux en Republique Democratique du

Congo et en Republique du Rwanda (1959 à 1965). Gerfaut 55: 394-457

BOTKIN, D.B. & R.S. MILLER 1974 Mortality rates and survival of birds. Am. Nat. 108: 181-192

BOWEN, W.W. 1926 Is Pyromelana franciscana (Isert) polygamous? Ibis 2(12th ser.): 441-444

BRÉMOND, J.C. 1971 Communications acoustiques chez les oiseaux. J. Psychol. norm. path. 4: 353-380

BRENNER, F.J. 1966 The influence of drought on reproduction in a breeding population of Redwinged Blackbirds. Am. Midl. Nat. 76: 201-210

BRENNER, F.J. 1967 Seasonal correlations of reserve energy of the Redwinged Blackbird. Bird-banding 38: 195-211

BROOKE, R.K. 1966 Nuptial moult, breeding season and clutch size of Rhodesian Red Bishops Euplectes orix, and congeners in relation to rainfall. Ostrich suppl. 6: 223-235

BROOKE, R.K. 1970 Birds eating winged termites. Honeyguide 64: 17-18, 38

BROOKE, R.K., J.H. GROBLER, M.P. STUART IRWIN & P. STEYN 1972 A study of the migratory eagles Aquila nipalensis and A. pomarina (Aves: Accipitridae) in Southern Africa, with comparative notes on other large raptors. Occ. Pap. natn. Mus. Rhod. 5B: 61-114

BROSSET, A. 1971 Recherches sur la biologie des Pycnonotidés du Gabon. Biologia Gabonica 7: 423-460

BROSSET, A. 1974 La nidification des oiseaux en forêt gabonaise: architecture, situation des nids et predation. Terre Vie 28: 579-610

BROSSET, A. 1976 Observations sur le parasitisme de la reproduction du coucou émeraude Chrysococcyx cupreus au Gabon. Oiseau Revue fr. Orn. 46: 201-208

BROWN, F.A. & M. ROLLO 1940 Light and moult in weaver finches. Auk 57: 485-498

BRUSH, A.H. & D.M. POWER 1976 House Finch pigmentation: carotenoid metabolism and the effect of diet. Auk 93: 725-739

BULLOCK, E. 1938 Breeding the Orange Bishop Weaver. Avicult. Mag. 5: 15-16

BURKHOLDER, T.J. 1974 The relation of serum calcium levels to the reproductive cycle and egg production of female Red-winged Blackbird, Agelaius phoeniceus. Physiol. Zool. 47: 242-251

BURTT, H.E. & M.L. GILTZ 1970 The sex ratio for the Redwinged Blackbird. Inld Bird-banding News 42: 83-85

BUTLER, A.L. 1905 A contribution to the ornithology of the Egyptian Soudan. Ibis 19(8th ser.): 301-401

CAREY, M. & V. NOLAN 1975 Polygyny in Indigo Buntings: a hypothesis tested. Science 190: 1296-1297

CATCHPOLE, C.K. 1973 Conditions of co-existence in sympatric breeding populations of Acrocephalus warblers. J. Anim. Ecol. 42: 623-635

CATCHPOLE, C.K. 1974 Habitat selection and breeding success in the Reed Warbler (Acrocephalus scirpaceus). J. Anim. Ecol. 43: 363-380

CHAPIN, J.P. 1954 The birds of the Belgian Congo. Part 4. Bull. Am. Mus. Nat. Hist. 75B: 1-846

CHAPPUIS, C. 1971 Un exemple de l'influence du milieu sur les émissions vocales des oiseaux: l'evolution des chants en forêt équatoriale. Terre Vie 118: 183-202

CHEESEMAN, R.E. & W.L. SCLATER 1936 On a collection of birds from North-western Abyssinia. Part IV. Ibis 6(13th ser.): 163-197

CLAUSING, P. 1976 Biometrische Untersuchungen an Populationen des Feldsperlings, Passer montanus (Aves). Zool. Anz. 196: 212-220

CODY, M.L. 1966 A general theory of clutch size. Evolution 20: 174-184

CODY, M.L. 1969 Convergent characteristics in sympatric species: a possible relation to interspecific competition and aggression. Condor 71: 222-239

COLEMAN, J.D. & A.B. ROBSON 1975 Variations in body weight, fat-free weights and fat deposition of starlings in New Zealand. Proc. N.Z. ecol. Soc. 22: 7-13

COLLIAS, N.E. 1963 A spectrographic analysis of the vocal repertoire of the African Village Weaverbird. Condor 65: 517-527

COLLIAS, N.E. & E.C. COLLIAS 1964 Evolution of nest-building in the weaverbirds (Ploceidae). Univ. Calif. Publs Zool. 73: 1-162

COLLIAS, N.E. & E.C. COLLIAS 1970 Some experimental studies of the breeding biology of the Village Weaver *Ploceus (Textor) cucullatus* Müller. Ostrich suppl. 8: 169-177

COMMINS, D.M. 1953 An account of the plant ecology of the Albert Falls area of the Natal Midlands. M.Sc. Thesis; University of Natal, Pietermaritzburg.

CONRADS, K. 1971 Über die Rufe des Ortolans (*Emberiza hortulana* L.). Vogelwarte 26: 169-175

COULSON, J.C. 1960 A study of the mortality of the Starling based on ringing recoveries. J. Anim. Ecol. 29: 251-271

COULSON, J.C. 1961 The post-fledging mortality of the Blackbird in Great Britain. Bird Study 8: 89-97

COULSON, J.C. 1968 Differences in the quality of birds nesting in the centre and on the edges of a colony. Nature, Lond. 217: 478-479

COULSON, J.C. & J. HOROBIN 1976 The influence of age on the breeding biology and survival of the Arctic Tern *Sterna paradisaea*. J. Zool., Lond. 178: 247-260

COULSON, J.C. & R.D. WOOLLER 1976 Differential survival rates among breeding Kittiwake Gulls *Rissa tridactyla* (L.). J. Anim. Ecol. 45: 205-213

CRAIG, A.J.F.K. 1973 Breeding behaviour and polygyny in the Red Bishop Bird *Euplectes orix* (L). M. Sc. Thesis; University of Cape Town.

CRAIG, A.J.F.K. 1974 Reproductive behaviour of the male Red Bishop Bird. Ostrich 45: 149-160

CRAIG, A. & C. BURMAN 1973 Stork killing birds in mist nets. SAFRING News 2: 5

CROOK, J.H. 1960 Studies on the social behaviour of *Quelea q. quelea* (Linn.) in French West Africa. Behaviour 16: 1-55

CROOK, J.H. 1961 The basis of flock organisation in birds. In W.H. Thorpe & O.L. Zangwill (eds), Current problems in animal behaviour, 125-149. Cambridge University Press, Cambridge.

CROOK, J.H. 1964 The evolution of social organisation and visual communication in the weaver birds (Ploceinae). Behaviour suppl. 10: 1-178

CROOK, J.H. 1969 Functional and ecological aspects of vocalization in weaver-birds. In R.A. Hinde (ed.), Bird vocalizations, 265-290. Cambridge University Press, Cambridge.

CROOK, J.H. & P.A. BUTTERFIELD 1970 Gender role in the social system of Quelea. In J.H. Crook (ed.), Social behaviour in birds and mammals, 211-248. Academic Press, London & New York.

