

A COMPARATIVE STUDY OF THE GREY-HEADED SPARROW
(PASSER GRISEUS L) AND THE HOUSE SPARROW
(PASSER DOMESTICUS L) IN MALAWI

THESIS

Submitted in fulfilment of the
requirements for the Degree of
DOCTOR OF PHILOSOPHY
of Rhodes University

by

MARTIN EDWIN DARWIN NHLANE

November 1996

This thesis is my original work
and has not been submitted for a
degree in any other University.

MARTIN EDWIN DARWIN NHLANE

ACKNOWLEDGEMENTS

I would like to express my sincere thanks to the Chief Museums Officer Mr M.G. Kumwenda for giving me financial support in the data collection over the study period. Sincere thanks are also extended to the Ministries of Education and Youth, Sports and Culture for willingly approving educational advances which enabled me to complete my studies through Rhodes University.

Without guidance, suggestions and criticism from my supervisor Professor Adrian Craig, this work would not have been successfully completed. In my final year of study in 1995, I was greatly assisted with school fees by my supervisor. My travel to Rhodes University for thesis revision was made possible by Professor Craig. For all this, I sincerely thank him. Ms Karen Kuck drew the Geographical Information System (GIS) maps of sparrow distribution in Blantyre City. My sincere thanks are extended to her for assistance.

Dr Martin Villet of the Entomolgy Department at Rhodes University assisted with the statistical analysis and I sincerely thank him for the time he spared to guide me on the best method to analyse some of the data. Professor Pat Hulley assisted in many ways during my stay at Rhodes and I sincerely thank him for the attention he accorded me during the absence of my supervisor.

Graham Steele and Craig Whittington-Jones assisted with entering data on the computer and I also extend my sincere thanks to them.

My thanks are also extended to Management of Chikunda Farm where breeding studies were conducted on the House Sparrow and also general observations on Grey-headed Sparrows.

My wife Ephrina gave me the much-needed support and encouragement during the field work and also during the write-up. My daughters Zalerapi and Fanny Nhlane in their small way gave me the excitement to continue work. They particularly exhibited their knowledge in identifying the House Sparrow and asked me about the birds; I willingly told them.

Data collection in the field was assisted by Mr Victor Chilembo, of the technical staff at the Museums of Malawi. Data analysis on the computer was assisted by Mr Daniel Menyamenya of the Agriculture Development Division. I extend my sincere thanks to both of them for their assistance.

My final thanks go to all other people who provided assistance to me in many ways.

ABSTRACT

The House Sparrow Passer domesticus, an introduced species, and the Grey-headed Sparrow Passer griseus, an indigenous species, are sympatric in Malawi. Their distribution in the country and any possible interactions were studied, principally in southern Malawi.

A morphological analysis of museum specimens confirmed that grey-headed sparrows in Malawi belong to the Northern Grey-headed Sparrow Passer griseus as distinct from the Southern Grey-headed Sparrow Passer diffusus. This species was widely distributed in the country in association with human dwellings, both in rural areas as well as urban centres. In the northern region Grey-headed Sparrows were more abundant in the urban centres than rural areas, but in the central and southern regions numbers in the rural and urban areas were more or less the same. In Blantyre City, where they are in sympatry with the House Sparrow, they were found in the low density and industrial areas and were absent from the high density areas.

The House Sparrow, arrived in Malawi in 1967 at Chileka in the southern region. Since then it has spread northwards, moving from the southern to the central and northern regions. House Sparrow numbers were found to be progressively larger in the southern region and lowest in the northern region. House Sparrows were found at sites where food was readily available, as in the immediate vicinity of houses.

In the central and northern regions they were restricted mainly to urban areas. In the southern region, they occur both in rural and urban areas, probably as a reflection of the larger period of colonization in the south. In the northern region their movement has apparently been restricted by geographical barriers.

In Blantyre City Grey-headed Sparrows preferred areas where tree density was high and house density was low, while House Sparrows preferred areas where house density was high and tree density was low. There was a positive correlation between Grey-headed Sparrow numbers and tree density and a negative correlation with house density. House Sparrow abundance was negatively correlated with tree density and positively correlated with house density. Grey-headed Sparrows bred in the rainy season, whereas House Sparrows bred throughout the year. There were differences in nest site selection: Grey-headed Sparrows used artificial structures such as fencing poles, and wooden telephone or electricity poles. The House Sparrow used mostly buildings and nested in crevices, holes in walls and between the walls and rafters. Nest height also differed : Grey-headed Sparrows nested at heights ranging from 1 - 8 m while House Sparrow nests were at heights of 1 - 5 m.

Moult data suggests that although the House Sparrows breed throughout the year, they moult at a particular time of the year when breeding is less common. Grey-headed Sparrows were found to moult mainly from May to September in southern Africa and from June to September in central Africa. In both cases the breeding season extends over a similar period from about October to April/May of the following year. Peak moult periods differed between the House Sparrows and Grey-headed Sparrows. House Sparrows moulted mainly in the first half of the year, and Grey-headed Sparrows in the second six months.

The clutch sizes of the two species were similar (mean 3.9 eggs for the House Sparrow and 3.4 for the Grey-headed Sparrow). The clutch size of the House Sparrow varied seasonally and was larger from November to May. The average incubation period for the House Sparrow was 11.5 days and the fledging period 15.4 days. The Grey-headed Sparrow fledging period was 14.7 days. Chick mortality of the House Sparrow at Chikunda farm was attributed to starvation resulting from brood reduction, abandonment, predation, low birth weight, accidental deaths and parasitism by fly larvae.

Both Grey-headed and House Sparrows fed their young on insect food. Male House Sparrows fed actively initially, but their contribution declined from about day five onwards. In the Grey-headed Sparrow, both parents fed their young equally throughout the nestling period.

House Sparrows fed on the ground near houses; Grey-headed Sparrows fed both on the ground away from houses and in tree canopies. The Grey-headed Sparrow walked as it fed on the ground as opposed to the House Sparrow which hopped. Grey-headed Sparrows fed mainly as pairs and singletons while House Sparrows fed as family groups. Larger feeding groups of Grey-headed Sparrows were seen in the northern region at areas where food was plentiful. Where the two sparrows were seen feeding together, there was no direct competition for food. Where individual distance was violated; male House Sparrows displaced Grey-headed Sparrows which landed too close to them. Overall it appears that the distribution of the two species is determined more by their responses to habitat conditions than by interspecific interactions.

TABLE OF CONTENTS

TITLE	i
DECLARATION	ii
ACKNOWLEDGEMENTS	iii
ABSTRACT	v
LIST OF TABLES	xv
LIST OF FIGURES	xvii
LIST OF PLATES	xviii
LIST OF APPENDICES	xix

CHAPTER ONE

1.0	INTRODUCTION	1
-----	--------------	---

CHAPTER TWO

2.0	The Grey-headed Sparrows	4
2.1	Introduction	4
2.2	Materials and methods	6
2.3	Results	7

2.3.1	Plumage characteristics	7
2.3.2	Numerical data on different populations of grey-headed sparrows	8
2.3.3	Discussion	16

CHAPTER THREE

3.0	Sparrow distribution in Malawi	18
3.1	Introduction	18
3.2	History of the House Sparrow in southern Africa	18
3.3	History of the House Sparrow introduction to Malawi	20
3.4	Past records of Grey-headed sparrows	21
3.5	Methods	24
3.6	Statistical methods	25
3.7	Results	26
3.8	Current distribution by region	26
3.9	Northern region	26
3.9.1	Mzimba district	29
3.9.2	Rumphi district	29
3.9.3	Chitipa district	31
3.9.4	Karonga district	31
3.9.5	Nkhata Bay district	32
3.10	Central region	32
3.10.1	Salima district	36
3.10.2	Lilongwe district	36
3.10.3	Kasungu district	37

3.10.4	Dowa district	37
3.10.5	Mchinji district	38
3.10.6	Dedza district	38
3.10.7	Ncheu district	39
3.11	Southern region	39
3.11.1	Mwanza district	43
3.11.2	Chikwawa district	43
3.11.3	Nsanje district	44
3.11.4	Thyolo district	44
3.11.5	Mulanje district	44
3.11.6	Zomba district	44
3.11.7	Machinga district	45
3.11.8	Mangochi district	45
3.12	Interactions in sympatry	45
3.13	Discussion	49

CHAPTER FOUR

4.0	Distribution of Grey-headed and House Sparrows in Blantyre City	52
4.1	Introduction	52
4.2	Study areas and methods	52
4.2.1	High density areas	53
4.2.2	Low density areas	53
4.2.3	Mid-density areas	53

4.2.4	Commercial area	54
4.2.5	Industrial area	54
4.3	Bird counts	54
4.4	Results	59
4.4.1	Grey-headed Sparrows	59
4.4.2	Sparrow correlation to house density	62
4.4.3	Tree density	62
4.5	Discussion	66

CHAPTER FIVE

5.0	Sparrow breeding biology	68
5.1	Introduction	68
5.2	Methods	68
5.2.1	Breeding records	68
5.2.2	Parental care	72
5.2.3	Climatic data	73
5.2.4	Moult data	75
5.3	Results	75
5.3.1	Breeding season of Grey-headed and House Sparrows	75
5.3.2	Environmental factors and other factors affecting breeding	76
5.3.3	Moult	77
5.3.4	Clutch size	86
5.3.5	Incubation and fledging period	88

5.3.5.1	House Sparrow	88
5.3.5.2	Grey-headed Sparrow	90
5.3.6	Chick mortality	92
5.3.7	Egg measurements	93
5.3.7.1	House Sparrow	93
5.3.7.2	Grey-headed Sparrow	93
5.3.8	Hatching period	97
5.3.8.1	House Sparrow	97
5.3.9	Causes of hatching failure	97
5.3.10	Nestling food	99
5.3.11	House Sparrow chick and adult dispersal from breeding site	99
5.3.12	Feeding of nestlings	102
5.3.12.1	Grey-headed Sparrows	102
5.3.12.2	House Sparrow	102
5.3.13	Breeding behaviour	107
5.3.13.1	Grey-headed Sparrow	107
5.3.14	Nest defence (House and Grey-headed Sparrow)	107
5.4	Discussion	109

CHAPTER SIX

6.0	Feeding Biology	121
6.1	Introduction	121
6.2	Methods	122

6.2.1	Feeding observation (behaviour)	122
6.3	Results	122
6.3.1	Comparative morphology	122
6.3.2	Feeding groups of House Sparrows	127
6.3.3	Grey-headed Sparrows	127
6.3.4	Feeding interactions	128
6.3.5	Social behaviour	129
6.4	Discussion	130

CHAPTER SEVEN

7.0	Traditional competition theory	132
7.1	Recent views on competition theory	138
7.2	Do sparrows compete in Malawi?	143
7.3	Studies on other <u>Passer</u> species	144
7.4	Conclusion	148

APPENDICES	150
-------------------	-----

REFERENCES	160
-------------------	-----

LIST OF TABLES

2.1	Average measurements of the different taxa of grey-headed sparrows	9
2.2	Principal components analysis	11
2.3	Classification results of discriminant function analysis for populations	15
3.1	Number of Grey-headed and House Sparrows observed in rural and urban habitats in the northern region.	30
3.2	Number of Grey-headed and House Sparrows observed in rural and urban habitats in the central region.	34
3.3	Number of Grey-headed and House Sparrows observed in rural and urban habitats in the southern region.	41
3.4	Population density of Malawi in 1994.	48
4.1	Grading system of density of houses and trees in Blantyre City.	60
4.2	Total numbers of Grey-headed Sparrows counted in each month against locality in Blantyre City during 1992 and 1993	61
4.3	Total numbers of House Sparrows counted in each month against locality in Blantyre City during 1992 and 1993.	63

4.4	Grey-headed and House Sparrow sightings against grading system of house density in Blantyre City 1992/1993.	64
4.5	Grey-headed and House Sparrow sightings against grading system of tree density in Blantyre City 1992/1993.	65
5.1	Monthly distribution of wing-moult in Grey-headed Sparrows and House Sparrows.	80
5.2	Nest site selection of Grey-headed and House Sparrows in Blantyre City and nest records of BirdLife South Africa at Cape Town.	82
5.3	Nest height of Grey-headed and House Sparrows in Blantyre City and nest records of BirdLife South Africa at Cape Town.	85
5.4	Frequency of different clutch sizes of <u>Passer domesticus</u> and <u>Passer diffusus</u>	87
5.5	Breeding data for the House Sparrow at Chikunda farm.	89
5.6	Mean clutch size of House Sparrows per month at Chikunda combined for 1989 and 1990.	91
5.7	Causes of chick mortality in 1989 and 1990	95
5.8	Age at which death occurred in days	96
5.9	Causes of eggs failing to hatch	98
5.10	House Sparrows ringed and recaptured at Chikunda farm.	101

5.11	Feeding visits of Grey-headed Sparrows at one nest with two 5-6 day old chicks.	105
5.12	Feeding observations of House Sparrows on broods of different sizes and ages.	106
6.1	Comparative dimensions of adult sparrows.	124
6.2	Observed feeding places and activity of Grey-headed and House Sparrows in Blantyre City and elsewhere.	125
6.3	Feeding groups of sparrows observed in Blantyre City and elsewhere.	126

LIST OF FIGURES

2.1	Principal components analysis of five grey-headed sparrow taxa.	12
2.2	Discriminant function analysis of five grey-headed sparrow taxa	14
3.1	Map of Malawi showing districts where Belcher (1930) recorded Grey-headed Sparrows and the sightings of the House Sparrow in Malawi after introduction.	23
3.2	Map of the northern region	28
3.3	Map of the central region	35
3.4	Map of the southern region	42
4.1	Study areas in Blantyre City	55
5.1	Mean climatic data as recorded at Chileka International Airport	74

5.2	Breeding season of the Grey-headed Sparrow in 1993 and climatic data.	79
5.3	Breeding season of the House Sparrow in 1989/1990 and climatic data.	81

LIST OF PLATES

4.1	High density area in Blantyre City.	56
4.2	Low density area in Blantyre City.	56
4.3	Mid-density area in Blantyre City.	57
4.4	Commercial area in Blantyre City.	57
4.5	Industrial area in Blantyre City	58
5.1	Wooden electricity poles.	83
5.2	Fencing poles.	83
5.3	House wall crevice/hole	84
5.4	House rafters	84

APPENDICES

1.1	Number of Grey-headed and House Sparrows observed in Mzimba district.	150
1.2	Number of Grey-headed and House Sparrows observed in Rumphu district.	150
1.3	Number of Grey-headed and House Sparrows observed in Nkhata Bay district.	151
1.4	Number of Grey-headed and House Sparrows observed in Chitipa district.	151
1.5	Number of Grey-headed and House Sparrows observed in Karonga district.	152
2.1	Number of Grey-headed and House Sparrows observed in Salima district.	152
2.2	Number of Grey-headed and House Sparrows observed in Lilongwe district.	153
2.3	Number of Grey-headed and House Sparrows observed in Kasungu district.	153
2.4	Number of Grey-headed and House Sparrows observed in Dowa district.	154
2.5	Number of Grey-headed and House Sparrows observed in Mchinji district.	154
2.6	Number of Grey-headed and House Sparrows observed in Dedza district.	155
2.7	Number of Grey-headed and House Sparrows observed in Ncheu district.	155
3.1	Number of Grey-headed and House Sparrows observed in Mwanza district.	156

- 3.2 Number of Grey-headed and House Sparrows observed 156
 in Chikwawa district.
- 3.3 Number of Grey-headed and House Sparrows observed 157
 in Nsanje district.
- 3.4 Number of Grey-headed and House Sparrows observed 157
 in Thyolo district.
- 3.5 Number of Grey-headed and House Sparrows observed 158
 in Mulanje district.
- 3.6 Number of Grey-headed and House Sparrows observed 158
 in Zomba district.
- 3.7 Number of Grey-headed and House Sparrows observed 159
 in Machinga district.
- 3.8 Number of Grey-headed and House Sparrows observed 159
 in Mangochi district.

CHAPTER ONE

1.0 INTRODUCTION

Sparrows of the genus Passer are widespread in the Afrotropical, Palaearctic and Indomalayan regions (Summers-Smith 1988). Several species have been introduced to other areas and have proved highly successful in man-modified environments. Traditionally sparrows have been included in the weaver family (Ploceidae) but several authors have proposed that they should be placed in their own family Passeridae (Pocock 1966, Bock & Moroney 1978). Pocock (1966) considered the resemblance between Passer and the Ploceidae to be the result of convergence. Summers-Smith (1988) mentioned that the sparrows are sufficiently different from Ploceidae to warrant them being given full family rank. Sibley & Ahlquist (1988), based on the results of DNA x DNA hybridisation, erected a family Passeridae which included weavers and waxbills as sub-families. More recently, Dowsett & Forbes-Watson (1993) have also recognized the family Passeridae but they included Petronia as well, as did Sibley & Monroe (1990).

The situation where a widespread indigenous species occurs alongside a congeneric introduced species is of special interest. Conventional competition theory would suggest that in such a situation one species would exclude the other, unless they occupy separate niches (Wiens 1977). Competition theory assumes that population sizes of competing species are limited by the available resources (Pulliam 1983). Anderson & Koopman (1981)

accepted that species compete and that this competition operates on both ecological and evolutionary time scales, but no two species responded in exactly the same way to all environmental conditions. They pointed out that one result of competition may be specialisation. Specialisation by a species for the use of some subset of resources may increase its probability of survival.

In Africa the House Sparrow Passer domesticus is an introduced species which has spread in association with human activities. It is the world's most successful introduced species and it probably occupies more than two thirds of the earth's surface (Long 1981). It is now widely sympatric with the endemic African grey-headed sparrows, a species-complex in which some authors recognize five species (Hall & Moreau 1970, Summers-Smith 1988) and others only two (Dowsett & Forbes-Watson 1993).

Malawian grey-headed sparrows are generally assigned to the species Passer griseus, the Northern Grey-headed Sparrow (Benson & Benson 1977). These birds are now found in close association with man in many areas, where they are in direct contact with the House Sparrow. The aim of this study was to review the current distribution of the two taxa in Malawi, and to investigate their ecology in the City of Blantyre and its surroundings. Here they may compete directly for limited resources, such as breeding sites. From this it may be possible to predict the future pattern of distribution of these species, in relation to human modification of their environment. I have also attempted to

clarify the taxonomic status of the grey-headed sparrow population under study.

CHAPTER TWO

2.0 THE GREY-HEADED SPARROWS

2.1 INTRODUCTION.

In the first major checklist of the birds of Africa, Sclater (1930) recognized two species of grey-headed sparrow: Passer griseus and its races P. g. suahelicus, P. g. mosambicus, P. g. diffusus and the Parrot-billed Sparrow P. gongonensis though he noted that this species might be only a race of P. griseus. Two of these taxa P. g. suahelicus and P. g. mosambicus would occur within Malawi. White (1963) included all grey-headed sparrows (including gongonensis) in the single species P. griseus and noted that the two taxa P. g. diffusus and P. g. mosambicus intergrade extensively in Malawi (Nyasaland); he did not mention P. g. suahelicus as occurring in this area.

Hall & Moreau (1970) recognised five species of grey-headed sparrows on the grounds that small areas of overlap occur where two taxa live side by side without inter-breeding, although in other parts of their range these two taxa may apparently intergrade. The five species that they recognised are Passer griseus, P. swansonii, P. gongonensis, P. suahelicus, P. diffusus. They indicated that P. suahelicus occurred in the northern part of Malawi, P. diffusus in the southern part, and P. griseus throughout the country. In contrast Benson & Benson (1977) recorded only two populations of grey-headed sparrows,

Passer griseus mosambicus and P. g. stygiceps (now Passer diffusus stygiceps) from Malawi.

Clancey (1980) and Clancey et al. (1991) recognized two populations of the Southern Grey-headed Sparrow in southern Africa: Passer diffusus stygiceps which he indicated as extralimital in southern Malawi and Zambia, and P. d. diffusus. Meanwhile in East Africa, Britton (1980) recognized a single species with the following races: P. g. gongonensis, P. g. suahelicus, P. g. mosambicus, and P. g. swaisonii. Summers-Smith (1988) recognized the same five grey-headed sparrow species as Hall & Moreau (1970). The species which he indicated as occurring in Malawi are Passer g. ugandae, P. suahelicus, P. d. diffusus and P. d. mosambicus. Dowsett & Forbes-Watson (1993) however recognised only two species Passer griseus and Passer diffusus, and stated that both occur in Malawi. Clearly a decision must be reached on the taxon or taxa involved in the present study.

2.2 Material and methods

Apart from birds handled in Malawi (eight), I have examined grey-headed sparrow specimens from Durban Natural Science Museum (148), Transvaal Museum (121) and Albany Museum (12). The taxa represented and the geographical areas are listed in Table 2.1.

For each specimen, standard wing, tail, tarsus and culmen (from the base of the skull) measurements were taken. In addition I measured the depth and width of the culmen at the anterior border of the nostril, using vernier callipers. To avoid discrepancies in the measurements, all measurements were taken personally by me. I then compared populations from different regions using the (principal component analysis, followed by discriminant function analysis) Statgraphics statistical package.

The principal components are variables in a data set whose combination explains most of the variability. Discriminant function analysis on the other hand finds one or more quantitative measurements that will help to discriminate among groups when data are classified into two or more groups. The objective is to provide a method for predicting which group a case is most likely to fall into.

All birds handled were also examined for moult in their primary feathers. Moult was simply recorded as present or absent. These data were merely to serve as an indication of the relationship of moult to the breeding season of the birds.

2.3 Results

2.3.1 Plumage characteristics

There are some plumage differences between the different populations of grey-headed sparrows. Passer griseus ugandae is very distinct from the rest of the grey-headed sparrows. It is larger in size and the head is much greyer with a very conspicuous brown rump, and a whitish belly. P. g. suahelicus is the same size, but unlike ugandae, its ventral feathers are dark grey in appearance. P. d. mosambicus and P. g. stygiceps are similar in size. P. d. mosambicus has a wider band of rufous brown feathers on the scapula than P. g. stygiceps. The grey head feathers of P. d. mosambicus tend towards brownish while those of P. g. stygiceps are not. P. d. diffusus has a greenish grey head with reddish brown back which is very distinct from P. d. stygiceps. The head of the latter is very grey which goes all the way down to the mantle feathers. The underparts are not obviously different. Passer d. diffusus has a grey head, with the white wing bar very conspicuous. It is smaller in size than P. g. ugandae. P. g. mosambicus has a darkish grey head and the wing bar is not conspicuous. The back feathers are browner in appearance.

2.3.2 Numerical data on different populations of grey-headed sparrows.

Table 2.1 gives a summary of the average measurements taken on the grey-headed sparrow populations from different regions. The general pattern is that the males within all the geographical areas were larger than females. Raw data for all the species from the different regions were entered into the Statgraphics statistical package to carry out principal component and discriminant analysis.