CUNNINGHAM-VAN SOMEREN, G.R. 1971 Euplectes diadematus Fischer and Reichenow; courtship, nest and eggs. Bull. Br. Orn. Club 91: 119-121

DARLEY, J.A. 1971 Sex ratio and mortality in the Brown-headed Cowbird. Auk 88: 560-566

DARLING, F.F. 1938 Bird flocks and the breeding cycle. Cambridge University Press, Cambridge.

DARWIN, C. 1871 The descent of man and selection in relation to sex. John Murray, London.

DAVIES, C.J. 1910 Wild habits of the Giant Whydah. Avicult. Mag. 8: 224-225

DAWKINS, R. & T.R. CARLISLE 1976 Parental investment, mate desertion and a fallacy. Nature, Lond. 262: 131-13

DEAN, W.R. 1971 Breeding data for the birds of Natal and Zululand. Durban Mus. Novit. 9: 59-91

DELACOUR, J. & F. EDMOND-BLANC 1933 Monographie des Veuves (Revision des genres Euplectes et Vidua). Oiseau Revue fr. Orn. 3: 519-562, 687-726

DELIUS, J.D. 1965 A population study of Skylarks Alauda arvensis. Ibis 107: 466-492

DHONDT, A.A. 1970 The sex ratio of nestling Great Tits. Bird Study 17: 282-286

DIESSELHORST, G. 1971 Ein Fall interspezifischer Kompetition bei Webervögeln (Ploceus). J. Orn. 112: 227-229

DONNELLY, B.G. 1965 Longevity in the Yellow-backed Bishop, Euplectes capensis, in captivity. Ostrich 36: 14

DOWNHOWER, J.F. 1976 Darwin's finches and the evolution of sexual dimorphism in body size. Nature, Lond. 263: 558-563

DOWNHOWER, J.F. & K.B. ARMITAGE 1971 The Yellow-bellied Marmot and the evolution of polygamy. Am. Nat. 105: 355-370

DRUMMOND, D.C. 1960 The food of Rattus norvegicus Berk. in an area of sea wall, salt-marsh and mudflat. J. Anim. Ecol. 29: 341-347

DÜCKER, G. 1970 Untersuchungen über die hormonale Beeinflussbarkeit der Farbbevorzugung von Feuerwebern (Euplectes orix franciscanus). J. Orn. 111: 19-29

DUNBAR, R.I.M. & J.H. CROOK 1975 Aggression and dominance in the weaver bird, Quelea quelea. Anim. Behav. 23: 450-459

DUNCAN, A. 1906 Notes on the genus Pyromelana (Bishop Birds), with reference in particular to the seasonal changes of plumage and nidification in captivity of P. oryx (Red Bishop Bird). J. S. Afr. Orn. Un. 1: 57-61

DYRCZ, A. 1977 Polygamy and breeding success among Great Reed Warblers Acrocephalus arundinaceus at Milicz, Poland. Ibis 119: 73-77

ECKLEBEN, W. 1974 Überraschung durch unsere Feuerweber (Euplectes franciscana). Gefied. Welt 98: 22-23

ELGOOD, J.H. & P. WARD 1963 A snake attack upon a weaver-bird colony. Possible significance of synchronous breeding activity. Bull. Br. Orn. Club 83: 71-73

ELLIOTT, C.C.H. 1973 The biology of the Cape Weaver Ploceus capensis with special reference to its polygynous mating system. Ph.D. Thesis; University of Cape Town.

ELLIOTT, P.F. 1975 Longevity and the evolution of polygamy. Am. Nat. 109: 281-287

EMLEN, J.T. 1940 Sex and age ratios in survival of the California Quail. J. Wildl. Mgmt 4: 92-99

EMLEN, J.T. 1957 Display and mate selection in the whydahs and bishop birds. Ostrich 28: 202-213

EMLEN, S.T. & N.J. DEMONG 1975 Adaptive significance of synchronised breeding in a colonial bird: a new hypothesis. Science 188: 1029-1031

EMLEN, S.T., J.D. RISING & W.L. THOMPSON 1975 A behavioural and morphological study of sympatry in the Indigo and Lazuli Buntings of the Great Plains. Wilson Bull. 87: 145-179

EVANS, P.R. 1966 Autumn movements, moult and measurements of the Lesser Redpoll Carduelis flammea cabaret. Ibis 108: 183-216

FARKAS, T. 1966 The birds of Barberspan. III Some structural changes in the avifauna of the Barberspan Nature Reserve. Ostrich suppl. 6: 463-491

FARNER, D.S. 1959 Photoperiodic control of annual gonadal cycles in birds. In R.B. Withrow (ed.), A symposium on photoperiodism and related phenomena in plants and animals, 717-750. American Association for the Advancement of Science, Washington D.C.

FARNER, D.S. 1967 Day length as environmental information in the control of reproduction of birds. Colloques int. cent. natn. Rech. Scient. 172: 71-91

FERRY, C. & A. DESCHAINTRE 1974 Le chant, signal interspécifique chez Hippolais icterina et polyglotta. Alauda 42: 289-312

FISHER, H.I. 1975 The relationship between deferred breeding and mortality in the Laysan Albatross. Auk 92: 433-441

FITZSIMONS, F.W. 1927 Nuptial plumage of birds. S. Afr. J. Sci. 24: 382-383

FITZSIMONS, F.W. 1931 Further report on the nuptial plumage of birds. S. Afr. J. Sci. 27: 411

FOGDEN, M.P.L. 1972 The seasonality and population dynamics of equatorial forest birds in Sarawak. Ibis 114: 307-343

FOLK, C. & I. NOVOTNÝ 1970 Variation in body weight and wing length in the House Sparrow, Passer domesticus L., in the course of a year. Zool. Listy 19: 333-342

FRANCIS, W.J. 1971 An evaluation of reported reproductive success in Red-winged Blackbirds. Wilson Bull. 83: 178-185

FRIEDMANN, H. 1956 Further data on African parasitic cuckoos. Proc. U.S. natn. Mus. 106: 377-408

FRITH, C.B. 1976 A twelve-month field study of the Aldabran Fody Foudia eminentissima aldabrana. Ibis 118: 155-178

FRITH, H.J. 1976 (ed.) Readers' Digest complete book of Australian birds. Readers' Digest Services Pty Ltd, Sydney.

FRITH, H.J., S.M. CARPENTER & L.W. BRAITHWAITE 1976 Sexual cycles of pigeons in arid and semiarid Australia. Aust. J. Zool. 24: 331-351

FRY, C.H. 1969 Migration, moult and weight of birds in northern Guinea savanna in Nigeria and Ghana. Ostrich suppl. 8: 239-263

FRY, C.H. 1972 The social organisation of bee-eaters (Meropidae) and co-operative breeding in hot-climate birds. Ibis 114: 1-14

FUGGLES- COUCHMAN, N.R. 1943 A contribution to the breeding ecology of two species of Euplectes (bishop-birds) in Tanganyika territory. Ibis 85: 311-326

FURRER, R.K. 1975 Breeding success and nest site stereotypy in a population of Brewer's Blackbirds (Euphagus cyanocephalus). Oecologia 20: 339-350

GÖRANSSON, G., J. KARLSSON, S.G. NILSSON & S. ULFSTRAND 1975 Predation on birds' nests in relation to antipredator aggression and nest density: an experimental study. Oikos 26: 117-120

GOODWIN, D. 1967 Pigeons and doves of the world. Trustees of the British Museum (Natural History), London.

GRAY, A.P. 1958 Bird hybrids. A check-list with bibliography. Technical Communication 13 of the Commonwealth Bureau of Animal Breeding and Genetics, Edinburgh.

GRIMES, L.G. 1977 Nesting of the Red-headed Quelea Quelea erythrops on the Accra plains, Ghana. Ibis 119: 216-220

GRINDLEY, J., W.R. SIEGFRIED & C.J. VERNON 1973 Diet of the Barn Owl in the Cape Province. Ostrich 44: 266-267

GÜTTINGER, H.R. & J. NICOLAI 1973 Struktur und Funktion der Rufe bei Prachtfinken (Estrildidae). Z. Tierpsychol. 33: 319-334

GURNEY, J.H. 1860 On birds collected in the Colony of Natal in South-eastern Africa. Ibis 2: 203-221

GURNEY, J.H. 1861 On some additional species of birds received in collections from Natal. Ibis 3: 128-137

GWINNER, E. 1975 Circadian and circannual rhythms in birds. In D.S. Farner & J.R. King (eds), Avian biology, vol. 5: 77-128. Academic Press, New York & London.

GWINNER, E., P. BERTHOLD & P. KLEIN 1971 Untersuchungen zur Jahresperiodik von Laubsängern. II Einfluss der Tageslichtdauer auf die Entwicklung des Gefieders, des Gewichts und der Zugunruhe bei Phylloscopus trochilus und Ph. collybita. J. Orn. 112: 253-265

GWINNER, E. & H. BIEBACH 1977 Endogene Kontrolle der Mauser und der Zugdisposition bei südfinnischen und südfranzösischen Neuntötern (Lanius collurio). Vogelwarte 29: 56-63

GWINNER, E. & L-O. ERIKSSON 1977 Circadiane Rhythmik und photoperiodische Zeitmessung beim Star (Sturnus vulgaris). J. Orn. 118: 60-67

HAAGNER, A.C. 1901 Ornithological notes from the Transvaal. Ibis 2(8th ser.): 190-194

HAAGNER, A.C. 1910 The habits of the Great-tailed Widow Bird (Diatropura procne). J. S. Afr. Orn. Un. 6: 45-46

von HAARTMAN, L. 1951 Successive polygamy. Behaviour 3: 256-274

von HAARTMAN, L. 1955 Clutch size in polygamous species. Proc. 11. Int. Orn. Congr.: 450-453

von HAARTMAN, L. 1969 Nest-site and evolution of polygamy in European passerine birds. Ornis. Fenn. 46: 1-12 von HAARTMAN, L. 1971 Population dynamics. In D.S. Farner & J.R. King (eds), Avian biology, vol. 1: 391-459. Academic Press, New York & London.

HAASE, E. 1973 Zur Kontrolle von Fortpflanzungszyklen bei Vögeln. Untersuchungen an Bergfinken. J. comp. Physiol. 84: 375-431

HALL, B.P. & R.E. MOREAU 1970 An atlas of speciation in African passerine birds. Trustees of the British Museum (Natural History), London.

HALL, J.R. 1970a Observations on colonial breeding in the Black-headed Weaver and Vieillot's Black Weaver. Jl. E. Africa Nat. Hist. Soc. 28: 56-61

HALL, J.R. 1970b Synchrony and social stimulation in colonies of the Black-headed Weaver (Ploceus cucullatus) and Vieillot's Black Weaver (Melanopteryx nigerrimus). Ibis 112: 93-104

HALL, M.F. 1962 Evolutionary aspects of Estrildid song. Symp. zool. Soc. Lond. 8: 37-55

HARDING, J.P. 1949 The use of probability paper for the graphical analysis of polymodal frequency distributions. J. Mar. Biol. Assoc. U.K. 28: 141-153

HARMESON, J.P. 1974 Breeding ecology of the Dickcissel. Auk 91: 348-359

HARRISON, C.J.O. 1962 Solitary song and its inhibition in some Estrildidae. J. Orn. 103: 369-379

HAUKIOJA, E. 1969 Weights of Reed Buntings (Emberiza schoeniclus) during summer. Ornis Fenn. 46: 13-21

HAUKIOJA, E. 1970 Clutch size of the Reed Bunting Emberiza schoeniclus. Ornis Fenn. 47: 101-135

HAVLÍN, J. 1975 Das Geschlechterverhältnis ausgewählter Singvogelarten im Milieu von Anthropozönosen. Zool. Listy 24: 239-248

HILL, R.A. 1976 Sex ratio and sex-determination of immature Brown-headed Cowbirds. Bird-banding 47: 112-114

HOESCH, W. & G. NIETHAMMER 1940 Die Vogelwelt Deutsch-Südwestafrikas namentlich des Damara- und Namalandes. J. Orn. 88: Sonderheft

HOGAN-WARBURG, A.J. 1966 Social behaviour of the Ruff Philomachus pugnax (L.). Ardea 54: 109-229

HOLM, C.H. 1973 Breeding sex ratios, territoriality, and reproductive success in the Red-winged Blackbird (Agelaius phoeniceus). Ecology 54: 356-365

HOPKINSON, E. 1938 Breeding records: Summary II. Avicult. Mag. 5: 239-245

HORN, H.S. 1968 The adaptive significance of colonial nesting in Brewer's Blackbird. Ecology 49: 682-694

HORN, H.S. 1970 Social behaviour of nesting Brewer's Blackbirds. Condor 72: 15-23

HORNBY, H.E. 1967 The breeding cycle of the White-winged Widow Bird Euplectes albonotus. Ostrich 38: 5-10

HORNBY, H.E. 1970 Further notes on the Whitewinged Widowbird. Ostrich 41: 225-231

HOWE, H.F. 1976 Egg size, hatching asynchrony, sex, and brood reduction in the Common Grackle. Ecology 57: 1195-1207

HUNT, G.L. & M.W. HUNT 1976 Gull chick survival: the significance of growth rates, timing of breeding and territory size. Ecology 57: 62-75

HUSSELL, D.J.T. 1972 Factors affecting clutch size in Arctic passerines. Ecol. Monogr. 42: 317-364

IMMELMANN, K. 1963 Tierische Jahresperiodik in ökologischer Sicht. Zool. Jb. (Syst.) 91: 91-200

IMMELMANN, K. 1967 Untersuchungen zur endogen und exogenen Steurung der Jahresperiodik afrikanischer Vögel. Zool. Anz. suppl. 31: 340-357

IMMELMANN, K. 1968 Zur biologischen Bedeutung des Estrildidengesanges. J. Orn. 109: 284-299

IMMELMANN, K. 1970 Environmental factors controlling reproduction in African and Australian birds - a comparison. Ostrich suppl. 8: 193-204

IMMELMANN, K. 1971 Ecological aspects of periodic reproduction. In D.S. Farner & J.R. King (eds), Avian biology, vol. 1: 341-389. Academic Press, New York & London.

IMMELMANN, K. 1972 Erörterungen zur Definition und

und Anwendbarkeit der Begriffe "Ultimate Factor", "Proximate Factor" und "Zeitgeber". Oecologia 9: 259-264

JACKSON, F.J. 1938 The birds of Kenya Colony and the Uganda Protectorate. Vol. 3 Gurney & Jackson, London.

JACKSON, S.P. 1961 (compiler) Climatological atlas of Africa. Government Printer, Pretoria.