Principal component analysis identified two main components, wing and tail lengths, which accounted for 65.2% of the variability (Table 2.2). These two main components were plotted on a scatter diagram (Fig 2.1). The plot indicates that the five taxa of the grey-headed sparrows (Passer diffusus diffusus {1}, P. d. stygiceps {2}, P. griseus ugandae {3}, P. g. suahelicus {4} and P. g. mosambicus {5}) were clustered around a central axis with no obvious distinct grouping.

Table 2.1. Average measurements of the different grey-headed sparrows,
grouped according to countries.

COUNTRY	SPECIES	SEX	MEAN LENGTH (SAMPLE SIZE)			MEAN LENGTH (SAMPLE		
			Wing	Tail	Tarsus	Bill	width	Depth
ANGOLA	<u>P. d. diffusus</u>	female	82(1)	62(1)	18.5(1)	13.3(1)	5(1)	7(1)

BOTSWANA	<u>P. d. diffusus</u>	male	81.3(14)	63.4(14)	18.5(14)	13.4(14)	5.9(14)	6.8(14)
		female	79.2(10)	64.3(10)	18.5(10)	13.3(10)	5.7(6)	6.9(10)

CONGO	<u>P. g. ugandae</u>	male	85(2)	71.3(3)	19.1(3)	15.3(3)	6.3(3)	7.5(3)
		female	81.4(4)	68(4)	19.5(4)	14.9(4)	6.1(4)	7.4(4)

KENYA	<u>P. g. ugandae</u>	female	86(1)	67(1)	21(1)	15.3(1)	6.5(1)	8(1)
	<u>P. g. suahelicus</u>	male	89(2)	70(2)	21(2)	14.8(2)	6.3(2)	8(1)
		female	85.5(2)	67.5(2)	20.6(2)	14.9(2)	6.5(2)	7.5(2)

MALAWI	<u>P. g. ugandae</u>	male	84.6(8)	68.5(8)	21.2(8)	15.3(8)	6.4(8)	7.1(8)
		female	80(1)	64(1)	18.3(1)	15.3(1)	6(1)	7(1)
	<u>P. d. stygiceps</u>	male	84(2)	66.5(2)	19(1)	14.5(2)	6(2)	7.6(2)

MOZAMBIQUE	<u>P. d. stygiceps</u>	male	79(6)	60.7(6)	18.8(8)	13.3(6)	6.2(6)	7.2(6)
		female	79(2)	62(2)	19.5(2)	13.5(2)	6.3(2)	7.3(2)
	<u>P. g. mosambicus</u>	male	76(2)	55(2)	18.5(2)	12.5(2)	6(2)	7.3(2)
		female	76.5(2)	58.5(2)	19(1)	13(2)	5.5(2)	6.8(2)

SUDAN	<u>P. g. ugandae</u>	female	79(1)	67(1)	21(1)	14.8(1)	6.3(1)	8(1)

ZAMBIA	<u>P. g. ugandae</u>	male	77.5(2)	57.5(2)	18.3(2)	13.3(2)	5.8(2)	6.5(2)
		female	83(1)	65(1)	20(1)	14(1)	5.5(1)	7(1)

TANZANIA	<u>P. g. ugandae</u>	male	82(1)	64(1)	20(1)	16(1)	6.5(1)	8(1)
	<u>P. g. mosambicus</u>	male	82.4(15)	64.2(15)	19.3(15)	14.5(15)	6(15)	7.4(15)
		female	82.1(8)	63.4(8)	19.4(8)	14.4(8)	6.1(8)	7.6(8)
NAMIBIA	<u>P. d. diffusus</u>	female	80(5)	62.3(5)	18.3(5)	13.1(5)	5.6(5)	6.6(5)

		female	81.6(9)	65.4(9)	18.8(9)	13(9)	5.7(9)	6.9(9/
<hr/>								
ZIMBABWE	<u>P. d. stygiceps</u>	male	82.9(31)	65.5(31)	19.2(31)	13.4(31)	5.7(31)	6.9(31)
		female	80.9(17)	62.8(17)	19(17)	13.4(17)	6.2(17)	7.3(17)
	<u>P. d. diffusus</u>	male	83.8(4)	64(4)	19(4)	12.6(4)	5.1(4)	6.5(4)
		female	82.3(3)	63(3)	19.3(3)	13.8(3)	5.3(3)	6.5(3)
<hr/>								
SOUTH AFRICA	<u>P. d. diffusus</u>	male	80.3(12)	65.7(12)	19.5(12)	13.5(12)	5.9(12)	7(12)
(northern Cape)		female	77.5(8)	63(8)	18.6(8)	12.9(8)	5.9(8)	7.2(8)
(Transvaal)	<u>P. d. stygiceps</u>	male	81.8(15)	65.5(15)	18.8(15)	13.7(15)	6(15)	7(15)
		female	80.2(12)	62.1(12)	18.4(12)	13.6(12)	5.9(12)	6.9(12)
(eastern Cape)	<u>P. d. stygiceps</u>	male	73(4)	52.7(4)	18.7(4)	11.5(4)	5.4(4)	5.9(4)
(Natal)	<u>P. d. stygiceps</u>	male	80.9(35)	63(35)	18.7(15)	13.6(35)	5.8(35)	7(15)
		female	78(13)	59.7(13)	18.0(13)	13.5(13)	6(13)	7(13)
<hr/>								
Swaziland	<u>P. d. stygiceps</u>	male	83(1)	62(1)	18(1)	13(1)	5.5(2)	7(2)

Table 2.2. Principal component analysis

Component	Percentage of variance	Cumulative percentage
Wing length (mm)	42.7	42.7
Tail length (mm)	22.5	65.2
Tarsus length (mm)	12.9	78.1
Bill length (mm)	9.7	87.8
Bill width (mm)	7.4	95.2
Bill depth (mm)	4.8	100.0

Plot of First Two Principal Components

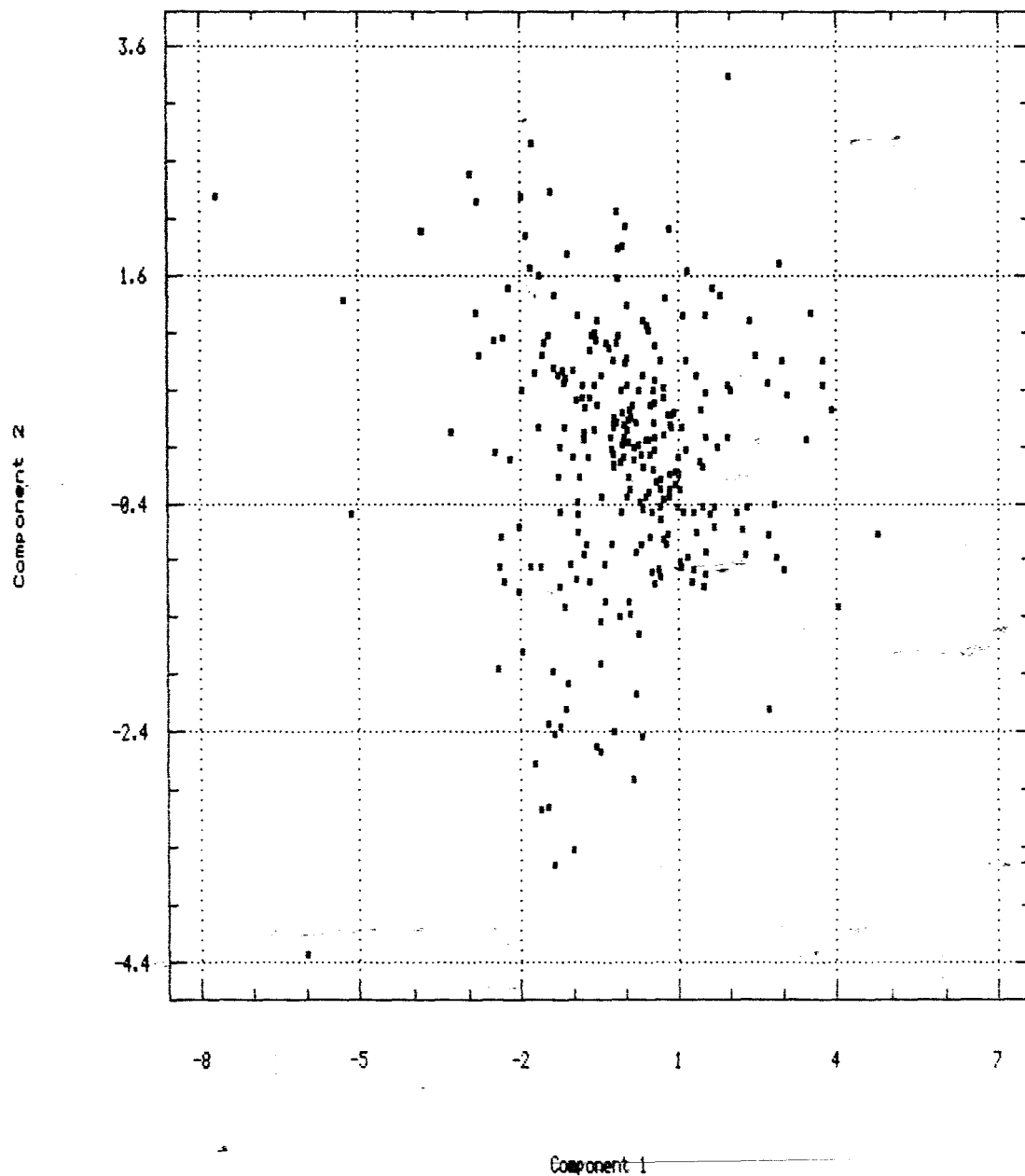


Fig 2.1 Principal component analysis
of five grey-headed sparrow taxa

Data were further analyzed using discriminant analysis and discriminating for the different races which were numbered from one to six as indicated above. As in the principal component analysis, two main discriminating functions were identified as wing length (discriminant 1) and tail length (discriminant 2). A plot of the analysis is shown in Fig. 2.2. The results show that P. d. diffusus and P. d. stygiceps overlap. P. g. ugandae, P. g. suahelicus and P. g. mosambicus are clearly seen outside the main nucleus of two other races and mainly in the positive sector of the two discriminants although some are spread out within the plotted diagram. They are separated from P. d. diffusus and P. d. stygiceps which are the southern races of the grey-headed sparrows while P. g. ugandae, P. g. suahelicus and P. g. mosambicus are the northern races. Classification results for the different races are shown in Table 2.3. Actual groupings entered into the computer are tabulated below.

	Group	Number
<u>Passer d. diffusus</u>	1	102
<u>Passer d. stygiceps</u>	2	111
<u>Passer g. ugandae</u>	3	24
<u>Passer g. suahelicus</u>	4	4
<u>Passer g. mosambicus</u>	5	27

Discriminant Analysis for BIRDS.Race_num

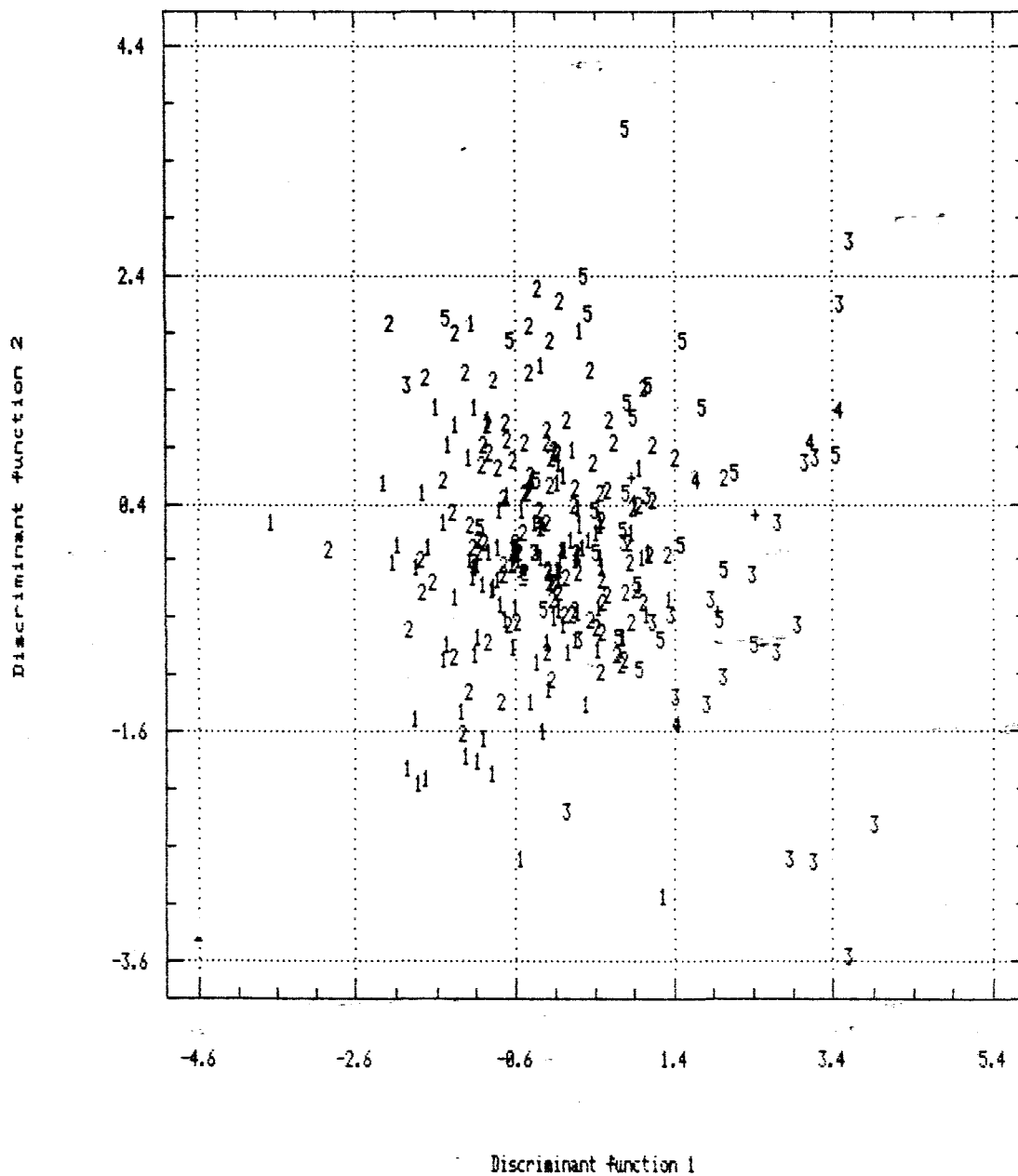


Fig 2.2 Discriminant component analysis of five grey-headed sparrow taxa

Table 2.3 Classification results of discriminant analysis
for populations based on measurements of wing and tail
lengths as main discriminants.

	Predicted Group									
	P.d.d		P.d.s		P.g.u		P.g.s		P.g.m	
	(Count,percentage)									
P.d.d	54	52.94	53	34.31	4	3.92	1	.98	8	7.84
P.d.s	35	31.53	46	41.44	8	7.21	2	1.80	20	18.02
P.g.u	2	8.33	2	8.33	15	62.50	4	16.67	1	4.17
P.g.s	0	.00	0	.00	1	25.00	3	75.00	0	.00
P.g.m	3	11.11	3	11.11	7	25.93	1	3.70	13	48.15

P. d. d = Passer diffusus diffusus

P. d. d = Passer diffusus stygiceps

P. g. u = Passer griseus ugandae

P. g. s = Passer griseus suahelicus

P. g. m = Passer griseus mosambicus

All five races were not accurately assigned by the computer as belonging to the various groupings based on the specimen labels. However for P. d. diffusus, P. g. ugandae and P. g. suahelicus more than 50% of the birds were assigned to the current taxon.

The general picture that emerges is that of the birds misidentified, the majority are assigned to other northern or southern races respectively. Of 268 total entries, the computer identified only 131 (48.9%) correctly.

2.3.3 Discussion

Both principal component and discriminant function analysis have shown that it is difficult to separate the five races consistently into five groups. However discriminant analysis when the results are classified (Table 2.3) has shown that two main groups can be identified: the northern population P. griseus and the southern P. diffusus. The above analysis also points to the confusion resulting from different taxonomists assigning different names to the grey-headed sparrows. It may not be necessary to have more than two basic taxa of the grey-headed sparrows.

Based on this analysis, I am following the most recent classification of the grey-headed sparrows by Dowsett & Forbes-Watson (1993), who recognized only two species P. griseus and P.

diffusus. Thus the birds in Malawi are the Northern Grey-headed Sparrow P. griseus, and this is the subject of my study. P. diffusus the Southern Grey-headed Sparrow is found in southern Africa from Zimbabwe southwards.

CHAPTER THREE

3.0 SPARROW DISTRIBUTION IN MALAWI

3.1 INTRODUCTION

3.2 History of the House Sparrow in southern Africa.

Long (1981) has reviewed the history of House Sparrow introductions throughout the world and its success, with the exception of a few places where it died out or was extirpated. Before looking at the distribution of the House Sparrow in Malawi, a look at introductions in southern Africa and its spread would give a better perspective on the situation. In South Africa introductions of House Sparrow P. d. indicus are reported from Durban (Summers-Smith 1963), while in East London the race P. d. domesticus was introduced at about the same time in 1890. Mackworth-Praed & Grant (1963) however reported that indicus was first liberated in 1893 and again in 1897 and the race domesticus in 1914 at Durban. Several other introductions were reported. Winterbottom (1966) stated that House Sparrows were introduced at Cape Town in 1902, Harwin & Irwin (1966) reported an introduction at East London in 1907 (this date was later given as 1927).

By the 1950's the House Sparrow is reported to have moved northwards reaching areas such as King Williams Town, Pretoria, Johannesburg and southern Zululand (Long 1981). It had spread more than 1 600 km, in three different directions; south-west to the Cape Peninsula, north-west to great Namaqualand and north to Zambia. Markus (1960) reported that in 1959 the House Sparrow had reached Springfontein, Bloemfontein and Kroonstad in the Orange Free State.

In Swaziland the first House Sparrows were observed in 1954, in Namibia they were first recorded at Grunau in 1961 (Uys 1962) and some spread northwards to several areas (Winterbottom 1971). In Botswana it was established at Lobatse by 1956 and to the north at Francistown in 1958 (Vernon 1962). In Zimbabwe the House Sparrow is reported to have been in Bulawayo in 1956 or earlier and they were released in Harare in 1957. Irwin (1981) stated that in Zimbabwe by 1965 the House Sparrow had spread to most parts of the country, though in some localities they were patchily distributed.

Long (1981) reported that there appear to be no records of the House Sparrow in Zambia until 1965, when they settled at Livingstone. It later appeared at Kalomo and Lusaka. This group is believed to have come from Zimbabwe. Dowsett (1971) gave subsequent records of the spread of the House Sparrow in Zambia. It was seen at Mbara and Petauke and Nyimba in November 1971, and Chadiza (which is only some 15 kilometres from Namitete in Malawi, in July 1971. In Chipata the House Sparrow was noticed

in 1974. Benson & Benson (1977) suggested that most probably the occurrences of House Sparrows in extreme eastern Zambia are an extension of the colonization of southern and central Malawi.

In Mozambique, the House Sparrow was released in 1955 from Portugal and it is reported that the status of the introduction is very poorly known (Long 1981).

3.3 History of House Sparrow arrivals in Malawi

Belcher (1930) did not record House Sparrows in Malawi. Thirty years later Long (1961) too had no records of the House Sparrow in the lower Shire and the country as a whole. The first House Sparrow was sighted at Chileka in Blantyre in 1967 (Benson & Benson 1975, 1977) see Fig 3.1. Payne & Payne (1967) recorded an occupied nest at Tete on 14 April 1967. It is believed that these House Sparrows may have invaded Malawi from Mozambique. Blantyre is only 100 miles (160 km) east-north-east of Tete. Benson & Benson (1975) suggested that the record at Chileka must have been between April and September, not long after that at Tete.

A year later it had spread as far as Blantyre which is 20 km away. In 1969 it had spread to Chikwawa in the south and northwards to Balaka. The northwards movement continued reaching Dedza 1970, Lilongwe 1971, Namitete and Bana 1974. In 1975 it was very common in Lilongwe, the capital of Malawi but uncommon

in Zomba 64 km from Blantyre (see Fig 3.1 for localities). Benson & Benson (1975) suspected that the House Sparrows may have colonized Zomba in 1973, but wondered why the population was still very small in 1975. There are no records of House Sparrow colonization in the northern districts of Malawi. The arrival of House Sparrows in the north could have taken place within the last ten years.

3.4 Past records of Grey-headed Sparrows.

The earliest records of bird distribution in Malawi were by Belcher (1930) whose records dated back to 1921. Belcher (1930) reported that the Grey-headed Sparrow "Pyrgilopsis griseus" was found throughout Nyasaland (Malawi) at all levels, but he gave no estimate of relative abundance. Belcher (1930) specifically mentioned the presence of Grey-headed Sparrows at Blantyre, Zomba, Liwonde, Luchenza, Karonga, Mchinji and Kasungu (see Fig. 3.1).

Long (1961) noted that Grey-headed Sparrows Passer griseus were very common in Nsanje district but their status and distribution was not known. He however recorded 41 localities from which the bird was sighted, and collected 12 specimens, of which ten were from villages and two in brachystegia woodland. From as early as 1961, the Grey-headed Sparrow had already adapted itself to human habitation in the lower Shire valley. From my childhood experience in Mzimba district (Northern

region), the Grey-headed Sparrow was common as shown in this study where it was found in the villages and trading centres where brick houses are usual. It could be speculated that this might have been the same in 1961 all over the country where similar conditions existed.

Benson & Benson (1975, 1977) observed that Grey-headed Sparrows were predominantly associated with human dwellings in Malawi as a whole. They were found below 5 000ft (1 500 m) and widespread in association with all kinds of man-made buildings, in which they also nested. In some localities birds were wholly or partially associated with woodland, probably nesting in holes in trees, as recorded at Nchalo, Liwonde and Monkey Bay. Benson & Benson (1977) suggested that the Grey-headed Sparrow probably occurred originally only in woodland, but that the human population increase in the last 100 years must have favoured it, and it had adapted to using man-made structures.