JENSEN, R.A.C. & M.K. JENSEN 1969 On the breeding biology of Southern African cuckoos. Ostrich 40: 163-181

JENSEN, R.A.C. & C.J. VERNON 1970 On the biology of the Didric Cuckoo in Southern Africa. Ostrich 41: 237-246

JOHANSSON, H. 1972 Clutch size and breeding success in some hole nesting passerines in Central Sweden. Ornis Fenn. 49: 1-6

JOHNSTON, D.W. 1970 Age and sex distribution in Indigo Buntings. Bird-banding 41: 113-118

JONES, P.J. 1976 The utilization of calcareous grit by laying Quelea quelea. Ibis 118: 575-576

JONES, P.J. & P. WARD 1976 The level of reserve protein as the proximate factor controlling the timing of breeding and clutch-size in the Red-billed Quelea Quelea quelea. Ibis 118: 547-574

JONES, P.J. & P. WARD 1977 Evidence of pre-migratory fattening in three tropical granivorous birds. Ibis 119: 200-203

KEAST, A. 1968 Moult in birds of the Australian dry country relative to rainfall and breeding. J. Zool., Lond. 155: 185-200

KELM, H. 1970 Beitrag zur Methodik des Flügelmessens. J. Orn. 111: 482-494

KEMP, A.C. 1976 Factors affecting the onset of breeding in African hornbills. Proc. 16. Int. Orn. Congr.: 248-257

KESSEL, B. 1957 A study of the breeding biology of the European Starling (Sturnus vulgaris L.) in North America. Am. Midl. Nat. 58: 257-331

KLEEFISCH, T. 1971 Einige meiner Zuchterfolge 1970. Gefied. Welt 95: 50-53

KLOMP, H. 1970 The determination of clutch size in birds. A review. Ardea 58: 1-124

KLUYVER, H.N. 1952 Notes on body weight and time of breeding in the Great Tit, Parus m. major L. Ardea 40: 123-141

KLUYVER, H.N. 1957 Roosting habits, sexual dominance and survival in the Great Tit. Cold Spring Harb. Symp. quant. Biol. 22: 281-285

KONTOGIANNIS, J.E. 1967 Day and night changes in body weight of the White-throated Sparrow, Zonotrichia albicollis. Auk 84: 390-395

KOK, O.B. 1971 Vocal behaviour of the Great-tailed Grackle (Quiscalus mexicanus prosopidicola). Condor 73: 348-363

KOK, O.B. 1972a Behaviour of the Great-tailed Grackle (Quiscalus mexicanus). Acta Academica 5: 55-76

KOK, O.B. 1972b Breeding success and territorial behaviour of male Boat-tailed Grackles. Auk 89: 528-540

KREBS, J.R. 1974 Colonial nesting and social feeding as strategies for exploiting food resources in the Great Blue Heron (Ardea herodias). Behaviour 51: 99-134

KRITZLER, H. 1943 Carotenoids in the display and eclipse plumages of Bishop Birds. Physiol. Zool. 16: 241-255

KRUUK, H. 1964 Predators and anti-predator behaviour of the Black-headed Gull (Larus ridibundus L.). Behaviour suppl. 11: 1-129

LACK, D. 1935 Territory and polygamy in a bishop-bird, Euplectes h. hordeacea (Linn.). Ibis 5(13th ser.): 817-836

LACK, D. 1954 The natural regulation of animal numbers. Clarendon Press, Oxford.

LACK, D. 1966 Population studies of birds. Clarendon Press, Oxford.

LACK, D. 1968 Ecological adaptations for breeding in birds. Metheun, London.

LANDAUER, W. 1957 Primary sex ratios of fowl. Nature, Lond. 180: 1139-1140

LA RIVERS, I. 1944 Observations on the nesting mortality of the Brewer Blackbird, Euphagus cyanocephalus. Am. Midl. Nat. 32: 417-437

LAWSON, W.J. 1965 A melanistic variant of the Red-shouldered Widow Bird. Ostrich 36: 44

LE BOEUF, B.J. 1974 Male-male competition and reproductive success in Elephant Seals. Am. Zool. 14: 163-176

LEINONEN, M. 1973a On the breeding biology of the White Wagtail Motacilla alba in central Finland. Ornis Fenn. 50: 53-82

LEINONEN, M. 1973b Comparisons between the breeding biology of year-old and older females of the White Wagtail Motacilla alba in central Finland. Ornis Fenn. 50: 126-133

LEOPOLD, A.S. 1945 Sex and age ratios among Bob-white Quail in southern Missouri. J. Wildl. Mgmt 9: 30-34

LEUTHOLD, W. & B. LEUTHOLD 1972 Blutschnabelweber (Quelea quelea) als Beute von Greif- und Stelzvögeln. Vogelwarte 26: 352-354

LILL, A. 1974 Sexual behaviour of the lek-forming White-bearded Manakin (Manacus manacus trinitatis Hartert). Z. Tierpsychol. 36: 1-36

LÖHRL, H. 1974 Die Tannenmeise. Neue Brehm-Bücherei 472. A. Ziemsen, Wittenberg Lutherstadt.

LOFTS, B. 1962 Photoperiod and the refractory period of reproduction in an equatorial bird, Quelea quelea. Ibis 104: 407-414

LOFTS, B. 1964 Evidence of an autonomous reproductive rhythm in an equatorial bird, Quelea quelea. Nature, Lond. 201: 523-524

LOFTS, B. & R.K. MURTON 1966 The role of weather, food and biological factors in timing the sexual cycle of Woodpigeons. Br. Birds 59: 261-280

LOFTS, B. & R.K. MURTON 1968 Photoperiodic and physiological adaptations regulating avian breeding cycles and their ecological significance. J. Zool., Lond. 155: 327-394

LOFTS, B., R.K. MURTON & R.J.P. THEARLE 1973 The effects testosterone propionate and gonadotrophins on the bill pigmentation and testes of the House Sparrow (Passer domesticus). Gen. Comp. Endocr. 21: 202-209

LYNES, H. 1924 On the birds of North and Central Darfur, with notes on the West-central Kordofan and North Nuba provinces of British Sudan. Ibis 6(11th ser.): 648-719

McILHENNY, E.A. 1940 Sex ratios in wild birds. Auk 57: 85-93

MACKWORTH-PRAED, C.W. & C.H.B. GRANT 1955 Birds of Eastern and North Eastern Africa. Vol. 2 Longmans, London.

MACKWORTH-PRAED, C.W. & C.H.B. GRANT 1962 Birds of the southern third of Africa. Vol. 2 Longmans, London.

MACKWORTH-PRAED, C.W. & C.H.B. GRANT 1973 Birds of West Central and Western Africa. Vol. 3 Longmans, London.

McLACHLAN, G.R. & R. LIVERSIDGE 1958 Roberts' birds of South Africa. Central News Agency, Cape Town.

McLAREN, I.A. 1972 Polygyny as the adaptive function of breeding territory in birds. Trans. Conn. Acad. Arts Sci. 44: 189-210

MACLEAN, G.L. 1970 The breeding seasons of birds in the southwestern Kalahari. Ostrich suppl. 8: 179-192

MACLEAN, G.L. 1973 The Sociable Weaver, Part 3: Breeding biology and moult. Ostrich 44: 219-240

MÄRKI, H. & O. BIBER 1975 Flugellänge und Gewichtsschwankung beim Zitronenzeisig Serinus c. citrinella (PALLAS 1764) vor und während des Herbstzuges. Jb. naturh. Mus. Bern 5: 153-164

MARKUS, M.B. 1964 A note on Euplectes ardens (Boddaert) during the post-nuptial regeneration phase. Ostrich 35: 297-298

MARLER, P. 1955 The characteristics of certain animal calls. Nature, Lond. 176: 6-7

MARLER, P. 1957 Specific distinctiveness in the communication signals of birds. Behaviour 11: 13-39

MARSHALL, A.J. 1960 The environment, cyclical reproductive activity and behaviour in birds. Symp. zool. Soc. Lond. 2: 53-67

MARSHALL, A.J. & J. de S. DISNEY 1957 Experimental induction of the breeding season in a xerophilous bird. Nature, Lond. 180: 647-649

MARTIN, S.G. 1974 Adaptations for polygynous breeding in the Bobolink, Dolichonyx oryzivorus. Am. Zool. 14: 109-119

MASON, C.F. 1976 Breeding biology of the Sylvia warblers. Bird Study 23: 213-232

MAYFIELD, H.F. 1975 Suggestions for calculating nest success. Wilson Bull. 87: 456-466

MAYNARD SMITH, J. & M.G. RIDPATH 1972 Wife sharing in the Tasmanian Native Hen Tribonyx mortierii: a case of kin selection? Am. Nat. 106: 447-452

MAYR, E. 1939 The sex ratio in wild birds. Am. Nat. 73: 156-179

MENDELSOHN, J. 1976 The testicular cycle of the Red-shouldered Widow-bird Euplectes axillaris (Smith). Unpublished Thesis B.Sc. (Hons.), Dept. of Zoology, University of Natal, Pietermaritzburg.

MILLER, R.S. 1968 Conditions of competition between Redwings and Yellowheaded Blackbirds. J. Anim. Ecol. 37: 43-67

MITCHELL, I.G. 1966 Courtship patterns in some species of Coliuspasser. Ostrich 37: 47-53

MOREAU, R.E. 1944 Clutch-size: a comparative study with special reference to African birds. Ibis 86: 286-347

MOREAU, R.E. 1950 The breeding seasons of African birds. I Land birds. Ibis 92: 223-267

MOREAU, R.E. 1960 Conspectus and classification of the Ploceine weaver-birds. Ibis 102: 298-321, 443-471

MOREAU, R.E. & W.M. MOREAU 1938 The comparative breeding ecology of two species of Euplectes (Bishop birds) in Usambara. J. Anim. Ecol. 7: 314-327

MOREL, G. 1968 L'impact ecologique de Quelea quelea (L.) sur les savanes saheliennes. Raisons du pullulement de ce ploceide. Terre Vie 22: 69-98

MOREL, M-Y. 1969 Contribution a l'étude dynamique de la population de Lagonosticta senegala L. (Estrildides) a Richard-Toll (Senegal). Interrelations avec le parasite Hypochera chalybeata (Müller) (Viduines). Thèse du Grade de Docteur des Sciences Naturelles, Université de Rennes.

MOREL, M-Y. & G. MOREL 1973 Elements de comparaison du comportement reproducteur colonial de trois espèces de Plocéidés: Passer luteus, Ploceus cucullatus et Quelea quelea, en zone semi-aride de l'ouest africain. Oiseau Revue fr. Orn. 43: 315-329

MORRIS, D. 1954 The reproductive behaviour of the Zebra Finch Poephila guttata with special reference to pseudo-female behaviour and displacement activities. Behaviour 6: 271-321

MOURITZ, L.B. 1913 Notes on Euplectes xanthomelas, Rüpp. J. S. Afr. Orn. Un. 9: 79-83

MUNDINGER, P.C. 1972 Annual testicular cycle and bill colour change in the Eastern American Goldfinch. Auk 89: 403-419

MURRAY, B.G. 1971 The ecological consequences of interspecific territorial behaviour in birds. Ecology 52: 414-423

MURRAY, B.G. 1976 A critique of interspecific territoriality and character convergence. Condor 78: 518-525

MUSIL, A. 1969 15 Jahre alte Napoleonweber. Gefied. Welt 93: 99

NEUNZIG, K. 1921 Die fremdländische Stubenvögel. (Neudruck 1965). A. Asher, Amsterdam.

NEWTON, I. 1966 The moult of the Bullfinch Pyrrhula pyrrhula. Ibis 108: 41-67

NEWTON, I. 1968 The temperatures, weights and body composition of moulting Bullfinches. Condor 70: 323-332

NEWTON, I. 1969 Winter fattening in the Bullfinch. Physiol. Zool. 42: 96-107

NEWTON, I. 1972 Finches. Collins, London.

NEWTON, R. 1937 Notes on Bishop-birds and Whydahs in the Cameroons. Niger. Fld 6: 151-156

NICE, M.M. 1937 Studies in the life history of the Song Sparrow, vol. 1. Trans. Linn. Soc. N.Y. 4: 1-247

NICE, M.M. 1957 Nesting success in altricial birds. Auk 74: 305-321

NICOLAI, J. 1964 Der Brutparasitismus der Viduinae als ethologisches Problem. Z. Tierpsychol. 21: 129-204

NICOLAI, J. 1969 Beobachtungen an Paradieswitwen (Steganura paradisaea L., Steganura obtusa Chapin) und der Strohwitwe (Tetraenura fischeri Reichenow) in Ost-afrika. J. Orn. 110: 421-447

NICOLAI, J. 1973 Das Lernprogramm in der Gesangausbildung der Strohwitwe Tetraenura fischeri Reichenow. Z. Tierpsychol. 32: 113-138

NIEMEYER, H. 1969a Versuch einer biometrischen Analyse der Flugellänge Helgoländer Fitislaubsänger (Phylloscopus trochilus) unter Berücksichtigung des Einflusses von Alter, Geschlecht. Zool. Anz. 183: 326-341

NIEMEYER, H. 1969b Statistische Untersuchungen zu Geschlechtsverhältnis und Zugordnung des Fitislaubsängers (Phylloscopus trochilus) auf Helgoland. Zool. Anz. 183: 342-354

NØRGAARD-OLESEN, E. 1970 Breeding the Fire-fronted Bishop Euplectes diademata. Avicult. Mag. 76: 94-95

NORRIS, F.G. 1968 Breeding the Giant Whydah (Diatropura progne). Foreign Birds 34: 109-110, 114-116, 137-139

NORRIS, R.A. 1958 Comparative biosystematics and life history of the nuthatches Sitta pygmaea and Sitta pusilla. Univ. Calif. Publs Zool. 56: 119-300

NOWIKOW, B.G. 1939 Einfluss der Gonaden auf die Entwicklung der Geschlechtsmerkmale bei Fringilla montifringilla (L.). Dokl. Akad. Nauk. SSSR for. Lang. Edn 25: 550-553

OATLEY, T.B. & D.M. SKEAD 1972 Nectar feeding by South African birds. Lammergeyer 15: 65-74

O'CONNOR, R.J. 1972 Patterns of weight change in the House Sparrow, Passer domesticus (L.). In S.C. Kendeigh & J. Pinowski (eds), Productivity, population dynamics and systematics of granivorous birds, 111-125. Polish Scientific Publishers, Warszawa.