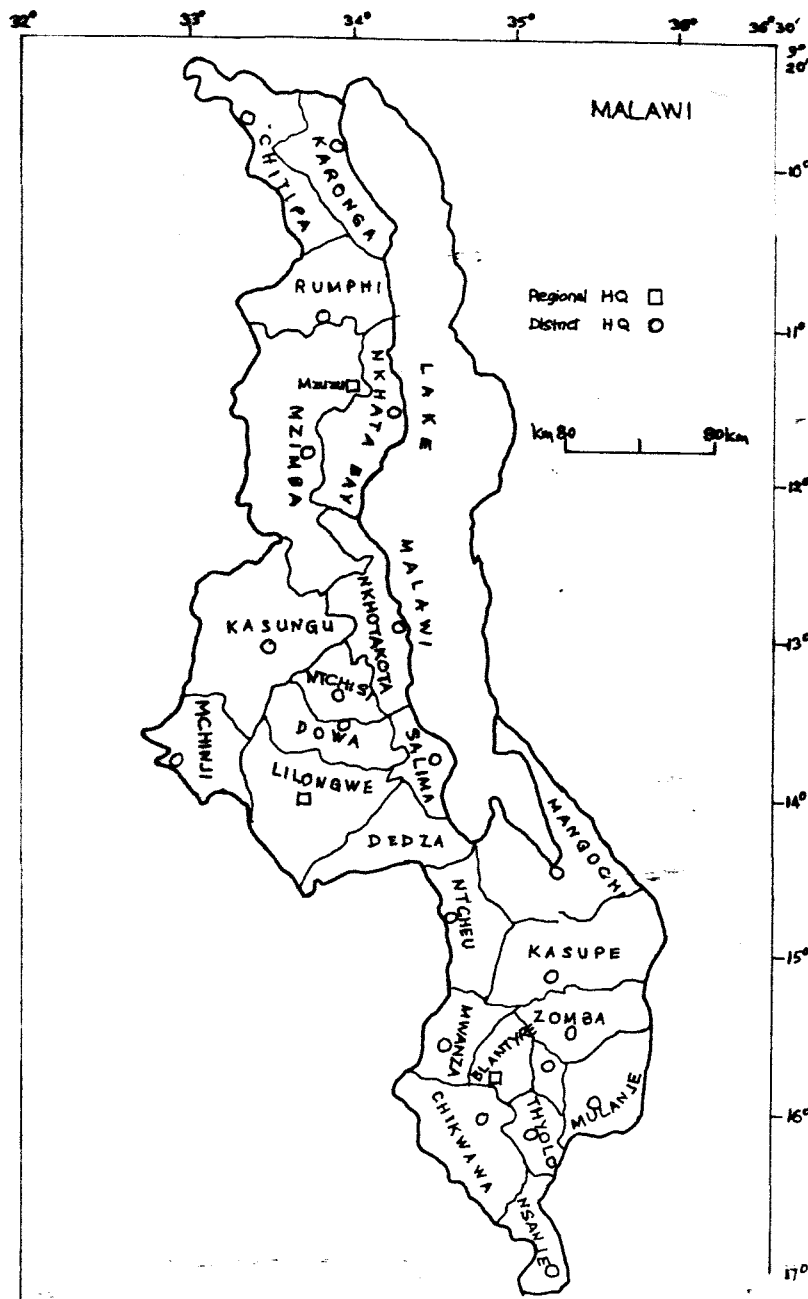


Fig.3.1 Map of Malawi showing districts where Belcher (1930) recorded Grey-headed Sparrows and the sightings of the House Sparrows in Malawi after introduction

Grey-headed Sparrows

Karonga, Kasungu,
Kasupe, Zomba,
Blantyre, Thyolo

House Sparrows

Blantyre (1967), Chikwawa (1969),
Zomba (1973), Kasupe, Dedza (1970),
Lilongwe (1971), Mchinji (1974), Kasungu

3.5 Methods

Counts of the relative abundance of sparrows in all the regions were done in May 1994 for northern region and May 1995 for the central and southern regions. Counts in the regions were undertaken soon after the rainy season to avoid any discrepancy in the number of Grey-headed Sparrows counted. Grey-headed Sparrows are more conspicuous during the breeding season because they sing or call at nesting places. The House Sparrows are conspicuous throughout the year. The results are therefore comparable between regions.

In each district, relative abundance of the Grey-headed and House Sparrows was surveyed in the built-up area which comprised the town centre, with shops and other buildings around. The built-up areas in towns and cities of Blantyre, Lilongwe and Mzuzu were taken as urban areas. Human activity in urban areas was much higher as compared to the rural areas. The rural areas comprised places which were about 20 km away from towns or cities. Here there were a few buildings comprised of shops and residential houses of either brick or poles, thatched or roofed with iron sheets. The human activity here was lower as compared to areas in town. The rural areas were populated by a peasant community. Two to five sites in the urban and rural areas were surveyed for the presence of both the Grey-headed and House Sparrow by walking along a transect of 100 m. Numbers of sparrows were recorded visually in each of the areas with the aid of 8x40 binoculars. Observations were made in the morning and

afternoon from 0800 to 1000 hours and from 1400 to 1600 hours respectively. Each observation period lasted up to 30 minutes. Since the counts were from different areas, and there was no likelihood of duplication, the numbers reflected in each district were summary counts of these different sites within the district.

3.6 Statistical methods.

Most of the statistical calculations were done on both the SPSS and STATGRAPHICS statistical packages at the 5% level of significance. For bird counts, the Wilcoxon test of ranks, a non-parametric test was used. The Wilcoxon signed-rank test ranks the absolute differences between each data value pair and calculates average ranks. It was used here because it takes care of the disparities between the data that may arise from the collection methods used. It is more sensitive than the sign and unpaired tests.

3.7 RESULTS

3.8 Current distribution by region

I examined the present distribution of House and Grey-headed Sparrows in all the regions of the country, which was subdivided into the northern, central and southern regions (Figs 3.2 - 3.4). The House Sparrow first arrived in Malawi in the southern region, and there has been a steady northwards movement. The human population density is progressively larger towards the south. It was therefore appropriate to follow the administrative division of the country into three regions and compare the numbers of sparrows in these regions.

3.9 Northern region.

The distribution of Grey-headed and House Sparrows in the northern region (Fig 3.1) is summarised in Table 3.1. Raw data for each of the districts are in Appendix 1. House Sparrows were absent in the rural areas of the northern region except for Mzimba, and were also absent from Karonga town and uncommon in Chitipa. In the urban areas, the highest number of House Sparrows was found in Mzimba, followed by Nkhata Bay and Rumphi district. The difference in the numbers of House Sparrows between urban and rural sites for the whole region was significant ($P = 0.04$, $Z = -2.01$, $N = 5$, Wilcoxon test of ranks).

As for Grey-headed Sparrows, they were found both in urban and rural areas. The numbers for all the districts were higher in the urban areas than rural areas although for Karonga it was more or less equal. The highest numbers were recorded in Mzimba district and the lowest in Rumphi district. The distribution of Grey-headed Sparrows between urban and rural areas was significantly different with more Grey-headed Sparrows in the urban centres than in the rural areas ($P = 0.03$, $Z = -2.16$, $N = 5$, Wilcoxon test of ranks).

The Grey-headed Sparrow numbers recorded for the region were much higher than the House Sparrows, representing approximately 70% of the total numbers. The comparison between Grey-headed and House Sparrows for the rural areas showed a significant difference ($P = 0.03$, $Z = 2.16$, $N = 5$, Wilcoxon test of ranks). However when the two species were compared in urban areas, there was no significant difference ($P = 0.18$, $Z = 1.35$, $N = 5$, Wilcoxon test of ranks).

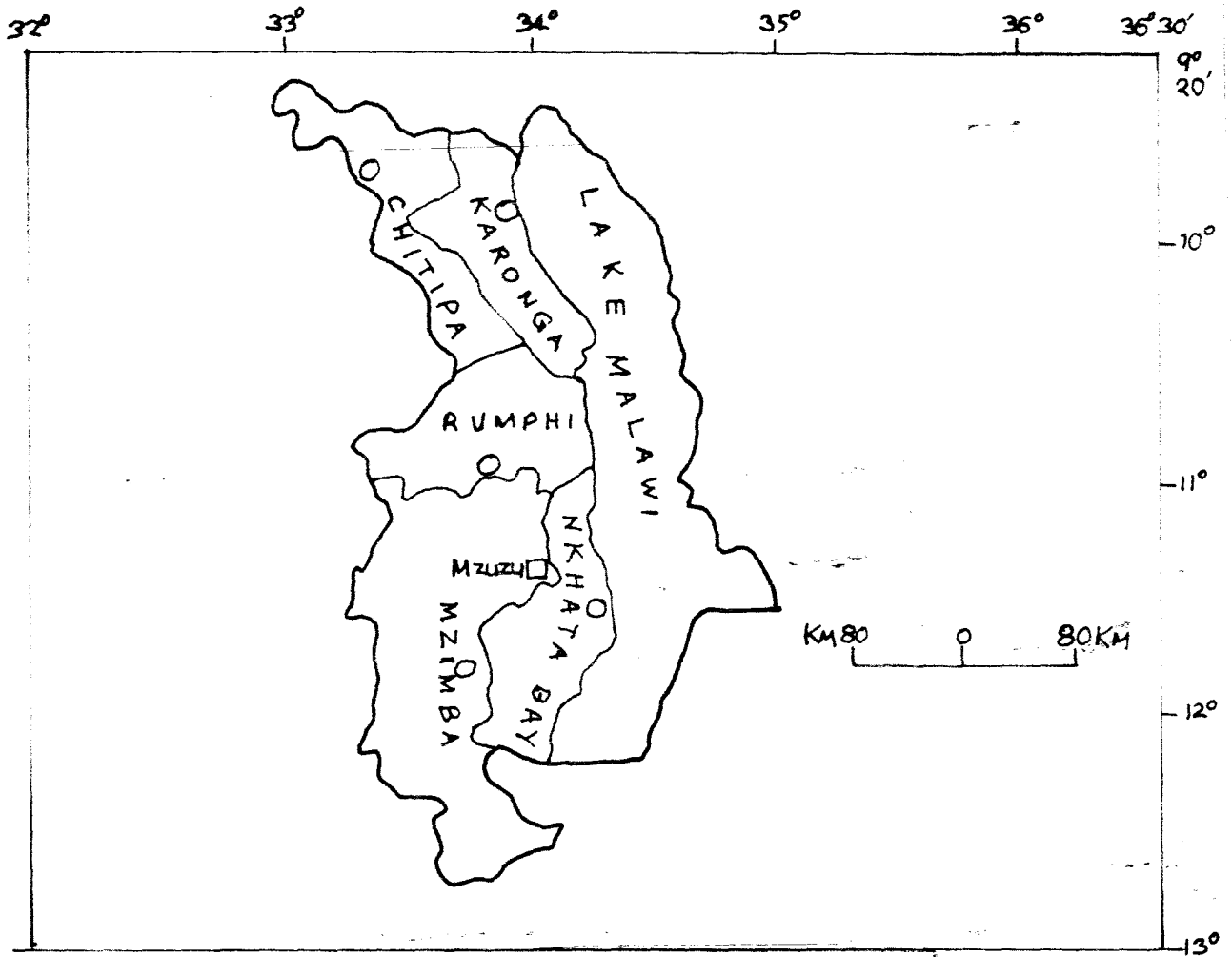


Fig 3.2 Map of Northern region showing the districts where data on relative abundance of the two sparrows were collected.

3.9.1 Mzimba district.

Except for Mzimba town, there were more Grey-headed Sparrows than House Sparrows in the areas visited. In the rural areas, the House Sparrow was absent except for Edingeni which is 20 km from the Zambian border town of Lundazi, a probable source..

The House Sparrow presumably reached Mzimba on its northwards movement before Mzuzu, and as a result the birds are better established at Mzimba than Mzuzu. The House Sparrow was sighted in built-up areas of town in the immediate vicinity of houses where garbage is thrown and from which they could easily find food whereas as the Grey-headed Sparrow was mostly found in wooded areas where buildings were far apart. Here they also collected food.

3.9.2 Rumphi district.

At Rumphi district both Grey-headed and House Sparrows were present, but at Livingstonia which is higher up on the plateau, there were no House Sparrows. The hills separating Livingstonia from Rumphi town appear to act as geographical barriers to House Sparrow movement.

Table 3.1 Number of Grey-headed and House Sparrows observed in the rural and urban habitats in the northern region

District	Number of birds recorded			
	Grey-headed and House Sparrows			
	Urban	Rural	Urban	Rural
Mzimba	70	21	79	5
Rumphi	8	5	14	0
Chitipa	52	17	5	0
Karonga	32	30	0	0
Nkhata Bay	55	7	27	0
TOTAL	217	80	125	5

3.9.3 Chitipa district

In Chitipa district there were significantly more Grey-headed Sparrows than House Sparrows. In the rural areas of Kameme (20 km from Chitipa town) and Nthalile (90km away), House Sparrows were conspicuously absent. Nthalile and Kameme are rural areas with both thatched and iron-roofed houses. The number of House Sparrows was very low at Chitipa town, which is surrounded by hills on all sides except on the western side. These hills possibly act as geographical barriers to the movement of House Sparrows, and the few birds at Chitipa may have come from the Zambian side. The population is very small; in 1989 a few House Sparrows were seen at Chitipa, and on a recent visit in May, 1993, there had been no increase in numbers.

3.9.4 Karonga district

In Karonga district the House Sparrow was absent both in town and at Kaporo which is 25 km from Karonga towards the Tanzanian border. Karonga district is bordered by Lake Malawi on the eastern side and lies in a lake shore valley. Kaporo area is within the lake shore valley, lying within the low land areas along Lake Malawi. Here rice is widely cultivated for both commercial and domestic consumption. The rice provides abundant food for the Grey-headed Sparrows. It appears that movement of House Sparrows is again restricted by geographical barriers such as hills on the Chitipa and Mzuzu side and the lake on the eastern side.

3.9.5 Nkhata Bay district

In Nkhata Bay town, there were more Grey-headed Sparrows than House Sparrows. Most of the Grey-headed Sparrows were sighted at a maize mill where they fed on maize fragments. As in Karonga the number of Grey-headed Sparrows is directly related to the food source. In Nkhata Bay, during rice drying, the birds congregate in even larger numbers (personal communication with residents at Nkhata Bay district).

3.10 Central region.

Table 3.2 summarizes the distribution of Grey-headed and House Sparrows in the central region (Fig 3.2). Grey-headed Sparrows were found in both urban and rural areas at all the sites that were visited. In Salima at Livingstonia Beach Hotel, there were more House Sparrows than Grey-headed Sparrows. Livingstonia Beach hotel is 25 km away from Salima town, and the House Sparrows have evidently established themselves at the hotel due to the availability food.

The numbers of Grey-headed Sparrows in rural and urban sites in the central region were not significantly different ($P = 0.11$, $Z = -1.61$, $N = 7$, Wilcoxon test of ranks). However there were more sightings in the urban areas than in the rural areas, suggesting that the Grey-headed Sparrows are moving into the urban areas. There was no significant difference between Grey-

headed Sparrows and House Sparrows in the urban areas, ($P = 0.21$, $Z = -1.27$, $N = 7$, Wilcoxon test of ranks).

The House Sparrows were mostly found in the urban areas, and were absent in some rural areas of some districts except in Salima, Kasungu and Dowa. The comparison between rural and urban areas was however not significant ($P = 0.11$, $Z = -1.61$, $N = 7$, Wilcoxon test of ranks). When rural distribution of the House Sparrows was compared with Grey-headed Sparrows, again there was no significant difference ($P = 0.09$, $Z = -1.69$, $N = 7$, Wilcoxon test of ranks), but Grey-headed Sparrows were more numerous in the rural areas.

Table 3.2 Numbers of Grey-headed and House Sparrows observed in the rural and urban habitats in the central region.

District	Numbers of birds recorded			
	Grey-headed Sparrows		House Sparrows	
	Urban	Rural	Urban	Rural
Salima	15	9	3	27
Lilongwe	45	7	41	0
Kasungu	29	27	26	7
Dowa	18	22	14	4
Mchinji	21	26	13	0
Dedza	18	11	8	0
Ncheu	14	5	37	0
TOTAL	160	107	142	38

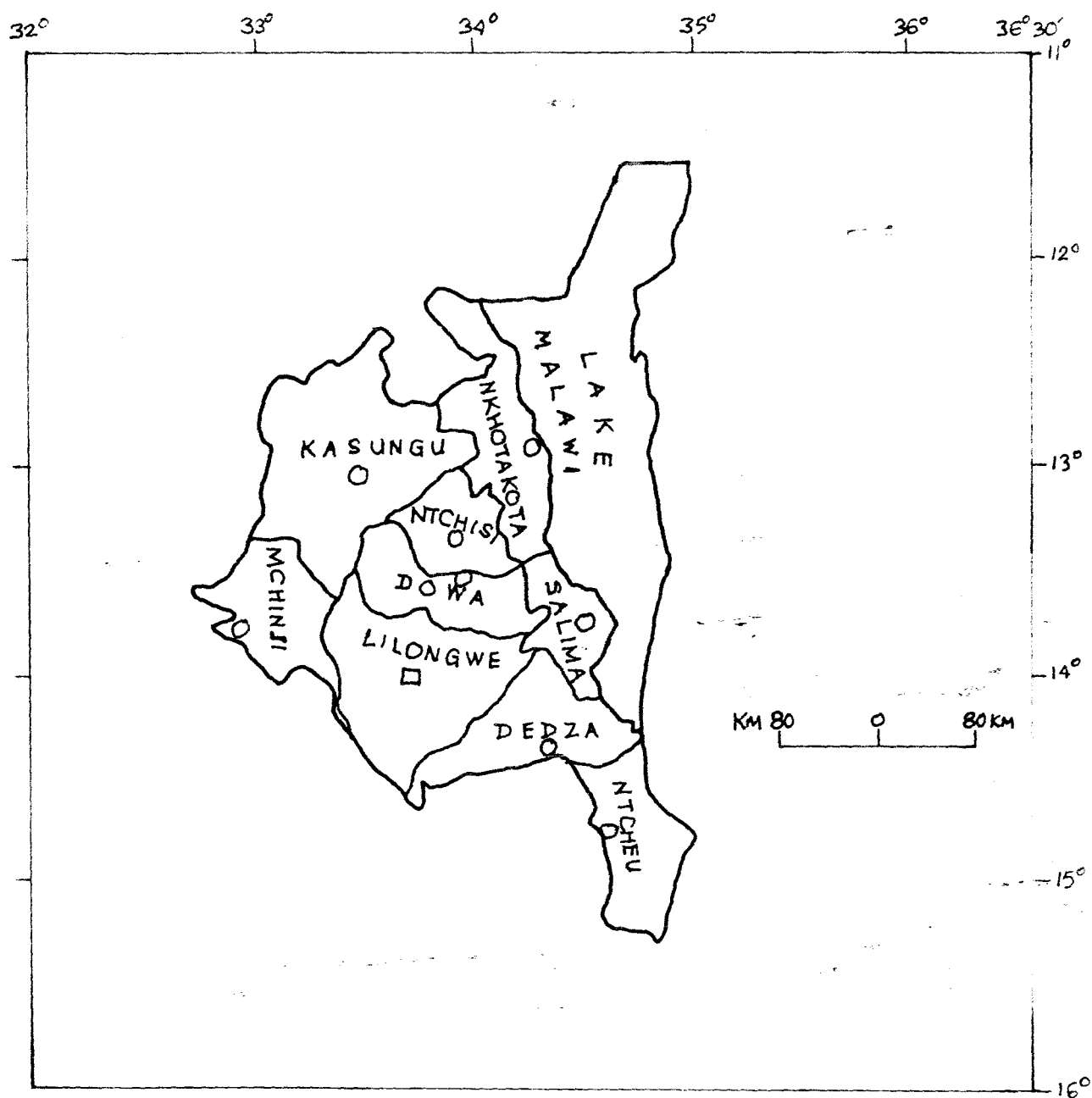


Fig 3.3. Map of central region showing the districts where data on relative abundance of the two sparrows were collected

3.10.1 Salima district.

The House Sparrow at Salima town was not well established, but it was common at Livingstonia Beach Hotel 23 km away from Salima because food was readily available, even though this is a rural area. The birds seen there comprised a family group with several juveniles. House Sparrows have failed to establish themselves in the villages in between, probably due to unpredictable food supplies.

Salima town is heavily wooded with Acacia spp, even in the commercial areas. The Grey-headed Sparrows were sighted in the more open areas away from the Acacia trees, where there were restaurants and houses within which they fed.

3.10.2 Lilongwe district.

Both sparrows were found at most sites, but the House Sparrow was absent in the rural area. In the old town, with commercial buildings, there were more House Sparrows than Grey-headed Sparrows. In the new city centre, there were comparatively fewer buildings than in the old town and a lot of natural vegetation between buildings. The Grey-headed Sparrow numbers here were much higher than House Sparrows. In the townships where the houses were closely built and refuse is readily available, observation showed that the House Sparrow numbers were higher.

3.10.3 Kasungu district.

Grey-headed Sparrows were dominant at all the sites visited in Kasungu district, but in town the sparrow numbers were almost the same. The Grey-headed Sparrows were seen in pairs and very rarely singly or threes; the House Sparrows on the other hand were found in family groups comprised of adults and juveniles. The Grey-headed Sparrows were found throughout the town, while the House Sparrows were restricted to backyards of buildings where food was available. The majority of the House Sparrows recorded at Kasungu were found at a maize mill. In the rural areas like Dwangwa, the House Sparrows were virtually absent. This is the case in all parts of the country where there are few brick buildings and mostly thatched houses. In such areas usually single pairs of Grey-headed Sparrows are seen. Dwangwa is 23 km from Kasungu and Nkhamenya is 54 km away on the road to Mzimba. This suggests that the House Sparrows at Nkhamenya may have come from a different source, probably from Zambia.

3.10.4 Dowa district.

In Dowa district Grey-headed Sparrows were found at all the sites and in larger numbers than the House Sparrows. The House Sparrows were absent in the rural areas. Most of the House Sparrows sighted were in family groups, the majority being juveniles.

3.10.5 Mchinji district.

Grey-headed Sparrows occurred in both urban and rural areas. The House Sparrow however was not present at Mchinji town nor in the rural areas. However, House Sparrows were present at Kamwendo, a semi-rural area which is 80 km from Lilongwe and only 20 km from Mchinji town. The House Sparrows are present in Lilongwe, and thus may have moved westwards to Kamwendo, or they could have come from Zambia. Mchinji is only 12 km from the Zambian boarder, and the nearest town is Chipata in Zambia which is about 45 km away. If the House Sparrows reached Zambia much earlier than Lilongwe in Malawi, the reason why they did not reach Mchinji from the Zambian border could be the geographical barrier (hills) on the western side of Mchinji on the Zambian border.

3.10.6 Dedza district.

In Dedza district Grey-headed Sparrows were found in all the areas visited. House Sparrows were absent in the rural areas but present at the town in very small numbers, suggesting that they were not well established.

3.10.7 Ntcheu district.

There were more House Sparrows at Ntcheu than Grey-headed Sparrows. Although the House Sparrows were more abundant, they were not evenly distributed within the town but concentrated on a building compound. This area provided adequate food as well as nesting places. There were a few breeding pairs, accompanied by juveniles. The Grey-headed Sparrows on the other hand were spread out evenly within the town. In the rural areas which were sampled, the House Sparrows were absent.

3.11 Southern region.

Table 3.3 gives a summary of sightings and distribution of both Grey-headed Sparrows and House Sparrows in the southern region (Fig 3.3). In the southern region, the distribution of Grey-headed Sparrows was more or less even both in the rural and urban areas. In Chikwawa, Nsanje and Mangochi, there were more Grey-headed Sparrows in the urban areas. The comparison of Grey-headed Sparrows between urban and rural sites is however statistically not significant ($P = 0.88$, $Z = -0.14$, $N = 8$, Wilcoxon test of ranks).