ORIANS, G.H. 1961 Social stimulation within blackbird colonies. Condor 63: 330-337

ORIANS, G.H. 1969 On the evolution of mating systems in birds and mammals. Am. Nat. 103: 589-604

ORIANS, G.H. 1972 The adaptive significance of mating systems in the Icteridae. Proc. 15. Int. Orn. Congr.: 388-398

ORIANS, G.H. 1973 The Red-winged Blackbird in tropical marshes. Condor 75: 28-42

ORIANS, G.H. & G. COLLIER 1963 Competition and blackbird social systems. Evolution 17: 449-459

OTTOW, J. & G. DUVE 1965 Zur Kenntnis der Fortpflanzung von Chrysococcyx caprius und Cuculus canorus gularis in Süd-Africa. J. Orn. 106: 431-439

PAYNE, R.B. 1969 Breeding seasons and reproductive physiology of Tricoloured Blackbirds and Redwinged Blackbirds. Univ. Calif. Publs Zool. 90: 1-137

PEEK, F.W. 1972 An experimental study of the territorial function of vocal and visual display in the male Red-winged Blackbird Agelaius phoeniceus. Anim. Behav. 20: 112-118

PERRINS, C.M. 1970 The timing of birds' breeding seasons. Ibis 112: 242-255

PERRINS, C.M. & P.J. JONES 1974 The inheritance of clutch size in the Great Tit (Parus major L.). Condor 76: 225-229

PHILLIPPS, R. 1905 Nesting of the Orange Bishop Pyromelana franciscana. Avicult. Mag. 3: 89-94

PIECHOCKI, R. 1954 Statistische Feststellungen an 20 000 Sperlingen (Passer d. domesticus). J. Orn. 95: 297-305

PIKE, W.J. 1974 (Letter). Bokmakierie 26: 52

PINTO, A.A. da R. & D.W. LAMM 1960 Contribution to the study of the ornithology of Sul do Save (Mozambique). Mem. Mus. Dr. Alvaro de Castro 5: 69-126

PITMAN, C.R.S. 1958 Snake and lizard predators of birds. Bull. Br. Orn. Club 78: 82-86, 99-104, 120-124

POWELL, G.V.N. 1974 Experimental analysis of the social value of flocking by starlings (Sturnus vulgaris) in relation to predation and foraging. Anim. Behav. 22: 501-505

POWETT, T. 1963 Red-eyed Bulbul Pycnonotus nigricans and Long-tailed Widow Bird Diatropura procne feeding on insects. Ostrich 34: 47

PRICE, F.E. & C.E. BOCK 1973 Polygyny in the Dipper. Condor 75: 457-459

PRIEST, C.D. 1936 The birds of Southern Rhodesia. Vol. 4 William Clowes, London.

PRÖVE, E. 1974 Der Einfluss von Kastration und Testosteronsubstitution auf das Sexualverhalten männlicher Zebrafinken (Taeniopygia guttata castanotis Gould). J. Orn. 115: 338-347

PULLIANEN, E. 1968 Sex and age ratios in a partridge (Perdix perdix L.) population in Ostrobothnia, West Finland. Ann. Zool. Fenn. 5: 179-182

RADTKE, G.A. 1957 Vogelliebhaberei und -zucht im Ausland. Gefied. Welt 81: 88-90

RALPH, C.L., D.L. GRINWICH & P.F. HALL 1967 Hormonal regulation of feather pigmentation in African weaver birds: the exclusion of certain possible mechanisms. J. Exp. Zool. 166: 289-294

REED, A. 1968 Studies of the Diederik Cuckoo, Chrysococcyx caprius, in the Transvaal. Ibis 110: 321-331

REICHENOW, A. 1904 Die Vögel Afrikas. Bd. 3 Neumann, Neudamm.

RICKLEFS, R.E. 1969 An analysis of nesting mortality in birds. Smithson. Contr. Zool. 9: 1-48

ROBERTS, N. 1909 Pyromelana oryx and its nesting parasites. J. S. Afr. Orn. Un. 5: 22-24

ROBERTSON, R.J. 1972 Optimal niche space of the Redwinged Blackbird (Agelaius phoeniceus). I Nesting success in marsh and upland habitat. Can. J. Zool. 50: 247-263

ROBERTSON, R.J. 1973 Optimal niche space of the Redwinged Blackbird: spatial and temporal patterns of nesting activity and success. Ecology 54: 1085-1093

ROBERTSON, R.J. & R.F. NORMAN 1976 Behavioural defences to brood parasitism by potential hosts of the Brown-headed Cowbird. Condor 78: 166-173

ROLLIN, N. 1962 Melanistic Orange Bishop Bird Euplectes franciscana. Ostrich 33: 35-37

ROLLO, M. & L.V. DOMM 1943 Light requirements of the Weaver Finch. Auk 60: 357-367

ROOKE, K.B. 1938 Unusual reproductive behaviour: the reactions of a male Bishop-bird in non-breeding plumage to nestling canaries. Ibis 80: 147-149

ROWAN, M.K. 1953 Early breeding of the Cape Weaver Ploceus capensis. Ostrich 24: 186-187

ROWAN, M.K. 1964 An analysis of the records of a South African ringing station. Ostrich 34: 160-187

ROWAN, M.K. 1966 Some observations on reproduction and mortality in the Cape Sparrow Passer melanurus. Ostrich suppl. 6: 425-434

ROWAN, M.K. 1970 The foods of South African birds. Ostrich suppl. 8: 343-356

ROWAN, M.K. & G.J. BROEKHUYSEN 1962 A study of the Karroo Prinia. Ostrich 33: 6-30

RUTGERS, A. 1973 Handbuch für Zucht und Haltung fremdländischer Vögel. (Deutsche Bearbeitung von Dr. W. & D. Winkel). Neumann, Neudamm.

RUWET, J-C. 1964a La periodicite de la reproduction chez les oiseaux du Katanga. Gerfaut 54: 84-110

RUWET, J-C. 1964b Quelques exemples de separation écologique d'espéces congeneriques sympatriques de l'avifaune Katangaise. Gerfaut 54: 159-166

RUWET, J-C. 1965 Notes écologiques et éthologiques sur les oiseaux des plaines de la Lufira supérieure (Katanga). Rev. Zool. Bot. afr. 72: 389-427

RYVES, B.H. & Mrs. RYVES 1934 The breeding habits of the Corn Bunting as observed in North Cornwall; with special reference to its polygamous habit. Br. Birds 28: 2-26

SAGE, B.L. 1965 Comments on plumage variations in the genus Euplectes Swainson. Bull. Br. Orn. Club 85: 42-44

SAITOU, T. 1976 Breeding biology of the Eastern Great Reed Warbler, Acrocephalus arundinaceus orientalis. Misc. Rep. Yamashina Inst. Orn. 8: 135-156

SAVIDGE, I.R. & D.E. DAVIS 1974 Survival of some common passerines in a Pennsylvania woodlot. Bird-banding 45: 152-155

SAXENA, R.N. & J.P. THAPLIYAL 1962 Male hormone and beak pigmentation in the Baya (Ploceus philippinus). Proc. 2. All India Congr. Zool.: 8

SCHIFTER, H. 1967 Bemerkenswertes aus der Schönbrunner Weberkollektion. Gefied. Welt 91: 25-27

SCHIFTER, H. 1970 Longevity in the Longtailed Widowbird in captivity. Ostrich 41: 255

SCHLUPP, W.F. 1922 The granivorous bird problem. J. Dep. Agric. sth. Afr. 4: 432-446

SCHMIDT, R.K. 1968 A colony of Red Bishop Birds Euplectes orix in the south western Cape. Ostrich 39: 25-27

SCHWARTZKOPFF, J. 1973 Mechanoreception. In D.S. Farner & J.R. King (eds), Avian biology, vol. 3: 417-477. Academic Press, New York & London.

SEBER, G.A.F. 1973 The estimation of animal abundance and related parameters. Griffin, London.

SEEL, D.C. 1968 Clutch-size, incubation and hatching success in the House Sparrow and Tree Sparrow Passer spp. at Oxford. Ibis 110: 270-282

SEEL, D.C. 1976 Moult in five species of Corvidae in Britain. Ibis 118: 491-536

SELANDER, R.K. 1958 Age determination and moult in the Boat-tailed Grackle. Condor 60: 355-376

SELANDER, R.K. 1960 Sex ratio of nestlings and clutch size in the Boat-tailed Grackle. Condor 62: 34-44

SELANDER, R.K. 1965 On mating systems and sexual selection. Am. Nat. 99: 129-141

SELANDER, R.K. 1972 Sexual selection and dimorphism in birds. In B. Campbell (ed.), Sexual selection and the descent of man, 180-230. Heinemann, London.

SELANDER, R.K. & D.R. GILLER 1961 Analysis of sympatry of Great-tailed and Boat-tailed Grackles. Condor 63: 29-86

SELANDER, R.K. & R.J. HAUSER 1965 Gonadal and behavioural cycles in the Great-tailed Grackle. Condor 67: 157-182

SIBLEY, C.G. 1970 A comparative study of the egg-white proteins of passerine birds. Bull. Peabody Mus. Nat. Hist., Yale Univ. 32: 1-131

SIEGFRIED, W.R. 1972 Breeding success and reproductive potential in the Cape Sparrow, _Passer melanurus_ (Müller). In S.C. Kendeigh & J. Pinowski (eds), Productivity, population dynamics and systematics of granivorous birds, 167-179. Polish Scientific Publishers, Warszawa.

SIEGFRIED, W.R. 1976 Sex ratio in the Cape Shelduck. Ostrich 47: 113-116

SIEGFRIED, W.R. & P.G.H. FROST 1975 Continuous breeding and associated behaviour in the Moorhen _Gallinula chloropus_. Ibis 117: 102-109

SIROKI, Z. 1974 Gelungene Zucht des Napoleonwebers. Gefied. Freund 21: 71-73

SKEAD, C.J. 1956 A study of the Red Bishop. Ostrich 27: 112-126

SKEAD, C.J. 1959 A study of the Redshouldered Widowbird _Coliuspasser axillaris axillaris_ (Smith). Ostrich 30: 13-21

SKEAD, C.J. 1965 The ecology of the ploceid weavers, widows and bishop-birds in the south-eastern Cape Province, South Africa. In D.H.S. Davis (ed.), Ecological studies in Southern Africa, 219-232. W.H. Junk, The Hague.

SKEAD, D.M. 1975 Ecological studies of four Estrildines in the central Transvaal. Ostrich suppl. 11: 1-55

SMITH, D.G. 1972 The role of the epaulets in the Red-winged Blackbird (_Agelaius phoeniceus_) social system. Behaviour 41: 251-268

SMITH, D.G. 1976 An experimental analysis of the function of Red-winged Blackbird song. Behaviour 56: 136-156

SMITH, H.M. 1943 Size of breeding populations in relation to egg-laying and reproductive success in the Eastern Red-wing (_Agelaius p. phoeniceus_). Ecology 24: 183-207

SMITH, M.J. & J. LE GAY BRERETON 1976 Annual gonadal and adrenal cycles in the Eastern Rosella, Platycercus eximius (Psittaciformes; Platycercidae). Aust. J. Zool. 24: 541-556

SNAPP, B.D. 1976 Colonial breeding in the Barn Swallow (Hirundo rustica) and its adaptive significance. Condor 78: 471-480

SNOW, D.W. 1956 The annual mortality of the Blue Tit in different parts of its range. Br. Birds 49: 174-177

SNOW, D.W. 1962 A field study of the Black and White Manakin, Manacus manacus, in Trinidad. Zoologica, N.Y. 47: 65-104

SNOW, D.W. 1970 Analysis of breeding success in the Blackbird, Turdus merula. Ardea 57: 163-171

SNOW, D.W. 1976 The relationship between climate and annual cycles in the Cotingidae. Ibis 118: 366-401

SNOW, D.W. & B.K. SNOW 1964 Breeding seasons and annual cycles of Trinidad land-birds. Zoologica, N.Y. 49: 1-39

SNOW, D.W. & B.K. SNOW 1973 The breeding of the Hairy Hermit Glaucis hirsuta in Trinidad. Ardea 61: 106-122

SOSSINKA, R. 1970 Domestikationserscheinungen beim Zebrafinken Taeniopygia guttata castanotis (GOULD). Zool. Jb. (Syst.) 97: 455-521

STARK, A.C. 1900 The fauna of South Africa. Birds. Vol. 1 R.H. Porter, London.

STEIN, H. 1974 Ein Beitrag zur Brutbiologie von Singdrossel, Turdus philomelos, Amsel, Turdus merula, und Mönchsgrasmücke, Sylvia atricapilla, mit besonderer Berücksichtigung der Brutverluste. Beitr. Vogelk. 20: 467-477

STEINBACHER, J. 1952 Jahreszeitliche Veränderungen am Schnabel des Haussperlings (Passer domesticus L.). Bonn. zool. Beitr. 3: 23-30

STEINER, G. 1967 Meine gelungene Zucht mit Orangewebern. Gefied. Welt 91: 202-204

STEWART, I.F. 1963 Variation of wing length with age. Bird Study 10: 1-9

STRESEMANN, E. & V. STRESEMANN 1966 Die Mauser der Vögel. J. Orn. 107: Sonderheft

TAYLOR, K.D. & M.G. GREEN 1976 The influence of rainfall on diet and reproduction in four African rodent species. J. Zool., Lond. 180: 367-389

TESCHEMAKER, W.E. 1910 The nesting of the Giant Whydah _Chera procne_. Avicult. Mag. 8: 81-90

THAPLIYAL, J.P. & R.N. SAXENA 1964 Absence of a refractory period in the Common Weaver Bird. Condor 66: 199-208

THIELCKE, G. 1970a Vogelstimmen. Springer, Berlin.

THIELCKE, G. 1970b Die sozialen Funktionen der Vogelstimmen. Vogelwarte 25: 204-229

THIOLLAY, J-M. 1974 Le peuplement avien de la savane de Lamto. Bull. de liaison des chercheurs de Lamto 4: 39-68

THIOLLAY, J-M. 1975 Exemple de predation naturelle sur une population nicheuse de _Quelea q. quelea_ (L.) au Mali. Terre Vie 29: 31-54

THOMPSON, W.A., J. VERTINSKY & J.R. KREBS 1974 The survival value of flocking in birds: a simulation model. J. Anim. Ecol. 43: 785-820

THORPE, W.H. 1961 Bird-song. Cambridge University Press, Cambridge.

THORPE, W.H. & B.I. LADE 1961 The songs of some families of the Passeriformes. II The songs of the buntings (Emberizidae). Ibis 103a: 246-259

TOMPA, F.S. 1967 Reproductive success in relation to breeding density in Pied Flycatchers, _Ficedula hypoleuca_ (Pallas). Acta Zool. Fenn. 118: 1-28

TRIVERS, R.L. 1972 Parental investment and sexual selection. In B.G. Campbell (ed.), Sexual selection and the descent of man, 136-179. Heinemann, London.