Unlike in the northern region and some parts of central region, House Sparrows were found both in the rural and urban areas except for Mwanza district. One explanation that is obvious is the longer period of colonization of the House

Sparrows in the southern region, and the higher human population density. As a result most of the rural areas are inhabited and food resources were readily available for the House Sparrows, so that they have moved further into the rural areas. The comparison of House Sparrows between rural and urban areas is not significant ($P = 0.67$, $Z = -0.42$, $N = 8$, Wilcoxon test of ranks).

There were significantly more House Sparrows than Grey-headed Sparrows in the urban areas ($P = 0.005$, $Z = -2.60$, $N = 8$, Wilcoxon test of ranks). This was expected as the House Sparrows in the south have established themselves over the past 27 years. In the rural areas the numbers of the two species also differ significantly ($P = 0.05$, $Z = 1.89$, $N = 8$, Wilcoxon test of ranks); whereas in the northern and central regions (Tables 3.1 & 3.2), Grey-headed Sparrows dominated, there were more rural House Sparrows in the southern region than in the other two sectors (Table 3.3).

Table 3.3 Numbers of Grey-headed and House Sparrows observed in rural and urban habitats in the southern region.

District	Number of birds sighted			
	Grey-headed Sparrows		House Sparrows	
	Urban	Rural	Urban	Rural
Mwanza	9	10	23	0
Chikwawa	14	3	39	79
Nsanje	7	5	18	11
Thyolo	7	12	28	31
Mulanje	6	13	27	9
Zomba	3	6	11	21
Mangochi	15	5	43	11
Machinga	12	14	22	29
<hr/>				
TOTAL	73	68	211	191
<hr/>				

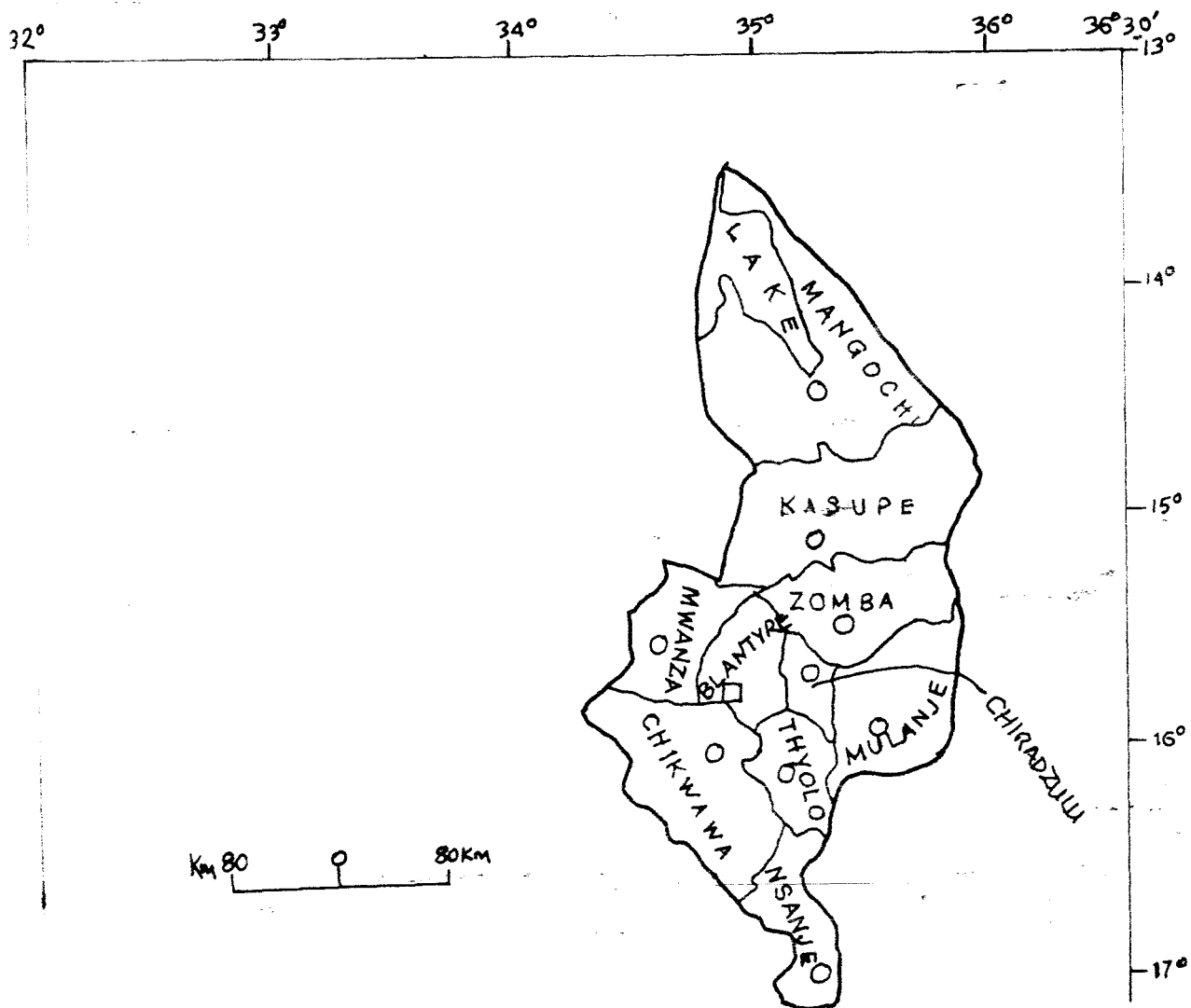


Fig 3.4 Map of southern region showing the districts where data on relative abundance of the two sparrows were collected

3.11.1 Mwanza district

At the three sites visited in Mwanza district, Grey-headed Sparrows were distributed both in the urban centres of Mwanza town and the two rural areas visited. The House Sparrow on the other hand was found only in the urban centre and absent in the rural areas.

3.11.2 Chikwawa district.

Both Grey-headed Sparrows and House Sparrows were present at Nchalo and Chikwawa. Chikwawa town had fewer House Sparrows than Nchalo, which is 25 km from Chikwawa in a southerly direction. This can be explained on the grounds that the town is sparsely populated and surrounded by villages and vegetation. The Shire River passes nearby with its riverine vegetation. Nchalo on the other hand is a trading centre which has grown out of Nchalo sugar company. There is more human activity here than in the town itself. As a consequence of this human activity, there is increased food availability within people's compounds, and hence a well established population of House Sparrows.

Grey-headed Sparrows are less abundant at Nchalo than at Chikwawa, which had natural vegetation and a riverine forest nearby. The Grey-headed Sparrows are apparently not affected by human activity at this locality.

3.11.3 Nsanje district.

Both Grey-headed Sparrows and House Sparrows were found at the two sites although the numbers were very small. The historical records indicate that the House Sparrows arrived at Chikwawa in 1969. This population probably moved to Bangula and then Nsanje.

3.11.4 Thyolo district.

Both sparrows were present at Thyolo and Luchenza. The House Sparrow numbers were higher than those of Grey-headed Sparrows. These were mostly family groups made up of juveniles and a few adults.

3.11.5 Mulanje district.

In Mulanje the Grey-headed Sparrows were absent at Muloza but present at the other two sites. The House Sparrows were absent at Phalombe which is a rural site, but present at the other two sites.

3.11.6 Zomba district.

Both Grey-headed Sparrows and House Sparrows were absent from the higher altitude area of Zomba plateau, but were present at the other sites. The number of House Sparrows sighted at Zomba was smaller than at Domasi which is 20 km away from Zomba

in a northern direction.

3.11.7 Machinga district.

Both sparrows were present at the three sites visited. The numbers of House Sparrows were larger than Grey-headed Sparrows.

3.11.8 Mangochi district.

In all the areas visited, both sparrows were present. House Sparrows were numerous in the rural areas of Mangochi.

3.12 INTERACTIONS IN SYMPATRY

The House Sparrows were virtually absent in the rural areas of the northern region (Table 3.1) and in the central region, they were present only in Kasungu, Salima and Dowa districts (Table 3.2). The Grey-headed Sparrows on the other hand were found both in the rural and urban areas. In the north, the spread of the House Sparrow has been recent in late 1970s and early 1980s. This is reflected in the low numbers of the House Sparrows (Table 3.1). At the extreme north, Chitipa and Karonga, House Sparrows were absent in Karonga and only 5 were seen in Chitipa. There could be competition over nesting places at Chitipa between the Grey-headed and House Sparrows. However no direct evidence of nest site competition was observed. Except

for Mzimba, the Grey-headed Sparrows were in majority.

Competition for food was unlikely in both the rural and urban areas. In Chitipa, numbers of House Sparrows were too low to suggest any competition for food or nesting places, and Grey-headed Sparrows nested freely on buildings. In Mzimba, Rumphi and Nkhata Bay, the birds fed in different sites. Feeding areas were segregated between the two sparrows (See sections 3.8 -3.10) in most district.

In Karonga where the House Sparrows were absent, the Grey-headed Sparrows fed within house compounds as at maize mills where maize husks were readily available. In Nkhata-Bay, large numbers of Grey-headed Sparrows were also seen feeding at a maize mill.

Generally, the Grey-headed Sparrows were not marginalized in their distribution in the northern and central regions. They fed freely both in the inner town and periphery of the town. This condition came about because the House Sparrows did not outnumber the Grey-headed Sparrows.

It is apparent that competition for feeding sites and breeding could be dependent on the number of House Sparrows. Where there are more House Sparrows, the Grey-headed Sparrows' feeding and breeding sites were restricted to low house density areas and industrial sites where House Sparrow activity was low as in Blantyre City (See Chapter four).

In the Northern region, observations showed that both Grey-headed and House Sparrows bred on the same houses with no obvious interference. The breeding sites were not competed for, except in one instance in Mzuzu City, where I observed a male House Sparrow harassing Grey-headed Sparrows at a nesting site. Both birds were prospecting for the same nesting site. When the Grey-headed Sparrows entered the hole, the male House Sparrow who was nearby also flew to the site harassing the Grey-headed Sparrows.

In the southern region House Sparrows and Grey-headed Sparrows were sighted both in the urban and rural environments (Table 3.3). In the northern and central regions, the House Sparrows were restricted to urban centres and absent in the rural areas except for a few places. In the southern region House Sparrows were found in both areas because they have been resident for much longer than in the northern and central regions. Their range expansion has been northwards. The southern region on the other hand is the most populous, with its population almost equal to the two other regions combined (table 3.4) Most of the areas in the southern region are inhabited both in the urban and rural areas. Consequently, food is readily available in most of the places.

Table 3.4

Population density of Malawi in 1994

Region	Total land (km ²)	Population	Density/km ²
North	26,931	1,145,100	43
Central	35,592	3,907,000	110
South	31,753	4,980,500	157

Historical records of the distribution of the Grey-headed Sparrow indicate that the birds were found all over the country (Belcher 1930), and the records of Long (1961) in the Nsanje district showed that the Grey-headed Sparrows were common in the villages and were also found in the woodlands. My own childhood experience in the northern region of Malawi, in the early 1960's is that the Grey-headed Sparrows were common in the villages as well as in trading centres where brick houses were common.

Benson & Benson (1975, 1977) made the same observation that the Grey-headed Sparrows were found associated with human dwellings as a whole. Although they do not mention specifically which human dwellings, brick or thatched ones, I assume they meant both.

The present distribution of the Grey-headed Sparrows as observed in this study shows that the birds are still associated with human dwellings. They were distributed both in rural and urban centres. They were found to be more common in the urban centres than in rural areas. This greater association with human dwellings is probably a result of destruction of their original habitats. The human dwellings provide them with readily available nesting sites. They are also found within settlements where food is more readily available. Human dwellings thus afford the Grey-headed Sparrows a two-fold advantage.

The distribution of House Sparrows has mostly been confined to the urban centres, with birds absent from most rural habitats except in the southern region. The likely cause of this distribution pattern of the House Sparrow is the availability of food. This is evident in the south. The southern region is densely populated with the result that most of the natural forests or woodlands have been replaced by cultivation and the opening of trading centres. This has resulted in the House Sparrow being found in rural areas far from urban centres. This pattern is lacking in the north and central region.

Another factor which could explain the presence of House Sparrows in the rural areas of the southern region is the period of colonization. Dispersal of House Sparrows in the southern region led to population of the rural areas. In the other two regions, the numbers of House Sparrows were smaller in the urban centres and thus did not disperse to rural areas, which in any case would not supply food for the House Sparrow. The House Sparrows are associated with man and as a result habitat change does affect them indirectly. With destruction of natural habitats and opening of more centres, suitable feeding sites and nesting places are made available to them. This affords them a chance to disperse from one place to another and became established in new places.

In the north, most of the woodlands are intact. With large stretches of uninhabited countryside the House Sparrow has been unable to move further out from the main trading centres. Most

of the area surrounding Karonga district for example is hilly. There are very few villages in these areas and the House Sparrows have failed to establish a foothold.

There was no indication in the districts to suggest that the two species competed for food or nesting sites. The only exception to this was in Blantyre district where most of the observations were made (See Chapter four).

CHAPTER FOUR

4.0 Distribution of sparrows in Blantyre City.

4.1 Introduction

Distribution needs to be studied at different spacial scales, since overlap in geographical terms may still imply habitat separation at a smaller scale. Here the focus is on the urban environment where the Grey-headed Sparrow is a more recent arrival.

4.2 Study areas and methods

The study areas for sparrow distribution in Blantyre City were sub-divided into five categories and the sparrow numbers in these sectors were related to the study areas, breeding and nonbreeding seasons. The study areas are shown in Fig 4.1. Tree and house densities were estimated from aerial maps of Blantyre City and also visually. A grading scale of one to five was used, from highest density (1) to lowest density (5) based on 10 samples of 10 cm² counts on the aerial maps.

4.2.1 . High density areas

The high density areas comprise residential areas where houses are built very close to each other, in an unplanned fashion. Here the poorest of the city residents live. The houses in most cases are built with unburned bricks and roofed either with iron sheets of low grade or thatch. Hygiene is below standard, and refuse is scattered freely. These areas are known as townships, and are located about 10 km from the main commercial area (See plate 4.1)

4.2.2 Low density areas

The low density areas are suburbs where houses are built on designated plots, spaced far apart and surrounded by trees and exotic plantations. This is where the upper and middle class residents of Blantyre City live. Refuse is controlled and put in dustbins which are removed by City refuse collectors (See plate 4.2)

4.2.3 Mid-density areas

These areas are suburbs within the City built by the Malawi Housing corporation. The houses are built on plots which are serviced with proper roads. Refuse is collected by the City. Tree cover is scanty except for some exotic plantations and hedges (See plate 4.3).

4.2.4 Commercial areas

The commercial areas consisted of the City centre of Blantyre City. The buildings consist of shops and office blocks. Tree cover is scanty, mostly consisting of exotic plants lining the streets (See plate 4.4).

4.2.5 Industrial areas

The industrial area comprised factories and warehouses. Tree density was higher than in the commercial areas of the City where exotic trees are mainly planted (See plate 4.5).

4.3 Bird counts.

Abundance of House and Grey-headed Sparrows was counted in 1992 and 1993 in Blantyre City. Pre-determined routes were followed with stops at fixed intervals. The total distances covered ranged between five to 25 km in the selected areas in the City. Stops were made every 1.5 km for a period of five minutes during which time sparrows were counted. Counts were done at least once a week in each of the areas.

- House Sparrows breeding
- Grey-headed Sparrows breeding
- ⊠ House Density = 1
- ⊠ House Density = 2
- ⊠ House Density = 3
- ⊠ House Density = 4
- ⊠ House Density = 5
- ▲ Tree Density = 1
- ▲ Tree Density = 2
- ▲ Tree Density = 3
- ▲ Tree Density = 4
- ▲ Tree Density = 5

Fig 4.1 Study areas in

Blantyre City

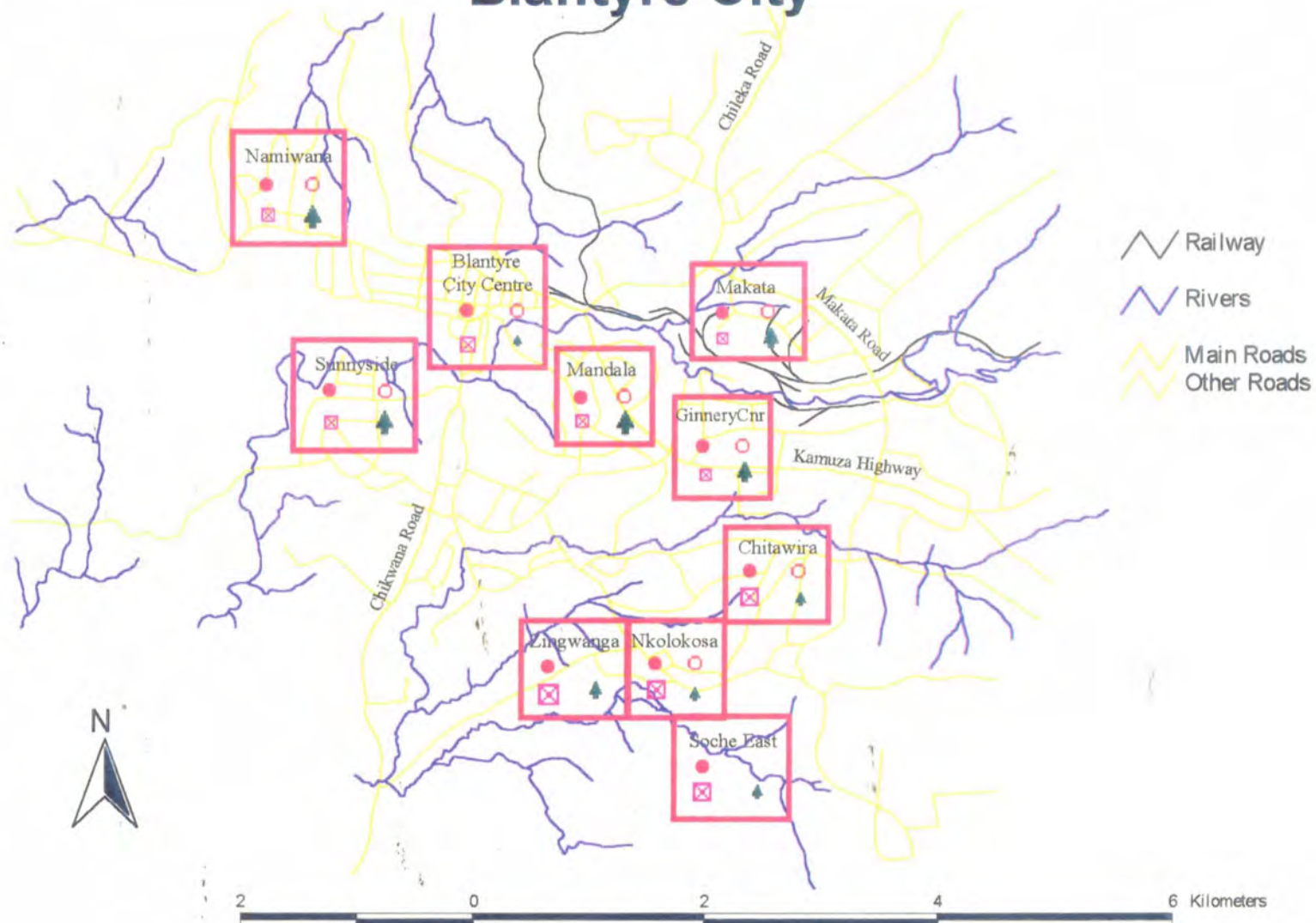




Plate 4.1 & 4.2 High and low density areas in the City of Blantyre respectively.



Plate 4.3 & 4.4 Mid-density and commercial areas in the City of Blantyre respectively



Plate 4.5 Industrial area in the City of
Blantyre

4.4 Results

4.4.1 Grey-headed Sparrows

The results in table 4.2 indicate that the Grey-headed Sparrow was found chiefly in the low density and industrial areas. They were absent from the high density areas except for one record in February, present in all months in the low density areas, but absent in some months in the other areas. The numbers were higher from January to April and also from October to December. Grey-headed Sparrows bred from about October to May. The numbers counted were higher then because during the breeding season the Grey-headed Sparrows sing a lot and are therefore conspicuous and easily sighted. The higher numbers appearing in the industrial areas in July and November were a result of birds concentrating at a food manufacturing company which provided easy foraging opportunities. The factory stores maize, millet, and sorghum which are used for making "Chibuku shake shake" beer. The Grey-headed and House Sparrows fed around the storage areas where food residues were found.

Table 4.1 Grading system of density of
houses and trees in Blantyre City

House density	Grade	Tree density (Grade)
Industrial	1	4
Low	2	5
Commercial	3	1
Mid	4	2
High	5	3

Table 4.2 Total numbers of Grey-headed Sparrows
counted in each month in Blantyre City
during 1992 and 1993

Month	Locality (HOUSE DENSITY)				
	High	Low	Mid	commercial	Industrial
Jan	0	19	3	2	9
Feb	1	31	1	1	9
Mar	0	21	0	4	8
Apr	0	10	3	3	3
May	0	4	0	0	0
Jun	0	7	2	2	0
Jul	0	3	0	0	20
Aug	0	2	0	0	1
Sep	0	1	2	2	7
Oct	0	13	0	0	3
Nov	0	5	5	1	14
Dec	0	10	0	6	6
TOTAL	1	126	16	21	80
%	0.4	51.9	6.6	8.6	32.8

4.4.2 Sparrow correlation to house density.

Table 4.2 and 4.3 shows that the number of Grey-headed Sparrows was significantly negatively correlated to house density whereas that of the House Sparrow showed a strong positive correlation (Spearman's correlation coefficient $r = -0.81$ and 0.79 respectively).

4.4.3 Tree density

Table 4.5 shows that the numbers of Grey-headed Sparrows were significantly positively correlated to tree density whereas that of the House Sparrow showed a slight negative correlation (Spearman's correlation coefficient $r = 0.82$ and -0.09 respectively).

Table 4.3 Total numbers of House Sparrows counted
in each month in Blantyre City during
1992 and 1993.

Month	Locality (House Density)				
	High	Low	Mid	Commercial	Industrial
Jan	174	13	64	5	14
Feb	167	10	70	11	24
Mar	214	9	40	9	19
Apr	315	16	60	27	36
May	298	19	54	18	39
Jun	183	10	37	19	13
Jul	152	11	48	20	20
Aug	167	3	17	25	40
Sep	172	4	45	19	13
Oct	197	1	64	21	11
Nov	201	2	77	12	33
Dec	180	5	80	9	28
<hr/>					
TOTAL	2 420	101	656	195	290
%	66.1	2.8	17.9	5.3	7.9
<hr/>					

Table 4.4 Grey-headed and House Sparrow
sightings according to house density
in Blantyre City 1992/93

Locality	Numbers Sighted	
	Grey-headed Sparrows	House Sparrows
Industrial	74	290
Low	126	101
Commercial	21	195
Mid	16	656
High	1	2420
TOTAL	238	3662

Table 4.5 Grey-headed and House Sparrow sightings
according to tree density in
Blantyre City 1992/93.