TRIVERS, R.L. & D.E. WILLARD 1973 Natural selection of parental ability to vary the sex ratio of offspring. Science 179: 90-92

ULBRICHT, H. 1975 Zur Brutbiologie der Rohrammer, _Emberiza schoeniclus_. Beitr. Vogelk. 21: 452-470

VAN EE, C.A. 1973 Cattle egrets prey on breeding Queleas. Ostrich 44: 136

VAN SOMEREN, V.D. 1945 The dancing display and courtship of Jackson's Whydah Coliuspasser jacksoni Sharpe. Jl. E. Africa Nat. Hist. Soc. 18: 131-141

VAN SOMEREN, V.G.L. 1956 Days with birds. Fieldiana, Zool. 38: 1-520

VAUGHAN, J.H. 1930 The birds of Zanzibar and Pemba. Ibis 6(12th ser.): 1-48

VAUGIEN, L. 1952 Sur l'activité testiculaire, la teinte du bec et la mue du moineau domestique soumis, en hiver, a l'éclairement artificiel continu. Bull. Soc. zool. Fr. 77: 395-407

VAUK, G. & H. SCHRÖDER 1972 Der Durchzug des Gartenrotschwanz' Phoenicurus ph. phoenicurus auf Helgoland unter Berücksichtigung von Alter und Geschlecht 1958-1968. Zool. Anz. 188: 291-300

VERHEYEN, R. 1953 Exploration du Parc National de l'Upemba. Fascicule 19. Oiseaux. Institut des Parcs Nationaux du Congo Belge, Bruxelles.

VERHEYEN, R. 1956 Les longeurs de l'aileron et de la queue en relation avec l'âge des oiseaux. Gerfaut 46: 65-74

VERNER, J. 1964 Evolution of polygamy in the Long-billed Marsh Wren. Evolution 18: 252-261

VERNER, J. 1975 Interspecific aggression between Yellow-headed Blackbirds and Long-billed Marsh Wrens. Condor 77: 328-330

VERNER, J. & G.H. ENGELSEN 1970 Territories, multiple nest building and polygyny in the Long-billed Marsh Wren. Auk 87: 557-567

VERNER, J. & M.F. WILLSON 1966 The influence of habitats on mating systems of North American passerine birds. Ecology 47: 143-147

VERNON, C.J. 1971 Owl foods and other notes from a trip to South West Africa. Ostrich 42: 153-154

VERNON, C.J. 1972 An analysis of owl pellets collected in Southern Africa. Ostrich 43: 109-124

VICTORIA, J.K. & N.E. COLLIAS 1973 Social facilitation of egg-laying in experimental colonies of a weaverbird. Ecology 54: 399-405

VINCENT, A.W. 1949 On the breeding habits of some African birds. Ibis 91: 483-507

VINCENT, J. 1936 The birds of Northern Portuguese East Africa. Ibis 6(13th ser.): 48-124

WAGNER, H.O. 1960 Beziehungen zwischen Umweltfaktoren und der Brutzeit, Zahl der Gelege sowie ihrer Grösse. Zool. Anz. 164: 161-172

WARD, P. 1965a Feeding ecology of the Black-faced Dioch Quelea quelea in Nigeria. Ibis 107: 173-214

WARD, P. 1965b The breeding biology of the Black-faced Dioch Quelea quelea in Nigeria. Ibis 107: 326-349

WARD, P. 1965c Seasonal changes in the sex ratio of Quelea quelea. Ibis 107: 397-399

WARD, P. 1969a The annual cycle of the Yellow-vented Bulbul Pycnonotus goiavier in a humid equatorial environment. J. Zool., Lond. 157: 25-45

WARD, P. 1969b Seasonal and diurnal changes in the fat content of an equatorial bird. Physiol. Zool. 42: 85-95

WARD, P. & G.E. POH 1968 Seasonal breeding in an equatorial population of the Tree Sparrow Passer montanus. Ibis 110: 359-363

WARD, P. & A. ZAHAVI 1973 The importance of certain assemblages of birds as "information centres" for food-finding. Ibis 115: 517-534

WELSH, D.A. 1975 Savannah Sparrow breeding and territoriality on a Nova Scotia dune beach. Auk 92: 235-251

WHYBROW, C. 1950 Effects of drought on the nesting of the Fire-crowned Bishop Euplectes hordacea. Ibis 92: 317

WILEY, R.H. 1974 Evolution of social organisation and life history patterns among grouse. Q. Rev. Biol. 49: 201-227

WILEY, R.H. & S.A. HARTNETT 1976 Effects of interactions with older males on behaviour and reproductive development in first-year male Red-winged Blackbirds Agelaius phoeniceus. J. Exp. Zool. 196: 231-242

WILLIAMS, J.G. 1962 An addition to our knowledge of Euplectes diademata. Bull. Br. Orn. Club 82: 172-173

WILLSON, M.F. 1966 Breeding ecology in the Yellow-headed

Blackbird. Ecol. Monogr. 36: 51-77

WILSON, G. 1973 Identifying, aging and sexing the Red Bishop and Cape Widow. SAFRING News 2: 22-23

WINKEL, W. & D. WINKEL 1976 Über die brutzeitliche Gewichtsentwicklung beim Trauerschnäpper (Ficedula hypoleuca). J. Orn. 117: 419-437

WINTERBOTTOM, J.M. 1936 Notes sur quelques veuves du nord de la Rhodésie. Oiseau Rev. fr. Orn. 6: 77-85

WINTERBOTTOM, J.M. 1971 Priest's eggs of Southern African birds. Winchester Press, Johannesburg.

WISEMAN, A.J. 1975 Changes in body weight of American Goldfinches. Wilson Bull. 87: 390-411

WITSCHI, E. 1936 Effect of gonadotropic and oestrogenic hormones on regenerating feathers of weaver finches (Pyromelana franciscana). Proc. Soc. exp. Biol. Med. 35: 484-489

WITSCHI, E. 1938 Hormonal control of seasonal phenomena in birds. Proc. 9. Int. Orn. Congr.: 431-435

WITSCHI, E. 1961 Sex and secondary sexual characters. In A.J. Marshall (ed.), Biology and comparative physiology of birds, vol. 2: 115-168. Academic Press, London & New York.

WITTENBERGER, J.F. 1976 The ecological factors selecting for polygyny in altricial birds. Am. Nat. 110: 779-799

WOODALL, P.F. 1971 Notes on a Rhodesian colony of the Red Bishop. Ostrich 42: 205-210

WRIGHT, P.L. & M.H. WRIGHT 1944 The reproductive cycle of the male Red-winged Blackbird. Condor 46: 46-58

WYDOSKI, R.S. 1964 Seasonal changes in the colour of starling bills. Auk 81: 542-550

YOM-TOV, Y. 1974 The effect of food and predation on breeding density and success, clutch size and laying date of the crow (Corvus corone L.). J. Anim. Ecol. 43: 479-498

YOM-TOV, Y. & J.G. OLLASON 1976 Sexual dimorphism and sex ratios in wild birds. Oikos 27: 81-85

YOUNG, H. 1961 A test for randomness in trapping. Bird-banding 32: 160-162

ZEDLITZ, O. Graf 1926 Vogelgewichte als Hilfsmittel für die biologische Forschung. J. Orn. 74: 296-308

ZEIDLER, K. 1966 Untersuchungen über Flügelbefiederung und Mauser des Haussperlings (Passer domesticus L.). J. Orn. 107: 113-153

ZIMMERMAN, J.L. 1966 Polygyny in the Dickcissel. Auk 83: 534-546

ZIMMERMAN, J.L. 1971 The territory and its density dependent effect in Spiza americana. Auk 88: 591-612

ZISWILER, V. 1965 Zur Kenntnis des Samenöffnens und der Struktur des hörnernen Gaumens bei körnerfressenden Oscines. J. Orn. 106: 1-48