Tree density	No of Sparrows	
	Grey-headed	House
1	21	195
2	16	656
3	1	2420
4	74	290
5	126	101

4.5 DISCUSSION

The overall pattern of distribution is the same as the results found in the regional district distribution (See chapter 3). However with a wide choice of habitats the two sparrows showed distinct preferences. The Grey-headed Sparrow numbers were highest in low density areas and industrial sites (Table 4.2) whereas the House Sparrow numbers were greater in the high density areas and mid-density areas (Table 4.3). The House Sparrows were however still found in smaller numbers in the other areas. The wide spread of the House Sparrows in the city indicates that they are adaptable to different environments.

This segregation was not prominent in the northern region. Both birds were found in town with little separation, which indicates that in Blantyre City, the situation could have been the same during colonization by the House Sparrow but changed when House Sparrows increased to outnumber Grey-headed Sparrows.

Greater numbers of House Sparrows could have brought competition for resources. It can therefore be argued that competitive interaction between the House Sparrow and Grey-headed Sparrow could have led to habitat segregation between the two species in Blantyre City.

In a study of intra- and interspecific aggression in the House Sparrow and House Finch Carpodactus mexicanus, Kalinowski (1975) found that the two species co-existed successfully in urban, suburban and rural agricultural areas in New Mexico.

However, the House Sparrow was a superior competitor in urban areas. Competition also occurred mostly over nesting sites. The co-existence was achieved by habitat division along a rural suburban-urban gradient with the House Finch being restricted by the House Sparrow to more suburban and rural habitats.

Penry (1978) in Zambia found that in Kitwe the numbers of Grey-headed Sparrow in the early days of House Sparrow colonization were higher than those of House Sparrows, but as the numbers of House Sparrows multiplied over the years, Grey-headed Sparrow numbers gradually decreased.

Cordero (1993) in Spain studied the House Sparrow and Eurasian Tree Sparrow Passer montanus on farms. He observed that both the House Sparrow and Eurasian Tree Sparrow showed differences in habitat use. The House Sparrow was predominantly an urban and suburban species while the Eurasian Tree Sparrow was more rural. They were found to coexist along a suburban-rural gradient where there was extensive dietary overlap, and nest-site segregation was found to be due to interactive competition.

CHAPTER FIVE

5.0 SPARROW BREEDING

5.1 Introduction

The study on the breeding ecology of the two species aimed at determining whether they competed for nesting places, if their breeding seasons overlapped, and if there was exclusion of one species from the territory of the other. I also looked into whether there was direct competition for nestling food. I also wished to compare the breeding biology of the House Sparrow to studies done elsewhere.

5.2 METHODS

5.2.1 Breeding records

Extensive searches for Grey-headed Sparrow nests were undertaken in each month in the study areas. For the House Sparrows, the history of each nest at Chikunda farm was recorded on a card monthly. Nests where egg laying was expected were visited daily to record exact dates when the clutch was started. The breeding season was considered to extend from the date the first egg was laid to the latest date on which a nest of the year was occupied.

Whenever possible, breeding birds were mist-netted at their breeding place and ringed with both a numbered metal ring and coloured celluloid rings so that they could be identified easily during observations at the nest, and in subsequent breeding seasons. Data on the number of clutches raised per year could be determined. House Sparrows are known to use the same nest in further breeding attempts (Seel 1968a). If this is the case in Grey-headed Sparrows, nest site fidelity could be established when the birds are banded.

Where both species were breeding within the same habitat, I recorded the nesting site of each sparrow species to see whether birds used similar sites for nesting which would lead to competition. I noted whether the breeding seasons differed between the two species or whether there was any overlap, and also how successful breeding was.

Nest record data were obtained from the study area. For the House Sparrow most of the breeding data were collected at Chikunda Farm. Nest building was looked for in each month of the year and records of breeding activity recorded as state of the nest, whether being built or already built. Nest contents, whether there was a full clutch or in the process of laying. Eggs were numbered with indelible ink, weighed on a 10 g Pesola balance to the nearest 0.5 g within 24 hours. Eggs were also measured by vernier callipers to the nearest 0.1 mm. I inspected nests two to three times a week in the morning between 0800-1000 hours. Numbered eggs were later used to calculate the incubation

and fledging period, hatching and fledging success. From the tenth day onwards, the nests were inspected daily to ascertain day of hatching. Eggs which had failed to hatch were broken to examine the embryo and record whether failure to hatch was due to death of the embryo or infertility.

Incubation period was taken as the time between the laying and hatching of the last egg laid in each clutch (Seel 1968a). This was calculated from numbered eggs in which the last egg was identifiable. To determine the day of hatching, some clutches were inspected daily from the tenth day onwards until all the eggs hatched.

Fledging period was taken as the time between chick hatching and leaving the nest. Not all eggs hatched the same day. In some nests hatching took up to three days. Fledging period was calculated for all nests in 1989 and 1990 for the House Sparrow. For the Grey-headed Sparrow, fledging period was calculated for those nests which were accessible on fencing poles. These nests were discovered during the building period and egg laying was closely followed up to fledging time. Fledging success was calculated as a percentage of the number of chicks leaving the nest divided by the total number of chicks which hatched.

Breeding and nesting success were calculated following the formulae as described by Siegfried (1972). Nest success was calculated as the number of nests fledging at least one chick divided by the number of nests in which at least one egg was laid

multiplied by 100. Breeding success was calculated as a percent of the total number of chicks fledged divided by total number of eggs laid.

For Grey-headed Sparrows, each month I made surveys every week throughout Blantyre residential areas recording breeding activity and distribution of the birds. Breeding activity was monitored where the adults were calling continuously. Most nests of Grey-headed Sparrows were in inaccessible places. Data were collected on the state of nest whether in the laying, brooding or nestling period. Nests with chicks could easily be identified because the adults brought in food. Where possible, contents of the nests were recorded. Those nests in fencing pole holes, were examined by a torch to record nest contents.

I tried to follow activities in all accessible nests from the time when nest was discovered to fledging period. Visits were made two to three times a week. Additional nest records were obtained from the Avian Demography Unit (ADU) in Cape Town.

5.2.2 Parental care.

Adult activity at nests was observed through 10x40 binoculars by using focal animal observation: one single nest was picked and observation focused on this one for the length of the observation period. These nests had known numbers of chicks aged between one and 16 days. Observation time was 30-60 minutes continuously, and the following measures of parental care were determined (a) the rate of feeding visits and (b) the proportion of observation time adults were inside the nest (probably brooding the young). Visiting frequencies were divided into brood size and age. Data collected from nests of different ages for these categories were grouped together. The visiting frequencies represented a measure of the feeding activity of the adults although the quality and quantity of the food brought to the nest could not be known. The effect of parental feeding rates on nestlings depends on both food delivery rate and brood size and is therefore best measured by the rate at which food is being delivered to nestlings (Wittenberger 1982).

Where the number of broods was known, number of feeds per chick for specific ages was calculated. The total visiting frequency for both adults was recorded on the assumption that this represented a measure of the feeding activity of adults to their nestlings. As pointed out by Seel (1968a), the method suffers from the difficulty that it gives no guide to the quality of food brought to the nest at each visit. However close examination through binoculars revealed that food quantities

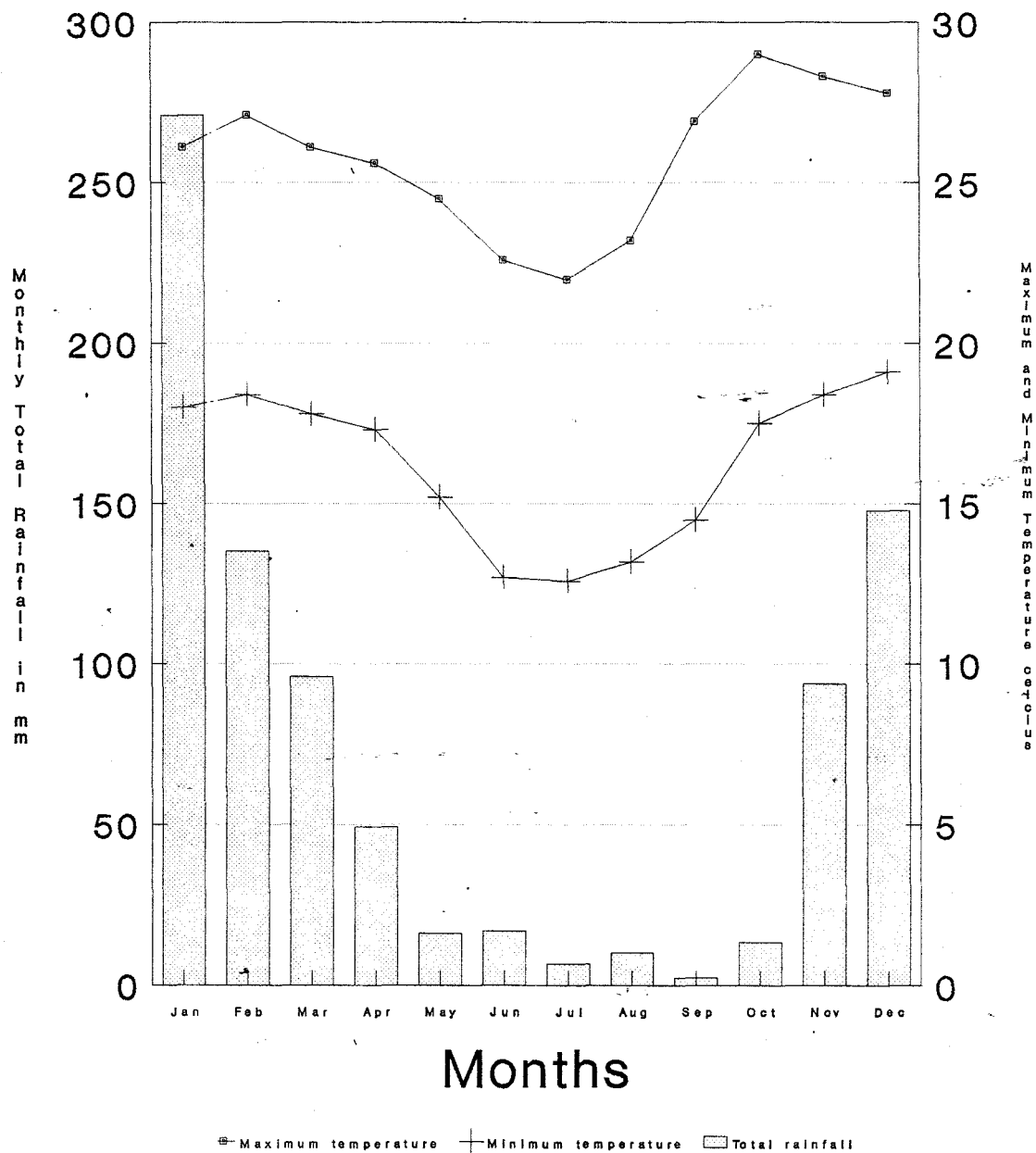
brought can be estimated roughly and correlated with the age of the chicks.

Adult House Sparrows are easily sexed because the males have a black patch on the throat. In the case of Grey-headed Sparrow, unringed adults were separated by behaviour as shown by their approach to the nest. Food items brought to the nest were crudely identified and recorded.

5.2.3 Climatic data.

Climatic data (temperature and rainfall) were taken from the nearest weather station at Chileka International Airport 15 km away from Blantyre City. As shown in Fig 5.1, the rainy season extended from about November to April and the dry season from May to October.

Fig 5.1
Mean climatic data as recorded at
Chileka International Airport 1989-1993



5.2.4 Moulting data.

Some House Sparrows breeding at Chikunda farm were caught and their moult recorded before they were released. Eight Grey-headed Sparrows shot in Mangochi were examined for moult. Additional material on moult on Grey-headed Sparrows was collected from museum skins from Transvaal, Durban, and Albany Museums in South Africa, and from ringing records in the Eastern Cape, South Africa, for both Grey-headed and House Sparrows. During this study, no Grey-headed Sparrows were collected due to lack of trapping material at the Museums of Malawi. Shooting in town was avoided in view of the situation that existed at the time, which was a transition period from one party rule to a multiparty system.

5.3 RESULTS

5.3.1 Breeding season of Grey-headed and House Sparrows.

The breeding season of Grey-headed and House Sparrows and climatic data are shown in Figs 5.2 and 5.3 respectively. Grey-headed Sparrows bred from January to May with peaks in February, March and May. January and April registered the lowest number of breeding records. From June to December there were no breeding records for 1993. The House Sparrow on the other hand bred throughout the year with a peak in May. There were fewest records in January, and none in February. The breeding season

of the Grey-headed Sparrow was restricted to the rainy season, whereas House Sparrows bred both in the rainy and dry seasons. Nest record cards from BirdLife South Africa at the University of Cape Town show breeding mainly from October to April with the following: numbers January 44, February 45, March 23 April 15 May 0, June 0, July 1, August 3, September 9, October 14, November 11 and December 19 in southern Africa.

5.3.2 Environmental factors and other factors affecting breeding.

For the Grey-headed Sparrow, breeding was restricted to the rainy season. This could be due to the availability of insect food, which is fed to the chicks. From my observations at Chikunda farm, breeding activity of the House Sparrow was also affected by food availability. Birds at the farm bred in chicken barns. Food available consisted of chicken feed and maize husks. After chicken rearing was abandoned, breeding attempts were infrequent. When chicken food was readily available in the barns, nesting activity intensified.

5.3.3 Moults

In the course of the breeding study at Chikunda farm, 66 adult House Sparrows were handled. Moults records are shown in Table 5.1. The breeding season at Chikunda farm for the House Sparrows extended throughout the year (Table 5.6). Records of moults at the farm for the months in which they were collected shows that some birds were in moults while others were not. In July to October the majority of the birds were not moulting while in January the majority were in moults. House Sparrows from southern Africa show a similar trend. The data though not adequate may point to the fact that House Sparrows may breed throughout the year but may moults in particular months when breeding is less frequent.

Moults data from museum skins of Grey-Headed Sparrows have been grouped into three geographical areas; East Africa (Tanzania and Kenya), Central Africa (Malawi, Zambia and Zimbabwe) and Southern Africa (Namibia, Botswana, and South Africa (Table 5.1). In southern Africa most birds were in moults from April to September, although wing moults was recorded in all months of the year. In Central Africa, moulting was most frequent from June to September. All birds except one in September were in moults. In central and southern Africa, the breeding season extends over a similar period from about October to April/May of the following year. In east Africa, moults was recorded at the beginning of the year from January to June. All birds during this time were in moults. Breeding in east Africa may start a little earlier from

about July to December.

In both southern Africa and central Africa, moult in the grey-headed sparrows is less frequent in the breeding months, and there is no evidence of moult breeding overlap in individual birds. From the available data, it seems the moult season of the grey-headed sparrows is different from the House Sparrow. The House Sparrow recorded higher percentage of moult in January (southern African birds) when that of grey-headed sparrows were lesser (Table 5.1)

Fig 5.2
Breeding season of Grey-headed Sparrow
in 1993 and climatic data

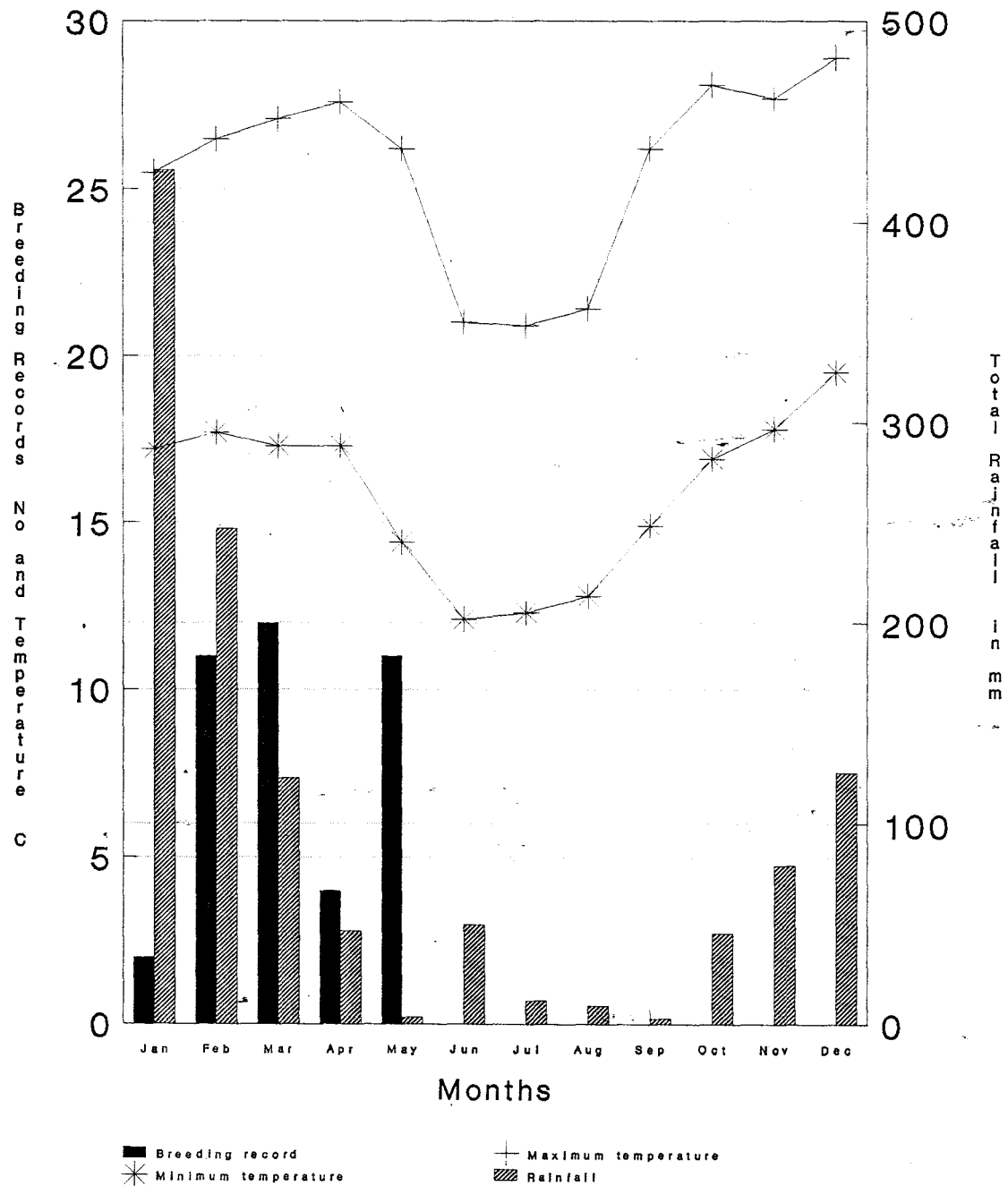


Table 5.1 Monthly distribution of wing moult in grey-headed sparrows

from southern, eastern and central Africa, and in House Sparrows at Chikunda farm in Blantyre and House Sparrows from South Africa.

		MUSEUM SKINS											
		Months											
Region		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Southern	Total number	66	31	17	7	27	53	32	40	32	11	11	32
	% moulting	37.9	51.6	29.4	57.1	59.3	47.2	59.4	27.5	81.3	27.3	18.2	21.9
Central	Total number	7	1	1	5	3	13	25	1	25	1	0	0
	% moulting	71.4	0	100	20	100	100	92	100	92	100	0	0
Eastern	Total number	7	3	7	0	4	2	4	0	0	1	0	0
	% moulting	100	100	100	0	100	100	100	0	0	100	0	0

HOUSE SPARROWS SOUTHERN AFRICA													
Number	42	5	9	0	0	0	0	7	2	0	1	1	2
% moulting	97.6	80	100	0	0	0	0	0	50	0	0	100	50

HOUSE SPARROWS THIS STUDY (Malawi)													
Number	14	10	0	0	0	0	10	12	9	10	0	0	0
% moulting	64.2	10	0	0	0	0	20	0	0	10	0	0	0

Fig 5.3
Breeding season of House Sparrow
in 1989/1990 and climatic variables

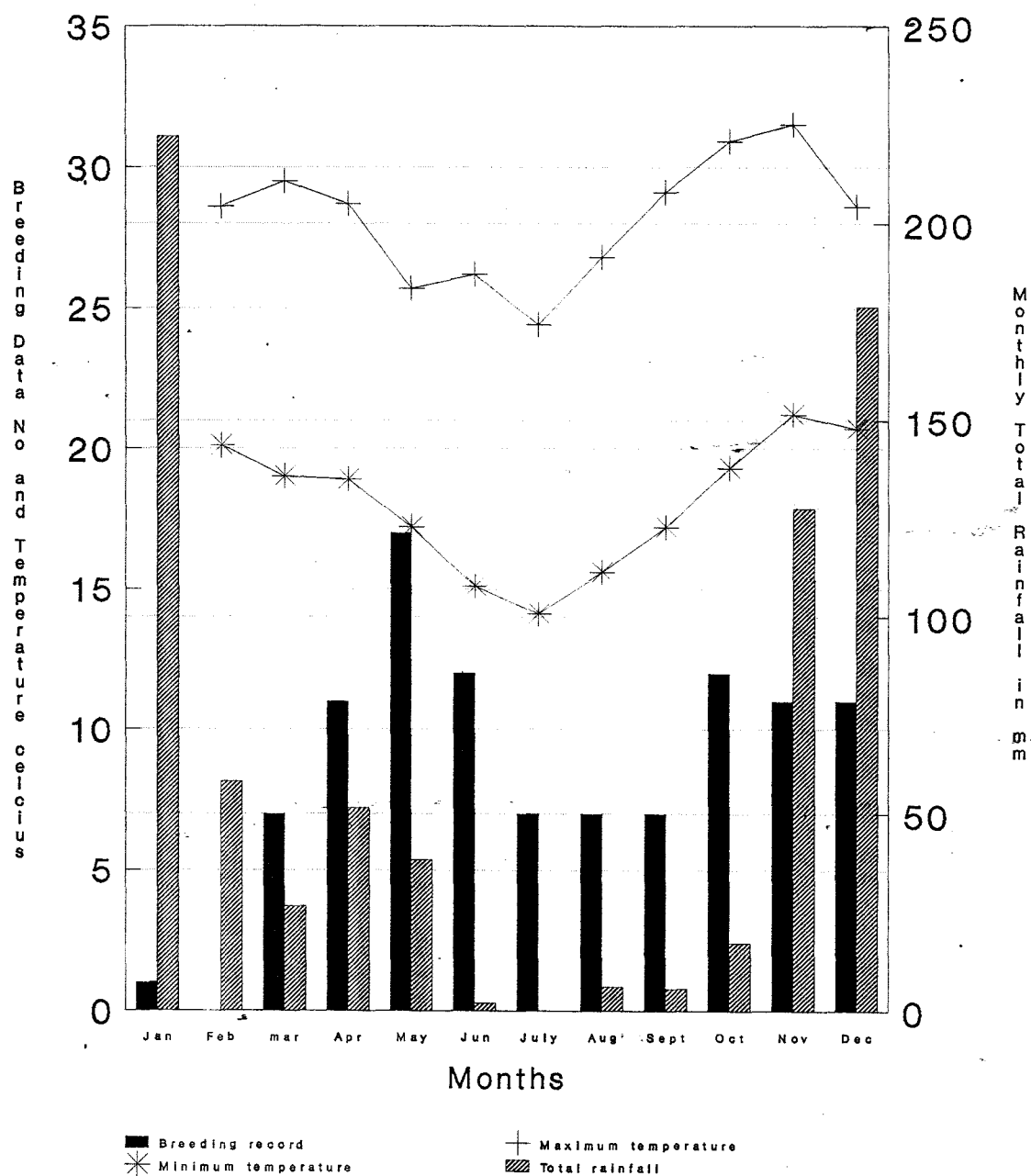


Table 5.2 Nest site selection of Grey-headed
and House Sparrows.

Nest site	Sparrow Numbers observed		
	Northern		Southern
	Grey-headed (Blantyre)	House (Blantyre)	Grey-headed (Southern Africa)
Wooden electricity			
poles	9	0	-
Crevice in house walls	20	25	51
Fencing poles	11	6	10
House rafters	-	167	-
Nest box	-	-	5
Tree hole	-	-	37
Bamboo fence	-	-	2
Hollow bridge	-	-	1
Swallow nest	-	-	7



Plate 5.1 & 5.2 Wooden electricity poles and
fencing poles respectively



Plate 5.3 & 5.4 House wall crevices and
rafters respectively.

Table 5.3 Nest heights of Grey-headed and House Sparrows

Nest height (meters)	Numbers		
	Northern Grey-headed (Blantyre)	House Sparrows (Blantyre)	Southern Grey-headed (Southern Africa)
1-2	9	6	37
3-5	27	192	43
6-8	4	0	6
> 8	0	0	5

5.3.4 Clutch size.

The average clutch size of the House Sparrow at Chikunda farm was 3.8 ± 0.1 in 1989 ($n = 81$, mode 4, range 2-6) and 4.0 ± 0.1 in 1990 ($n = 73$, mode= 4, range= 2-7) respectively. The modal clutch size for both years was four eggs. When data for the two years were combined, the average clutch size is 3.9 ± 0.1 ($n = 154$). Clutch sizes of two and six eggs were very rare. For those birds which had repeat clutches, the number of eggs remained more or less the same. Variation between clutches if any was ± 1 egg. In one nest a pair had six broods of which four had a clutch of five eggs, and two a clutch of four eggs. The clutch sizes during the breeding season ranged from two to seven eggs. The mean clutch size was not significantly different between the two years ($t = 0.07$, $P = 0.88$, two sample analysis test) Table 5.4.

The Grey-headed Sparrow nests were in sites which were inaccessible in most cases. The few nests which were accessible had a clutch size of three eggs ($n = 5$), or four eggs ($n = 3$). These nests were in fencing poles which could easily be examined by a torch. Measurement of eggs however was not possible. The average clutch size of this sample was 3.4 ± 0.2 ($n = 8$). Data from nest records cards in the Avian Demographic Unit at the University of Cape Town had an average clutch size of 3.3 with a clutch of three as most common.

Table 5.4 Frequency of different clutch sizes of House and Grey-headed Sparrows

House Sparrow

clutch size	2	3	4	5	6	7	Total No of clutches	Mean
Numbers observed in 1989	6	15	49	9	2	0	81	3.8 ± 0.1
Percentage of clutches	7.4	18.5	60.5	11.1	2.5	0		
Numbers observed in 1990	4	16	31	19	1	2	73	
Percentage of clutches	5.5	21.9	42.5	26.0	1.4	2.7		4.0 ± 0.1
combined for 1989/1990	10	31	80	28	3	2	154	3.9 ± 0.1

Grey-headed Sparrow

	12	31	23	6	0	0	72	3.3
Percent of clutches	17	43	32	8				

The mean clutch sizes of the House Sparrow combined for 1989 and 1990 at Chikunda farm are shown in table 5.6. Clutch sizes of the House Sparrow were on average larger from January to May with the exception of March, and also larger from November to December. They were smaller from June to October.

5.3.5 Incubation and fledging period

5.3.5.1 House Sparrows.

Data on incubation and fledging periods are presented in table 5. 5. The differences between the two years on the incubation and fledging periods is not pronounced. Other breeding variables indicated in Table 5.5 are the breeding, fledging, nesting and hatching success. Except for the fledging success in 1990, the breeding, nesting, and hatching success were higher in 1989 than 1990. The Chi-square test shows that the results were significantly different (Chi-square = 29.08, $P < 0.001$) One reason why fledging success was low in 1989 was predation of nestlings by farm labourers. In 1990, all the farm labourers had stopped vandalizing the nests.

In 1989, 267 eggs were laid during the breeding period, 197 eggs hatched and 136 chicks fledged. In 1990, 242 eggs were laid during the breeding season, 131 eggs hatched and 100 chicks fledged. In 1989 and 1990, there were 83 and 84 nests respectively with at least one egg. the number of nests fledging at least one chick were 49 and 47 respectively.

Table 5.5 Breeding data for the House Sparrow at
Chikunda farm.

		YEAR	
		1989	1990
Incubation period	(days)	11.6 (29)	11.5 (39)
Fledging period	(days)	15.7 (40)	11.0 (49)
Breeding success	%	50.9	41.3
Fledging success	%	69.0	76.3
Nesting success	%	59.0	56.0
Hatching success	%	69.0	54.0

5.3.5.2 Grey-headed Sparrows.

All the nests of the Grey-headed Sparrows were found with eggs already laid. It was therefore difficult to calculate the incubation period. The fledging period for the four nests whose hatching day was known, are 13, 14, 15 and 17 days. This gives an average of 14.7 ± 0.7 (n=4) days.

Table 5.6 Mean clutch size of House Sparrows per
month at Chikunda farm combined for 1989 and 1990 years

Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec
Mean clutch size	4.2	4.0	3.8	4.1	4.4	4.0	3.6	3.6	3.7	3.7	4.1	4.2
Nos Observed	9	5	15	21	17	16	16	9	10	19	16	6

5.3.6 Chick mortality

Table 5.7 gives the causes of chick mortality. Mortality was not significantly different between the two years ($t = -0.16$, $P = 0.88$ Two sample test analysis) Table 5.8 gives the ages at which chicks died. Slightly more chicks died between day one to day three and also between day four and day six in both years.

The causes of chick mortality at Chikunda Farm were identified as :

- (a) Starvation due to age differences. The younger chick(s) were unable to compete for food with the older chicks. This was common in November when food at the farm was scarce.
- (b) Chicks abandoned by parents. One reason why chicks were abandoned was territorial harassment when the nests were very close to each other. In November 1989 most of the nests had only one chick. This was evidently due to lack of food at the farm, which led to some adults abandoning their chicks.
- (c) Predation by farm labourers.
- (d) Weight at birth; chicks which weighed less than 2 g at birth did not survive more than two days after hatching.
- (e) Falling out of the nest.
- (f) Rain soaked chicks.
- (g) Strangling in nest material.

(h) Infestation by blood fly larvae. These parasites were commonly seen in nests which were used more than once. Heavily infested chicks lost a lot of blood, looked pale and had open wounds on their skins.

5.3.7 Egg measurements

5.3.7.1 House Sparrows

House Sparrow eggs at Chikunda farm in 1989 measured $20.4 \pm 0.1 \times 14.7 \pm 0.1$ mm ($n = 215$). The modal length was 21 mm and ranged from 17.0-25.0 mm while the modal width was 15.0 mm and ranged from 12-18 mm. The average weight of eggs was 2.3 ± 0.4 g ($n = 164$) and ranged from 1.5-3.0 g. The modal weight was 2.5 g and ranged from 1.5-4 g. Maclean (1985) recorded that in southern Africa, the eggs measured 21.5×15.2 mm ($n = 68$) and ranged from 19-24 x 13.6-19.7 mm.

5.3.7.2 Grey-headed Sparrows

It was difficult to get access to Grey-headed Sparrow nests and get egg measurements. One nest in Karonga on a house wall crevice which was abandoned had four eggs which measured 21×15.5 mm (x 2 eggs) and 21.5×14.5 mm (x 2 eggs). Belcher (1930) gave an average egg measurement of 22×16 mm for Malawi. Maclean (1985) recorded that in southern Africa, the eggs

measured 19.2 x 14.3 mm (n = 103) and ranged from 17-21.3 x 13.1-15.2mm.

Table 5.7 Probable causes of chick
mortality in 1989 and 1990.

<u>Cause of death</u>	Number of cases	
	1989	1990
Flooding	0	2
Abandoned by adults	2	4
Falling out of nest	0	2
Strangled in nest		
material	0	1
Starvation	5	1
Weight at birth		
less than 2g	3	1
Ecto parasites	2	0
Predation	2	4
<hr/>		
TOTAL	14	15
<hr/>		

Table 5.8 Age (in days) at which death
occurred

Number of chicks		
Age	1989	1990
1-3	3	8
4-6	1	8
7-9	1	2
10-12	1	1
<hr/>		
TOTAL	6	19
<hr/>		

5.3.8 Hatching period

5.3.8.1 House Sparrows

In one nest, hatching was witnessed early in the morning at 0913 hours. At this time the chick had broken the shell and half the body was out. The colour of the chick was deep red or reddish with a white gape. The chick started yawning or gaping for food ten minutes later. The weight of the chick at birth was 2.5 g. Two more eggs hatched during the day, and the fourth egg hatched the following day by 1000 hours. Hatching of all eggs took place within 24 hours.

5.3.9 Causes of hatching failure.

The causes of egg failure to hatch and the numbers which were observed in 1989 and 1990 are shown in Table 5.9. In 1989 more eggs were abandoned compared to 1990, and more eggs were taken by predators in 1990 than in 1989. Predation was blamed on mice which were seen around the chicken barns. There was no significant difference in failure to hatch between the two years ($t = 0.14$, $P = 0.89$ Wilcoxon two sample analysis test).

Table 5.9 Causes of House Sparrow eggs
failing to hatch.

	Number of cases	
	1989	1990
Infertility	5	5
Abandonment	7	5
Predation	3	6
Dead embryo	2	0
<hr/>		
TOTAL	17	16
<hr/>		

5.3.10 Nestling food

Both Grey-headed and House Sparrow chicks were fed exclusively on insect food. Initially (days 1-9) the nestlings were fed on tiny insects carried in billfuls. As the chicks grew older, one food item was fed to them at a time. Some food items were as long as 76 mm and as thick as 3 mm. This food consisted mostly of grasshoppers. Some insect food was as large as the length of the bill. The food items which were identifiable included grasshoppers, insect larvae, wasps and butterflies.

Between nine and 20 days, the chicks were fed single food items. Begging sounds commonly attracted the parents to feed them. In both species, adults collected faecal sacs soon after a feed. Faecal sacs were dropped as far as 10-15 m from the nest.

5.3.11 Chick and adult dispersal at a breeding site (House Sparrows).

A total of 32 adult House Sparrows and 89 chicks was ringed at Chikunda farm. Table 5.10 gives data on recapture of adults and chicks which had been ringed. The results show that both adults and fledged young stayed at the site of ringing/breeding. Chick No BC 07233 stayed at the site of ringing for 19 months when it was last recaptured for the fifth time. Adult bird No BC 07231 was recaptured 18 months after ringing. These few

results suggest that dispersal by both adults and young from the Chikunda farm breeding site was limited. This also showed that some adult House Sparrows stayed at their breeding site for more than one breeding season.

One explanation for the lack of dispersal of the House Sparrow at Chikunda farm was availability of food. Chikunda farm had plenty of chicken feed in the barns which was available to the House Sparrows. Food availability also affected nest site selection. Most of the birds built their nests at the chicken barns. In 1991, the management discontinued chicken farming, and the number of breeding birds declined. Even before this the effect of food was apparent. Of the two chicken barns, one was used for rearing sheep. Food in this barn was less abundant, and it held fewer breeding birds.

Table 5.10 House Sparrows ringed and recaptured at
Chikunda farm.

Bird No	Date of ringing	Last recapture	Interval (months)
BC 07205*	28/04/89	9/01/90	8.4
BC 07233*	15/08/89	05/03/91	18.6
BC 07229	29/01/90	31/01/91	12.1
BC 07206*	28/04/89	11/06/90	13.5
BC 10241	05/07/90	28/02/92	19.8
BC 07217	28/04/89	04/07/90	13.2
BC 07229	15/08/89	04/07/90	10.6
BC 10254	25/06/90	28/01/92	17.1
BC 07231	05/08/89	29/01/91	17.8
BC 07261	06/09/89	30/01/91	16.8
BC 10283	04/02/91	28/02/92	12.8

* Ringed at the nest as chicks.

5.3.12 Feeding of nestlings

5.3.12.1 Grey-headed Sparrows

Feeding visits to Grey-headed Sparrow chicks were observed at one nest. Observations were made in the morning and afternoon on two five to six day old chicks. The results (Table 5.11) showed that the chicks were fed at the rate of 7.75 feeds/hour/chick in the morning and eight feeds/hour/chick in the afternoon. There was no significant difference in the food provided by male and female to the chicks (Chi-square = 0.01, $P = 0.99$). General observation also indicated that adults visited the nest at intervals of one to 20 minutes. When prey items were abundant at the collecting sites, the adults visited the nest within a minute of each other. Not all visits by adults resulted in a feed.

5.3.12.2 House Sparrows

Feeding visits per 30 minute observation period of House Sparrow adults to nestlings of different age groups showed that the female contributed more to feeding chicks (Table 5.12). The female feeding rates to chicks of different age groups is significantly higher than male feeding rates (Chi-square = 22.88, $P < 0.001$). The male fed the chicks much more often from 1 - 3.5 days onwards, the male left the feeding mostly to the female. During this time he was often engaged in guarding the

nest.

In the Grey-headed Sparrow, there was very little difference in the feeding visits of both adults at the three nests which were observed in detail. At these nests one adult was ringed and therefore they could be separated. The House Sparrow is sexually dimorphic, so the parents could be distinguished easily.

During the early days of the chicks, the female brooded the young. Brooding periods in one nest extended from 10-20 min. for chicks aged between 1.5-2.5 days. When the female was brooding and the male came to feed the chicks, she came out to give way to the male. As soon as the male had fed the chicks, the female went back to brood or flew away to fetch food.

When the adults brought in food, they did not fly directly to the nest. They stopped a short distance away and then flew to the nest entrance, stopped for a short time and then entered the nest. The average time (seconds) taken feeding the chicks by the female ranged from two to 30 seconds with an average of 14.1 ± 0.8 ($n = 21$) seconds. Longer periods spent inside the nest indicated brooding of the young.

Food was collected as near as a meter away from the nest and as far as 100 m. The frequency of food collection depended on the foraging site. At a nest with three chicks aged 13.5 - 14.5 days the female fed eight times in 30 minutes, the average time between feeds was 4.1 ± 0.9 ($n = 7$). In another nest of four

chicks aged between 10.5 - 11.5 days, the chicks were fed 11 times by the female within 30 minutes and the average time between feeds was 2.5 ± 0.35 (n = 10).

Table 5.11 Feeding visits of Grey-headed Sparrows
at one nest with two 5-6 day old chicks

Sex	Feeds		Total
	Morning 0840-1030	Afternoon 1430-1505	
Female	17	14	31
Male	18	14	32
<hr/>			
TOTAL	35	28	63
<hr/>			

Table 5.12 Hourly feeding visits of House Sparrows
to broods of different ages.

Age (days)	No observations	Female	Males
0.5 - 3.5	11	3.3 ± 0.6	2.6 ± 0.9
0.5 - 7.5	18	3.9 ± 0.8	0.8 ± 0.4
8.5 - 11.5	9	3.2 ± 0.4	0.7 ± 0.2
12.5-15.5	10	3.1 ± 0.1	0.1 ± 0.1

5.3.13 Breeding behaviour

5.3.13.1 Grey-headed Sparrow

Grey-headed Sparrows were easy to locate during the breeding season (nesting, laying or brooding period). During this time, the male was usually perched on a vantage post and called persistently. A careful search of the area revealed where the birds nested. After the eggs hatched, calling within the nest area was much diminished. This behaviour could be adaptive in not advertising the nest site to predators.

5.3.14 Nest defence (House and Grey-headed Sparrows).

Nest defence was mostly carried out by the male House Sparrow. This took place during nest building through to fledging of the chicks. Female nest defence was usually directed at other females. The male when nest guarding called continuously near the nest. Nest defence was triggered when another bird, either female or male, came near the nest. At this time all the males flew to their nests with a characteristic call and wing vibration display. Nest guarding occurred when the female was incubating and when she was away foraging.

Female nest defence was prominent when a nest of another female was nearby. In one instance at Chikunda farm in the chicken barns, a nest with four chicks was less than 1 m away from a nest which had two eggs. The females at these nests vigorously defended their nests whenever the female engaged in feeding flew to its nest. They both called "che-che-che-che" rapidly. Each visit by the female feeding chicks elicited this response from the other female whose clutch was still incomplete.

Grey-headed Sparrows are not social nesters. As a result of this, there was no nest defence. The only time nest defence was observed was during the prospecting period, and this was directed at House Sparrows. Here the Grey-headed and House Sparrows were competing for a possible nesting place. The House Sparrows were the aggressors on all four occasions.

5.4 DISCUSSION

The breeding season of the House Sparrows extended throughout the year, while the Grey-headed Sparrows nested only during the rainy season, January to May. Irwin (1981) in Zimbabwe and Maclean (1985) in South Africa both recorded the House Sparrow breeding throughout the year. In South Africa, Maclean (1985) also mentions that for the Grey-headed Sparrow, breeding is mainly from September to December.

Summers-Smith (1988) pointed out that with a wide distribution from the tropics to the Arctic circle in the north, and south to the limits of the land masses in the southern hemisphere, there is a great variation in the breeding season of the House Sparrows. He noted that breeding probably correlates with the availability of sufficient invertebrate food to enable the female to build up the necessary protein for egg formation. Seel (1968b) in England in a study of the breeding season of the House Sparrow found that it extended from April to July or early August, Murphy (1978) in Canada recorded a breeding season which also extended from April to July (four months) and Veiga (1990) in Spain recorded April as the start of the breeding season.

In the temperate region, the breeding season does not extend throughout the year, as it did in Zambia (Anon. 1986a). My results in Malawi which is in the tropics show that the House Sparrow bred throughout the year. Murphy (1978) pointed out that several studies in the temperate regions have suggested that both

photoperiod and temperature are proximate factors which cue or control breeding phenology.

In temperate climates most of the arguments are centred on clutch size adjustment being responsive to the environment - birds breed when the conditions are optimal for the young in the nest and out of the nest in order for them to find enough food (Seel 1968b). In the tropics this may not apply. Seasons are clearly dry and wet seasons. The House Sparrow in Blantyre bred throughout the year, and was therefore not responsive to changes in the weather. Food may not affect it as much as in the temperate region. Within house compounds, food was readily available throughout the year to enable it to breed uninterruptedly. In Brazil, though also tropical, Summers-Smith (1988) reported that House Sparrows bred in the dry season from March to October, which is six months as compared to only four in the temperate region.

There is considerable annual variation in breeding of the House Sparrow. Summers-Smith (1988) reported that in some cases, breeding can abruptly stop due to adverse conditions like heavy rainfall, and dry spells. He also pointed out that in some cases there had been reports of breeding taking place throughout the year, but that generally in the temperate region the breeding season extended for 120 days (four months).

The Grey-headed Sparrow unlike the House Sparrow is a seasonal breeder which bred from January to May. Brown & Britton (1980) in East Africa, Irwin (1981) in Zimbabwe, Anon. (1986b) in Zambia and Craig (in press) all give the rainy season as the breeding season of the Grey-headed Sparrow. The actual months of breeding may differ slightly. Craig (in press) gives October to May in South Africa while Anon. (1986b) in Zambia records January to April as the main breeding season although there were some single records in other months and Irwin (1981) in Zimbabwe reported breeding from September to April. The Grey-headed Sparrow may be responding to food as a proximate and ultimate factor for breeding. During the rainy season insect food is abundant.

The few House Sparrows examined for moult in this study (Table 5.1) had active wing moult or worn plumage. In England the House Sparrow moults from late June to early November with a peak during July to mid-October (Summers-Smith 1963). Seel (1968b) reported that the House Sparrow lays eggs from beginning of April to late July or early August. Thus in the temperate region moult does not overlap with breeding, but takes place after breeding and lasts for about 83 days (Craig 1983). In India, Mathew & Naik (1985) found that the moult of the House Sparrow overlapped with nesting and was interrupted from time to time. They suggested that this overlap indicates that the initiation of moult is controlled by a mechanism independent of the breeding schedule.

It is generally accepted that most birds moult when they have stopped breeding or that the two processes are mutually exclusive (Payne 1972). Craig (1983) however argues that this may be true of birds in temperate climates but in southern Africa or in general in non-temperate zones it may not be the case. Moulting-breeding overlap has been reported in several African species (Payne 1969). Craig (1983) suggests that the timing of moult relative to breeding may vary regionally and that more information is needed for most Afrotropical species.

All eight Grey-headed Sparrows collected from Mangochi in September had some of their primary feathers in moult. Moult in the Grey-headed Sparrow at this time indicates that the birds start shedding their feathers after the breeding season. Craig (1983) reported that Grey-headed Sparrows have a complete moult after breeding.

Barrentine (1980) observed that House Sparrows which nested in trees in Canada, were able to tolerate other pairs within very short distances. He attributed tolerance in the spruce trees to the foliage. He pointed out that House Sparrow pairs could persist in building a nest next to other House Sparrow nests. This in the end led them to establish themselves. This behaviour he argues is typical of House Sparrows which can displace species from nests by constant harassment and then use the sites themselves. Such behaviour was observed in Blantyre during this study, between the Grey-headed and the House Sparrows. On all the four occasions it happened, the Grey-headed Sparrows ended

being the losers and abandoned the nest site.

Summers-Smith (1988) reports that a wide variety of nest sites is used by House Sparrows: holes, crevices in man made structures, or in trees, in cliffs and earth banks, under roofs, and free-standing nests built among the branches of trees or the tops of telegraph poles.

The clutch sizes of the House Sparrow in this study varied between the years. The modal clutch for both years was four eggs and the clutches ranged from two to seven eggs. For the combined data for 1989 and 1990, the average clutch size was 3.9 eggs. The mean clutch size for the Grey-headed Sparrows was 3.4 eggs. Maclean (1985) in South Africa reported that the clutch size for the Grey-headed Sparrow was usually three to four eggs. Anon. (1986b) in Zambia found an average clutch size of 3.9 eggs for the House Sparrow.

Seel (1968a) at Oxford in England found an average clutch size of 3.9 eggs for the House Sparrow. When he separated the results into early-laying birds and late-laying birds, he found average clutch sizes of 4.1 and 3.9 respectively. Veiga (1990) in Spain found a larger average clutch size of 4.9 eggs. He also found that the clutch sizes did not vary significantly seasonally for the House Sparrow. The average clutch size for the House Sparrow at Chikunda Farm in Malawi is similar to those in England (Seel 1968a) and in Zambia Anon (1986a).

Summers-Smith (1988) reports that clutch size for the House Sparrow normally ranges from two to five eggs. The modal clutch is usually four eggs in the UK, continental Europe and north America.

The clutch size varied throughout the season at Chikunda Farm. The clutches were larger from January to April and from October to December, smaller in the middle of the year. Lack (1947) proposed that clutch size in altricial species of birds is adjusted evolutionarily to produce the maximum number of surviving young. He further proposed that food is the limiting factor. He concluded that the clutch size of a species in a particular locality is therefore adapted to reflect the average food supply available for feeding the young in that locality. Cody (1966) suggested predation and competitive ability as factors which operate in the tropics. In the temperate region however he concluded that food is probably of overriding importance in determining the number of young that can be raised.

Murphy (1978) found seasonal changes in the clutch size of the House Sparrow at Calgary and Lawrence in Canada. He suggested that seasonal variation in clutch size was responsive to food supply but cautioned that this is true only when insects are scarce or moderately abundant. Anderson (1977) found no response of House Sparrows to food abundance during an emergent year of periodical cicadas, Magicicada spp over that in non-emergent years, and concluded that clutch size is not responsive to temporary changes in the food supply.

Other Passer species have average clutches similar to the House and Grey-headed Sparrows. Siegfried (1972) in South Africa found an average clutch size of 3.7 eggs for the Cape Sparrow Passer melanurus. Veiga (1990) in Spain found a clutch size of 4.7 eggs for the Tree Sparrow and Seel (1968a) found an average clutch size of 5.1 eggs for the Tree Sparrow at Oxford in England, slightly higher than that found in Spain.

Seel (1969) at Oxford in Britain found that the feeding rates of House Sparrows increased with age. The same was found by McGillivray (1981) in Canada. My results however indicated that the feeding rates were highest in the age group 4.5 - 7.5 days. The age group 12.5 - 15.5 days showed the lowest number of feeding visits, which differed from the observations of Seel (1969) in Britain.

At Chikunda farm I found that the male House Sparrow contributed less than the female to feeding the young. The male contributed mostly to the age group 0.5 - 4.5 days. The female contributed more less equally to all age groups. Similar observations were made by Seel (1969) in Britain and McGillivray (1981) in Canada. They found that the contribution of the male declined as the chicks grew older. In other species like the Field Sparrow Spizella pusilus which is a seed eater, Best (1977) found that the sexes shared the duties equally.

The incubation period for the House Sparrow at Chikunda farm was 11 days and the fledging period was 15 days. The incubation

period for the Grey-headed Sparrow could not be assessed because nests were already found with eggs. The fledging period was 14.7 days, ranging from 13-17 days. The results for the fledging period are similar for the two species. Maclean (1985) in South Africa reported an incubation period of 12-14 days for the Grey-headed Sparrows and a fledging period of 15 days. His records are similar to my findings at Chikunda farm.

Seel (1968a) found the incubation period for the House Sparrow at Oxford to be 11.5 days and the fledging period 14 days.

Murphy (1978) in Canada found the fledging period of the House Sparrow to be 14 days and the incubation period 10.7 days. Anon. (1986a) in Zambia reported an incubation period of 11-12 days and fledging period of 15-18 days for the House Sparrow. There is apparently not much variation in both the incubation and fledging periods of the House Sparrow in the temperate region and the tropics. Anon. (1986b) gave the incubation period of the Grey-headed Sparrow as 16 days and a fledging period of 19 days.

My results for the fledging period are similar to those found in Zambia. Data are lacking in the literature for the Grey-headed Sparrows, and as a result it is very difficult to make a comprehensive comparison.

In both species the adult male did a lot of surveillance during the incubation period. The males sang to advertise their territory and deter any possible competitors. Singing was much more conspicuous in the Grey-headed Sparrows during incubation, and decreased during the nestling period. In the House Sparrows,

the male continued singing near the nest. Pomeroy (1993) in a review of song in the lives of three common birds in Uganda, found that peak levels of song by males correspond with the fertile period of their mates.

Factors which reduce nesting competition are discussed below.

1. Nest site selection.

Nest site selection for both sparrows is shown in Table 5.2. Both sparrows used house wall crevices and fencing poles. However the Grey-headed Sparrows exclusively used wooden electricity poles and House Sparrows house rafters (see plates 5.1-5.4). Even though there is an overlap in use of nesting sites, competition for breeding was reduced because of segregation in the breeding areas. Grey-headed Sparrows preferred areas where human activity was less, such as low house density areas, and industrial areas where vegetation was more abundant. On the other hand the House Sparrows preferred areas where house density was high and refuse more abundant. These areas were in the townships and mid-density areas.

2. Nest height

Nest height also differed between the two sparrows. From Table 5.3 the commonest nest height for both sparrows was 3-5 m. This was on buildings. Segregation in the distribution of preferred areas allowed for reduction in the competition because

the heights may be the same but the areas were different from each other. Nesting heights of 6 - 8 m were exclusively used by Grey-headed Sparrows. This was on wooden electricity poles. The selection of nesting height depended on the nesting substrate. The House Sparrow nest height was restricted to 3 - 5 m because the house walls in the high density and mid-density areas were within this range. The nesting heights of Grey-headed and House Sparrows was significantly different overall (Chi-square = 42.96, $P < 0.001$)

3. Food of nestlings.

Although both species fed their young on insects, there was no evident competition for food. Food was collected in the case of Grey-headed Sparrows both far from and near to nesting sites. Since breeding was in segregated areas, competition for food was reduced. At Chikunda farm, where both sparrows were present, their feeding sites differed. Grey-headed Sparrows fed mostly at the periphery of the farm, roadside and fallow areas. The House Sparrows fed within house compounds and areas where there was refuse. At one time in 1990, at Chikunda farm, one Grey-headed Sparrow nested in a house wall crevice. During chick feeding, the parents collected food on the fallow areas and roadsides. They did not compete with the House Sparrows.

What is not clear however is why the Grey-headed Sparrows are restricted to areas of low house density and high tree

density. One explanation is that as birds of savannah, this is their preferred habitat. This was also evident in Lilongwe where they were plentiful in wooded areas like the Capital Hill and new City centre. In all other parts of the country, they preferred areas where there were tall trees.

In areas of the north and centre of the country where House Sparrows were less common than in the southern region, the Grey-headed Sparrows were plentiful in the inner town of Chitipa, Karonga, Nkhata Bay and Mzimba. This could provide indirect evidence that competition was a factor because House Sparrows were uncommon or absent. In Rumphi for instance, both sparrows bred in some cases on the same building with no harassment of each other. Numbers of House Sparrows could be the determining factor which affected the distribution of Grey-headed Sparrows in areas where the House Sparrows outnumber Grey-headed Sparrows. This is what was observed in Blantyre City and could apply to all areas of southern Malawi. The Grey-headed Sparrows for instance could not breed in the high house density areas because even if they found suitable areas, they would meet stiff competition from the House Sparrows. Grey-headed Sparrows have selected breeding sites on artificial objects like on top of Escom poles, and metal fencing poles (Table 5.2).

The Grey-headed Sparrows are timid birds compared to the House Sparrows. The House Sparrows are agile and very adaptable; when feeding within house compounds they are not bothered by human activity around them. They fed quickly and flew over to

the nearest hedges and trees if disturbed. The Grey-headed Sparrows on the other hand are shy birds which preferred to feed quietly. They do not tolerate the presence of human beings very close to them. The only places where they seemed to have adapted themselves to human activity were at the Capital Hill in Lilongwe, Mzimba at the secondary school and in Karonga. In these areas they have been in touch with people for a very long time.

In Blantyre, the House Sparrows may not necessarily exclude the Grey-headed Sparrows because of their larger numbers but food also determines their distribution. In the low house density areas, food is not as plentiful as in the high density areas. As such the birds will continue to inhabit these segregated areas of the City. It has to be seen however whether in the central and northern regions the situation which exists in Blantyre will repeat itself in future when the human population increases, more especially in the cities of Mzuzu and Lilongwe.

During this study, I observed only four cases of nest aggression between the two sparrows. Once in Mzuzu in the north, and then in Lilongwe, Kasungu and Blantyre. In each case the aggressor was a male House Sparrow.

CHAPTER SIX

6.0 FEEDING BIOLOGY

6.1 Introduction

Mackworth-Praed & Grant (1960) indicated that the Grey-headed Sparrow occurred in both bush country and in all forms of cultivation and did some damage to crops at times. However there was no mention of the type of crops which they fed on. Understandably they could have been referring to cereal crops. They also indicated that Grey-headed Sparrows were almost omnivorous and fed their young on insects and termites when available. No mention was made of the food of House Sparrows.

Benson & Benson (1977), McLachlan & Liversidge (1978) and Maclean (1985) all mentioned that the Grey-headed Sparrow feeds on seeds and insects. Maclean (1985) also provided information on the food of the House Sparrow. He stated that it fed on a variety of food, including seeds, soft buds, fruits, insects (adults and larvae) and spiders.

Summers-Smith (1988) mentioned that the House Sparrow is primarily a seed eater, specializing on the seeds of man's cultivated grain crops such as oats, wheat, barley, corn, sorghum, maize, millet and rice. He also pointed out that the House Sparrow fed on seeds of annual herbs such as Graminae and those House Sparrows living in inhabited areas supplemented

their diet with household scraps and a variety of other foodstuffs. The aim of this chapter is to document whether the two sparrows competed over food if they were found feeding in the same habitat and how they avoided competition.

6.2 Methods

6.2.1 Feeding observation (behaviour)

Observations on feeding interactions of the Grey-headed and House Sparrows were noted whenever both sparrows were found feeding together or feeding in the same area. I also noted the feeding behaviour of sparrows within Blantyre City and in the suburban areas. Additional information was collected during country surveys of the sparrows. If the sparrows did not compete over resources, I tried to find out factors which enabled coexistence.

6.3 Results

6.3.1 Comparative morphology

The data in Table 6.1 were collected from museum specimens, this study at Chikunda farm for the House Sparrows and Mangochi district for the Grey-headed Sparrows. For the morphological comparison it would have been preferable to compare specimens

collected from the same locality. In both the Grey-headed and House Sparrows, the male morphological data of wing, tarsus, tail and bill lengths (mm) and fresh weight (g) were significantly larger than the females (Table 6.1: Chi-square 984.79, $P < 0.001$, and 1118.44, $P < 0.001$ respectively). The Grey-headed Sparrows were morphologically larger than the House Sparrows. The difference was significant (Chi-square = 1053.38, $P < 0.001$). The average tarsus and bill lengths of the House Sparrow were 2.5% and 9.2% shorter than those of the Grey-headed Sparrow.

Table 6.1 Comparative dimensions of adult sparrows (values expressed as means \pm standard error, in brackets = number of observation.

Species	Fresh weight (g)	Tarsus length (mm)	Wing length (mm)	Tail length (mm)	Bill length (mm)
House					
(a) δ	25.2 \pm 0.2 (20)	20.2 \pm 0.1 (22)	74.2 \pm 1.1 (22)	59.1 \pm 0.6 (21)	11.1 \pm 0.2 (22)
(b) φ	24.6 \pm 0.4 (25)	19.8 \pm 0.1 (29)	70.3 \pm 1.3 (25)	55.4 \pm 0.5 (28)	10.6 \pm 0.1 (28)
(c) $\delta\varphi$	24.8 \pm 0.2 (46)	19.9 \pm 0.1 (51)	74.2 \pm 0.3 (48)	56.8 \pm 0.5 (51)	10.8 \pm 0.1 (51)
Grey-headed					
(a) δ	30 (1)	19.5 \pm 0.4 (4)	81.3 \pm 1.3 (4)	64.0 \pm 2.4 (4)	12.0 \pm 0.4 (4)
(b) φ	23.3 \pm 0.2 (2)	21.0 \pm 0.9 (3)	79.7 \pm 1.4 (3)	61.3 \pm 0.5 (3)	12.0 \pm 0.5 (3)
(c) $\delta\varphi$	27.3 \pm 1.0 (11)	20.4 \pm 0.3 (17)	82.7 \pm 0.8 (18)	62.7 \pm 1.0 (17)	11.9 \pm 0.3 (18)

Table 6.2. Observed feeding places and activity of

Grey-headed and House Sparrows in Blantyre City
and other places.

Species	Perched on					feeding			Total
	Tree	Escom/Telephone line	Houses	Fence poles	Hedges	Ground(NH)	Ground (AFH)	Tree Canopy	
House	21	29	149	5	65	255	0	0	524
Percentage of activity	4	5.5	28.4	1	12.4	48.7	0	0	
Grey-headed	49	58	34	27	0	35	90	17	310
Percentage of activity	15.8	18.7	11	8.7	0	11.3	29	5.5	

NH = near houses

AFH = away from houses

Table 6.3 Feeding groups of sparrows observed in
Blantyre City and else where

Species	Size of feeding group						Total
	1	2	3	4 - 20	21 - 30	> 30	
House	16	27	30	41	9	9	132
Percentage of feeding group	12.1	20.5	22.7	31.1	6.8	6.8	
Grey-headed	53	69	13	11	0	2	148
Percentage of feeding group	35.8	46.6	8.8	7.4	0	1.4	

6.3.2 Feeding groups of House Sparrows

The feeding group size of the House Sparrow is shown in Table 6.3. Smaller groups of one to ten birds were seen both in low and high density areas. The common feeding groups were 11-20 birds. Bigger feeding groups were common at maize grinding mills and food depots.

6.3.3 Grey-headed Sparrows

Grey-headed Sparrows were observed to feed on the ground and in tree canopies (Table 6.2). These feeding areas were mainly in the low, industrial, and mid-density areas. When feeding on the ground, the birds walked slowly within a limited area picking up food. When the area was examined, it was often found that they were feeding on small crawling insects.

Apart from picking up small grain near farm buildings or gardens, the Grey-headed Sparrows supplemented their food with insects throughout the year. Feeding sites where insect food was collected included the ground on roadsides, on short grass and tree branches of flowering trees. For instance on one occasion at Chikunda farm, a small group of 12 Grey-headed Sparrows was feeding on the ground at the periphery of the farm on a cleared piece of land. Examination indicated that the birds were feeding on small black ants. Flowering trees generally have been observed to attract Grey-headed Sparrows because of the abundant

insects which visit flowers. On one occasion a Grey-headed Sparrow was seen picking crawling insects off poles. The bird stood vertically alongside the pole. Grey-headed Sparrows were also seen using the flycatching technique to capture grasshoppers and small butterflies in a flowering tree.

Lone feeding Grey-headed Sparrows and pairs represented 83.0% of the total observations of feeding groups (table 6.3). Single feeding birds were observed during the breeding season and they could simply reflect absence of mates who may have been perched up a tree or at the nest. Feeding groups of 4 -20 birds may have included juveniles with parents. Larger feeding groups of more than 20 birds were observed in Chitipa and Nkhata Bay districts in the northern region. In both cases the Grey-headed Sparrows were feeding at a maize mill.

6.3.4 Feeding interactions

At Chikunda farm, both Grey-headed and House Sparrows occurred. The House Sparrows were present throughout the year while the Grey-headed Sparrows were present during the breeding season from about January to May. Both species were seen feeding together. The two sparrows have also been seen feeding together at an industrial site where food was processed. Out of 17 occasions when the two sparrows were observed feeding together, I noticed only two occasions when there was any antagonism. This involved Grey-headed Sparrows joining feeding House Sparrows on

the ground. In this case it was individual distance that mattered. The Grey-headed Sparrow landed too close to feeding male House Sparrows, which responded by chasing them. The Grey-headed Sparrows simply jumped backwards and continued feeding as if nothing had happened. Grey-headed Sparrows usually joined feeding House Sparrows. Only once did I observe a male House Sparrow joining three Grey-headed Sparrows. Grey-headed Sparrows were not seen reacting to House Sparrows. They are morphologically bigger than House Sparrows (Table 6.1) and in direct combat, they would be expected to win a fight.

6.3.5 Social behaviour.

Generally Grey-headed Sparrows fed in pairs, and sometimes as a family group when they had fledged young. In these instances the birds were found either in threes or fours. However where food was abundant, they congregated in large groups and fed together. The behaviour in this instance was like that of House Sparrows when they were feeding as a social group. When disturbed the birds flew to nearby trees, made chattering noises, jumped from branch to branch and chased each other. When one individual flew down to feed, it was soon followed by others.

The above behaviour was observed in Nkhata-Bay and Chitipa. In the natural habitats they fed in pairs. In both Chitipa and Nkhata-Bay, social feeding was observed at maize mills, where food was abundant. In Nkhata-Bay, local people indicated that

during rice growing and harvesting, the birds feeding in the rice fields are even more concentrated than flocks observed at Nkhata-Bay, which numbered up to 70 birds. In Karonga where there is rice-growing a similar situation occurs.

6.4 DISCUSSION

Summers-Smith (1988) pointed out that the food of the House Sparrow depended on circumstances and local conditions. He regarded the bird as an opportunist that fed on such a variety of food stuffs that it could be called omnivorous. The adult House Sparrow readily took animal food when it was available.

The food of House Sparrows in Malawi was not different from that reported in the temperate region. During breeding, they fed their young on a variety of insect food. I observed that the House Sparrow was an opportunist which fed at a variety of sites whenever food was available. For instance they were observed feeding at the sewage works on the drying beds. This was common mainly during the rainy season when the sludge pumped out took longer to dry, and became a fertile breeding ground for insects. The House Sparrows fed on adult flies and maggots.

The Grey-headed Sparrow is different from the House Sparrow, in that it does not rely on human habitation for food but mainly for breeding. Human dwellings were sometimes used for feeding

but this was confined to places where grain was spread out for drying, and also maize grinding mills. In other parts of the country the Grey-headed Sparrow may rely on cultivated foodstuffs like millet and rice. The birds fed in the gardens where these crops were grown. On a smaller scale, in some instances the Grey-headed Sparrow was seen patronizing places like educational institutes where students discarded food.

In some parts of the country like Mangochi, the Grey-headed Sparrows in the non-breeding season fed in the woodlands. They came to town to roost and early in the morning left again to feed. In the evening before they went to roost, some fed on tree canopies and on the ground where they picked up insects and any other food that might have been thrown out by people. The Grey-headed Sparrow was not an opportunist like the House Sparrow.

CHAPTER SEVEN

7.0 TRADITIONAL COMPETITION THEORY

Competition theory predicts that we may expect competition among closely related species over some set of limited resources. Wiens (1977) pointed out that closely related species differ in either habitat or size and thereby may avoid competitive elimination. In bird communities composed of similar-sized species occupying similar structural habitats, a variety of feeding methods is necessary to allow coexistence, if the variety and abundance of resources is assumed to be limited. Competition among closely related species results in the "best" phenotypes surviving in populations and such processes are often viewed as the forces dictating community structure. Coexisting species, the theory predicts, must differ to circumvent competition, and the degree of ecological overlap or divergence among coexisting species is the measure of competitive intensity (Wiens 1977).

Diamond (1978), reported that during the first half of the twentieth century, several naturalists independently made the following observation; the species coexisting at a locality were not only morphologically distinct but also ecologically distinct in the microhabitat where they lived and in what they ate and how. He points out that such early observations were made by Steere in 1894 for Philippine birds, and by David Lack (1944, 1945, 1946, & 1947) for Europe and Galapagos birds and by Elton (1946) for numerous plant and animal communities.

Alley (1982). defined this niche concept as the conditions necessary to support the vital activities of a type of organism. He defined a niche by the range of environmental variation in both biotic and abiotic factors under which that organismic unit can engage in the activities necessary for its survival.

Diamond (1978) gave a few examples of congeners which coexist by segregation in the food they eat or the habitat they occupy. For example he reported that eight species of pigeons that coexist locally in New Guinea lowland forest are ecologically similar except that their different sizes permit them to eat fruits of different diameters and perch on branches of different thickness. Congeners could also differ in the type of habitats they occupy and also the height above the ground at which they were active, the type of food they ate and the way they caught their food.

Feeding studies of birds by various ecologists have given support to the predictions of competition theory. A few examples of such results will be mentioned here, and later I will discuss recent views of competition theory as advanced by later ecologists. Catchpole (1973) in a study of conditions of coexistence in sympatric breeding populations of Acrocephalus warblers, found that in some areas, European Reed Warblers Acrocephalus scirpaceus and European Sedge Warblers A. schoenobaenus coexisted in close proximity during the breeding season. He observed interspecific aggression and territorialism. In such places habitat separation was lacking and the birds were

separated by behavioural mechanisms which led to horizontal separation by the maintenance of mutually exclusive territories. The two species were also separated vertically in habitat and nest site selection. Catchpole (1973) postulated that under conditions of considerable interspecific competition, each species would retreat into its optimal habitat and conversely under conditions of reduced interspecific competition or in areas of allopatry, each species would expand into sub-optimal habitats.

Pulliam & Scott (1977) studied the ecology of emberizids at a research station in southern eastern Arizona in the United States. In winter several species are common residents at the ranch. One reason these species coexisted was by microhabitat separation. Different species occupied different habitats within the ranch. For example some occupied woodland and woodland edge habitats, while others occupied tall grass and plains grassland habitat, which was typical of the ranch. Food also allowed coexistence as different species fed on different food sizes. The ecology of these seed eaters was further studied by Pulliam (1983, 1985) who investigated foraging efficiency and resource partitioning.

He observed that feeding behaviour enabled birds to feed at different distances from trees and shrubs which contributed to their coexistence. The sparrows were also seen to defend feeding sites aggressively. Pulliam (1985) found that during years of low food abundance at the ranch, only one species

existed but during high food production more than one species existed at the ranch. This led him to suggest that each species was best adapted to a few habitats where it could out-compete all other species in times of food scarcity, but each species could occupy a greater variety of habitats when food was abundant and competition for food was not important.

If competition actually restricts a species, one would expect shifts in the distribution, habitat use or foraging behaviour of a species when it is not limited by competition. Shifts in habitat use in the absence of other species are well documented among European tits. In Ireland, Coal Tits Parus ater feed regularly in the understorey of evergreen forests in the absence of the Marsh Tit P. palustris and Crested Tit Parus cristatus that normally pre-empt this niche (Gill 1995). It has generally been accepted that two closely related species cannot coexist in the same area indefinitely if their ecological requirements are the same. Catchpole (1973) says this has been refined as the principle of competitive exclusion; this theory predicts that one species will be more efficient than the other, and by competing for the same limited environmental resources, will eventually replace the other. According to this principle as stressed by David Lack in his studies, the separation of niches observed in nature is the outcome of the interspecific competition that Darwin stressed. The species that succeed in minimizing the struggle for existence and in surviving are those that occupy distinct niches. Diamond (1978) stated that niche differences are not a matter of differences in habitat or food,

but may also consist of differences in techniques for finding the same food in the same habitat. The niche differences between closely related species result from competition; they are the means by which species minimize competition in nature.

When the geographical ranges of two closely related species overlap partially but not entirely, competition is postulated to cause morphological, ecological, behavioural or physiological differences between the two species to be more marked in the sympatric population than in allopatric populations. This is generally termed character displacement (Diamond 1978).

Orians & Wilson (1964) in reviewing interspecific territorialism, mentioned that selection normally favours ecological divergence in modes of environmental exploitation either by character displacement or differential habitat selection and in these cases unnecessary interspecific aggression is eliminated. They predicted that interspecific aggression only arises in cases where such divergence cannot occur due to some environmental limitation. In this case the birds could resort to interspecific territorialism which would be advantageous by excluding other competing species (Catchpole 1978).

While Catchpole (1972) and others have interpreted interspecific territorialism as an adaptation to allow two closely related species to coexist together, Murray (1988) argued that this was not the case. Instead he advanced his own hypothesis that interspecific territoriality is simply an

adaptation for two closely related species to use similar habitats for breeding -i.e. territorial space. He supported his hypothesis by using data from Catchpole (1972) which showed that the Acrocephalus warblers used different nesting heights, and fed their young outside their territories. Moreover warblers could be ousted by aggressive late comers. He concluded that there was no interspecific competition.

Ecological community theory attempts to predict the number and relative abundance of co-existing species based on resource utilization and availability (Pulliam 1983). Some studies have supported the theory, but some have shown little agreement between predictions of the theory and the pattern of bird abundance and distribution: for example of grassland and shrubsteppe birds in America (Wiens 1977). The traditional theory assumes that population sizes of competing species are limited by the available resources.

Alley (1982) noted that the views of many ecologists on the nature of niches are beset with a number of difficulties related to competition. These problems concern the widely accepted proposition of competition theory which asserts that there can be no more than one species per niche (or per limited resource), and its corollary that communities exist at equilibrium. Alley (1982) argued that there is growing evidence that true competitive equilibrium occurs very rarely, if at all, in natural situations. He said this should come as no surprise since,

contrary to the prevalent view of earlier naturalists, it is clear that organisms do fluctuate greatly in numbers, and not simply because of human interference with "natural" conditions.

Anderson & Koopman (1981) accepted that species compete and that this competition operates on both ecological and the evolutionary time scales, but no two species responded in exactly the same way to all environmental conditions. They suggested that populations generally fluctuated in a stochastic manner, not because different species are equally well adapted but because the environment will fluctuate independently of the species characteristics. In other words, their lack of adaptation to a changed environment is more important in the outcome than their adaptation to a former environment. One result of competition may be specialisation. Specialisation by a species for the use of some subset of resources may increase its probability of survival.

7.1 RECENT VIEWS ON COMPETITION THEORY.

Interspecific competition has generally been accepted as an important process in structuring communities (Grant & Grant 1982). Lack's (1945) observations on Darwin's finches on Galapagos Islands showed that the bird species were different on different islands in bill shape and his hypothesis was that distribution and morphology were causally influenced by interspecific competition for food. His main assumption was that

the feeding niche of a population was reflected in the average beak characteristics. The corollary to this is that diet differences parallel beak differences.

Grant & Grant (1982) mentioned however that the evidence that interspecific competition was an important factor in determining niche relationships and community pattern has been critically debated if not challenged.

Wiens (1977) in the study of grassland birds found that differences in habitat occupancy between species were by no means uniform but depended very much upon which individuals were included in the comparisons and when the comparison was made. He noticed that bird numbers changed between years and between areas as close as 100 m apart. He found out that his results from the study of grassland birds were not in conformity with competition theory. He pointed out that the theory had largely been accepted by ecologists so that it was in danger of becoming an entrenched dogma. He concluded from his results that (1) competition may be less pervasive in its effects than is usually assumed, (2) that what we witness in nature may at times represent merely a coarse fit to the optimal states predicted by theory and (3) that documentation of the competition process in nature may be extremely difficult if environments vary through time.

Subsequent findings by various writers supported his views (Grant & Grant 1982). Wiens (1977) contended that related species differ in either habitat or size and thereby avoid competitive elimination. In bird communities composed of similar-sized species occupying similar structural habitats, the variety of feeding methods is necessary to allow coexistence. Wiens (1977) argued that the variety and abundance of resources are assumed to be limited, and such processes are often viewed as the forces dictating community structure. The above type of arguments develop predictions that are simply logical consequences of the initial premises, and as such they represent tautologies more than theories (Wiens 1977). He pointed out that the resources which are used to measure competition are rarely carefully measured nor is it established that the species differences relate directly or solely to competitive process.

Competition theory dictates that competition is the major selective force acting upon the resource-utilization traits or determining the distribution of species. Wiens (1977) argued however that if other factors prevent populations from reaching sizes at which competition is intense, the predictions of theory may not be realized. Examples include predation, which may prevent prey species from competing among themselves by depressing their populations, environmental harshness or variability may influence such predation effects and may cause continuous shifting of the direction of competition between species, producing an unstable equilibrium at population levels well below resource-defined carrying capacities.

Wiens (1977) suggested from the foregoing that the patterns we observe in nature may therefore be influenced or explained by processes other than competition alone. He further suggested that populations usually operate below the equilibrium, which is determined by resource levels. The factors which contribute to this are predation or frequent and recurrent disturbances. He argued that competition however plays only a minor role in such equilibrium solutions. The majority of studies that provided the evidence supporting a major role for competition in determining community patterns have been short-term, spending only a few weeks or a single season assaying populations in any given locality. The results generally indicated that populations were at equilibrium level yet long term studies have shown substantial variations in densities.

Natural environments are variable, and this variability thwarts the application of simple theory to nature. He further pointed out that environmental fluctuations occurring over short time intervals may affect the organism concerned within generations. The organism's behaviour will be adjusted according to seasons. Optimal behaviour may occur during winter or dry season, the selective pressures on these attributes may be relaxed or different during summer or wet seasons. What is optimum then in one annual cycle may not be optimal at another, but such short-term within-generation variations in responses are not considered by the current theory (Wiens 1977).

Alley (1982) further mentioned that the decline of a population due to competition will always take some time, and if the rate of decline is sufficiently slow, genetic change may spread through the population so as to decrease or even reverse the cause of competition. He pointed out that species are not static entities with fixed relations to the environment, but plastic elements, changing their genetic constitution under the influence of the physical factors of the environment and of the interactions with other species. Moreover when adverse conditions arise due to competition, a behavioural change may appear that will alter the competitive relationship between populations.

Competition theory predicts that coexisting species must differ to circumvent competition, and the degree of ecological overlap or divergence among coexisting species is often used as a measure of competitive intensity. In birds, bill size and body size in particular have been used to explain the coexistence of species. In the same vein, quantitative measures of the overlap in trophic morphology or feeding behaviours have been used as direct estimates of the intensity of competition among species. The critical link between overlap in actual utilization of limiting resources, however has not been satisfactorily documented (Alley 1982).

Thomson & Lawton (1983) stated that competition may be contemporary and apparent from studies of species population dynamics. However they pointed out that most studies including

theirs agree with a growing body of similar evidence which fails to support any simple relationship between morphology and feeding ecology, either in constant body size ratios between coexisting species or clear relationships between morphology and diet. They however suggested that it is possible that studies may use the wrong parameters when looking at bird morphology. Food preferences found at the time of investigation may not reflect the natural food preferences under situations of occasional severe resource limitation. They concluded that it is dangerous to presume that morphology can be used as an index to ecological relationships among species coexisting in the same habitat. Wiens (1977) came up with the same views as those of Thompson & Lawton (1983). He admitted that species do differ but he argued that it is wrong to attribute these differences indiscriminately to competitive pressures or to label them "coexistence mechanisms". While the theory may be justified in some cases, he cautioned that it often may simply not apply to real-world situations, largely because the underlying assumptions so greatly oversimplify nature.

7.2 DO SPARROWS COMPETE IN MALAWI?

During this study I found little direct evidence that competition for limited resources was crucial to the occurrence and success of House Sparrows or Grey-headed Sparrows at a local level. Individual House Sparrows may displace Grey-headed Sparrows at a food source, and at nest sites. However, the

species commonly feed at different spots and favour different areas for nesting. House Sparrows tolerate close co-habitation with man at higher densities than Grey-headed Sparrows can apparently accept at this stage. This behavioural response to man-modified environments seems to be crucial to their distribution in urban areas. In rural areas Grey-headed Sparrows appear to find food sources more readily than House Sparrows. There is no evidence to date that interactions between these species have led to either behavioural or morphological changes.

7.3 Studies on other Passer species and Emberizids.

Competition between the House Sparrow and other species has been studied and documented in Africa, Europe and America. Penry (1978) in Kitwe, Zambia, observed over a ten-year period that in the early years the numbers of Grey-headed Sparrows were larger at the hospital than House Sparrows. However in later years he noticed that the numbers of Grey-headed Sparrows had declined and those of House Sparrows had increased. He suggested that competition seemed to have taken place over nesting sites with the House Sparrows taking over a third of the niche previously occupied by Grey-headed Sparrows.

In South Africa in the Cape Province, the Southern Grey-headed Sparrow was absent in about 1940. This area had previously been occupied by an indigenous species, the Cape

Sparrow, and the House Sparrow, both of them potential competitors. In the 1950's the Southern Grey-headed Sparrow suddenly started to increase its range in the Cape Province. Craig et al. (1987) suggest that the likely cause of this is changes in land use. Although there had been other sparrow species in the area, Craig et al. (1987) reported that the Southern Grey-headed Sparrow coexists with the House Sparrow. In some cases House and Grey-headed Sparrows have been reported feeding and breeding at the same place. In some areas like Grahamstown, the birds feed in different areas of the town. House Sparrows were restricted to the commercial centre whereas the Grey-headed Sparrow was common in the suburban areas.

Kalinowski (1975) in the study of intra and interspecific aggression in the House Finch Carpodactus mexicanus and House Sparrow in an outdoor feeder and cages, found that the House Sparrow was generally dominant to House Finches especially in cages. The male House Finches interacted more with their own species than with House Sparrows. Kalinowski (1975) suggested three factors which accounted for interspecific aggression in these species. Individual distance was important. Any violation of this led to agonistic encounters at commonly utilized resources. He also noticed that the House Sparrows had evolved interspecific aggression towards other species over nesting places in a restricted habitat. Lastly, the larger size of the House Sparrow gave it an advantage over the House Finch in aggressive interactions. However this cannot be true with Grey-headed Sparrows. They are larger than House Sparrows, which

displace Grey-Headed Sparrows at nesting places by numerical superiority and persistent harassment.

Allaire & Fisher (1975) in study of three resident sympatric Emberizidae in eastern Texas, found that the species coexisted because they differed in their feeding behaviour. Bachman's Sparrow Aimophila aestivalis which fed on the ground was more methodical in the way it foraged. The Chipping Sparrow Spizella passerina was not as thorough as the Bachman's Sparrow. The three also differed in their food habits. Bachman's Sparrow ate mostly one kind of seed throughout the year, while the Chipping Sparrow and Field Sparrow Spizella pusilla selected different food in winter. the authors suggested that this could be a reflection of competition in winter.

Pulliam & Scott (1977) studied the use of space by eight species of Emberizidae in winter at a research ranch in southern Arizona. The question they asked was how these species coexisted. Different species occupied different habitats within the ranch. For example some occupied woodland and woodland edge habitats while others occupied tall grass and plains grassland habitat which was typical of the ranch. Food also allowed coexistence as the birds fed on different grain sizes. They also defended their feeding sites. There was a general indication that interference competition might also have played a part (Pulliam 1983).

Summers-Smith (1984) studied the three species of sparrows on the Cape Verde Islands. These were the House Sparrow, an endemic species the Iago Sparrow Passer iagoensis and the Spanish Sparrow P.hispaniolensis. The House Sparrow and the Spanish Sparrow are colonizers of the islands. At some of the islands the Iago Sparrow is absent and Summers-Smith (1984) suggested that the Spanish Sparrow may have competed with it leading to its disappearance at some of the islands. He also observed that where the Spanish Sparrow and Iago Sparrow occurred on the same island, they were segregated. For example at Santiago Island, the Spanish Sparrow occurs alone in the town of Praira, the larger villages and cultivated land with large trees, whereas the Iago Sparrow was found in arid, rocky country and the marginal cultivated land where the trees were smaller and less numerous. He found that the House Sparrow on Cape Verde competed with the Spanish Sparrow and this had led to the latter disappearing from Sao Vincente. The House Sparrow failed to colonize some of the islands due to a lack of suitable towns to give it a foothold.

Alonso (1986) in a study of ecological segregation between sympatric Spanish Sparrows and House Sparrows during winter, found that the two species coexisted because they differed in their food choice. The House Sparrow depended on cereal food such as wheat and corn seeds which comprised 41% of the total food ingested while the Spanish Sparrow took only 13% of such grains. He found that the birds also differed in their use of feeding sites and nesting sites. The House Sparrow preferred to feed on the ground and adjacent to farm buildings, wasteland and

roadsides while the Spanish Sparrow fed in the corn fields. He suggested that this is an efficient strategy when exploiting and defending predictable food resources such as waste cereals near granaries or cereal seeds in livestock food. In contrast he found that the Spanish Sparrows exhibited a highly gregarious and mobile behaviour that probably enabled them to exploit locally or temporally abundant food resources more efficiently.

Bennett (1990) reported that in the United States, there is some overlap in nest-site preference and diet between the House Sparrow and the House Finch. He pointed out that the House Sparrow however requires nest sites at or near a predictable and highly concentrated food source such as a livestock pen or fast food dumpster, whereas the House Finch has slightly broader dietary and nest-site preferences and forages over larger areas. Unlike the House Sparrow, the House Finch does not require nest-sites to be close to a single food source.

7.4 CONCLUSION

From the results of this study, I predict that on a local scale over a long period of time, the House Sparrow will eventually replace the Grey-headed Sparrow in commercial areas in the districts. This will be more pronounced in the cities of Blantyre, Lilongwe and Mzuzu where the House Sparrow numbers will overtake those of Grey-headed Sparrow. This prediction is supported by the current status of two species in Blantyre City

where they were studied closely. With anticipated development in these cities and influx of people to urban areas and population growth, the situation will favour the House Sparrow which is able to cohabit with the people while the Grey-headed is not. Eventually the Grey-headed Sparrow will be displaced from the inner city and pushed to the periphery or suburban areas.

In order to test this prediction, there is a need for follow-up research on the two species in order to document their population numbers and possible competition in the coming years. The major cities of Lilongwe and Mzuzu are of interest since they are at present expanding, and precise information can be collected which can elucidate the interactions that take place as numbers of House Sparrows increase in high density areas.

Another area which needs further examination is the present occurrence of the Grey-headed Sparrows in Malawi. While accepting that Passer griseus ugandae is widespread in the country, the other taxa which have been examined in Chapter 2 need further investigation to throw some light on their distribution in the country.

OBSERVATIONS SPARROWS IN APPENDIX I WERE IN MAY 1994

Appendix 1.1 Number of Grey-headed and House Sparrows observed in Mzimba district

Number of birds observed		
Locality	Grey-headed Sparrows	House Sparrows
Mzuzu City	27	14
Mpherembe (rural)	7	0
Ekwendeni (rural)	6	0
Mzimba town	43	65
Edingeni (rural)	8	5
<hr/>		
TOTAL	91	84
<hr/>		

Appendix 1.2 Number of Grey-headed Sparrows and House Sparrows observed in Rumphi district

Number of birds observed		
Locality	Grey-headed Sparrows	House sparrows
Rumphi town	8	14
Livingstonia (rural)	5	0
on plateau		
<hr/>		
TOTAL	13	14
<hr/>		

Appendix 1.3 Number of Grey-headed and House Sparrows
observed in Nkhata Bay district

Locality	Number of birds observed	
	Grey-headed Sparrow	House Sparrow
Nkhata Bay town	55	27
Chintheche (rural)	7	0
TOTAL	62	27

Appendix 1.4 Number of Grey-headed and House Sparrows
observed in Chitipa district.

Locality	Number of Birds Observed	
	Grey-headed Sparrows	House Sparrows
Chitipa town	52	5
Nthalile (Rural)	11	0
Kameme (Rural)	6	0
TOTAL	68	5

Appendix 1.5 Number of Grey-headed and House Sparrows
observed in Karonga district.

Number of Birds Observed		
Locality	Grey-headed Sparrows	House Sparrow
Karonga town	32	0
Kaporo (Rural)	30	0
<hr/>		
TOTAL	62	0
<hr/>		

OBSERVATIONS OF SPARROWS IN APPENDIX 2 WERE
DONE IN MAY 1995

Appendix 2.1 Number of Grey-headed and House Sparrows
observed in Salima District.

Number of Birds sighted		
Locality	Grey-headed Sparrow	House Sparrow
Salima (Boma)	15	3
Livingstonia Hotel (Rural)	9	27
<hr/>		
TOTAL	24	30
<hr/>		

Appendix 2.2 Number of Grey-headed and House Sparrows
observed in Lilongwe district.

Numbers of Sparrows sighted.		
Locality	Grey-headed Sparrows	House Sparrows
Old town	9	14
New City Centre	28	5
Suburbs (Townships)	8	22
rural areas	7	0
TOTAL	52	41

Appendix 2.3 Numbers of Grey-headed and House Sparrows
observed in Kasungu District.

Numbers of Sparrows		
Locality	Grey-headed	House
Kasungu Town	29	26
Dwangwa (rural)	18	0
Nkhamenya (rural)	9	7
TOTAL	56	33

Appendix 2.4 Numbers of Grey-headed and House Sparrows
observed in Dowa district.

Locality	Number of Sparrows	
	Grey-headed	House
Mponela trading	18	14
Madise (rural)	15	4
Mtengowanthenga (rural)	7	0
TOTAL	30	18

Appendix 2.5 Number of Grey-headed and House Sparrows
observed in Mchinji district

Locality	number of Sparrows	
	Grey-headed	House
Mchinji town	21	0
Kamwendo (semi rural)	15	13
Mkanda (rural)	11	0
TOTAL	47	13

Appendix 2.6 Number of Grey-headed and House Sparrows
observed in Dedza district.

Locality	Number of Sparrows	
	Grey-headed	House Sparrow
Dedza town	18	8
Chimbiya (rural)	4	0
Bembeke (rural)	7	0
TOTAL	29	8

Appendix 2.7 Number of Grey-headed and House Sparrows
observed in Ntcheu district.

Locality	Number of Sparrows	
	Grey-headed	House
Ntcheu Boma	14	37
Bawi (rural)	5	0
TOTAL	19	37

OBSERVATIONS OF SPARROWS IN APPENDIX 3 WERE DONE
IN MAY 1985

Appendix 3.1 Number of Grey-headed and House Sparrows
observed in Mwanza District.

Locality	No of Sparrows	
	Grey-headed	House
Mwanza town	9	23
Thambani (rural)	4	0
Neno (rural)	6	0
	19	23

Appendix 3.2 Number of Grey-headed and House Sparrows
observed in Chikwawa district

Locality	No of Sparrows	
	Grey-headed	House
Chikwawa town	14	39
Nchalo (trading)	3	79
TOTALS	17	118

Appendix 3.3 Number of Grey-headed and House Sparrows
observed in Nsanje district.

Locality	No of Sparrows	
	Grey-headed	House
Nsanje town	7	18
Bangula (rural)	5	11
TOTAL	12	29

Appendix 3.4 Number of Grey-headed and House Sparrows
Observed in Thyolo district

Locality	No of Sparrows	
	Grey-headed	House
Thyolo town	7	28
Luchenza	12	31
TOTAL	19	59

Appendix 3.5 Number of Grey-headed and House Sparrows
observed in Mulanje district.

Locality	No of sparrows	
	Grey-headed	House
Mulanje town	6	37
Muloza (rural)	0	9
Phalombe (rural)	13	0
TOTAL	19	46

Appendix 3.6 Number of Grey-headed and House Sparrows
observed in Zomba district.

Locality	No of Sparrows	
	Grey-headed	House
Zomba town	3	11
Zomba plateau	0	0
Domasi (semi rural)	6	21
TOTAL	9	32

Appendix 3.7 Number of Grey-headed and House Sparrows
observed in Machinga District.

Locality	No of Sparrows	
	Grey-headed	House
Machinga town	7	13
Liwonde	5	11
Balaka	8	30
TOTAL	20	54

Appendix 3.8 Number of Grey-headed and House Sparrows
observed in Mangochi district.

Locality	No of Sparrows	
	Grey-headed	House
Mangochi town	12	22
Ulongwe (rural)	9	13
Madeco (rural)	5	16
TOTAL	26	51

REFERENCES

- Allaire, P.N. & Fisher, C.D 1975. Feeding ecology of three resident sympatric sparrows in eastern Texas. Auk 92: 260-269.
- Alley, T.R. 1982. Competition theory, evolution, and the concept of an ecological niche. Acta Biotheoretica 31: 165-179.
- Alonso, J.C. 1986. Ecological segregation between Spanish Sparrow Passer hispaniolensis and House Sparrow Passer domesticus during winter. Ekologia Polska 34: 63-73.
- Anderson, S. & Koopman, K.F. 1981. Does interspecific competition limit the sizes of ranges of species? American Museum Novitates 2716: 1-10.
- Anderson, T.R. 1977. Reproductive responses of sparrows to a superabundant food supply. Condor 79: 205-208.
- Anon. 1986a. Breeding data: House Sparrow Passer domesticus. Zambian Ornithological Society Newsletter 16: 66-67.
- Anon. 1986b. Breeding data Grey-headed Sparrow, Passer: griseus. Zambian Ornithological Society Newsletter 16: 108-109.

Barrentine, C.D. 1980. Communal nesting in the House Sparrow.

Journal of Field Ornithology: 371-372.

Belcher, C.F. 1930. The birds of Nyasaland. Technical Press, London.

Bennett, W.A. 1990. Scale of investigation and the detection of competition: An example from the House Sparrow and House Finch introduction in North America. American Naturalist 135: 725-747.

Benson, C.W. & Benson, F.M. 1975. Studies of some Malawi birds. Arnoldia 32: 1-27.

Benson, C.W. & Benson, F.M. 1977. The birds of Malawi. Montfort Press, Limbe.

Best, B.L. 1977. Nesting biology of the Field Sparrow. Auk 94: 308-319.

Bock, W.J. & Moroney, J.T. 1978. Relationship of the passerine finches (Passeriformes : Passeridae). Bonner zoologischer Beitrage. 29: 122-145

Britton, P.L. (Ed.) 1980. Birds of East Africa, their Habitat, Status and Distribution. East Africa Natural History Society, Nairobi.

Brown, L.H. & Britton, P.L. 1980. The breeding seasons of east African birds. East Africa Natural History Society, Nairobi.

Catchpole, C.K. 1972. A comparative study of territory in the reed warbler Acrocephalus scirpaceus and sedge warbler Acrocephalus schoenobaenus. Journal of Zoology, London 166: 213-231.

Catchpole, C.K. 1973. Conditions of co-existence in sympatric breeding populations of Acrocephalus warblers. Journal of Animal Ecology 42: 623-635.

Catchpole, C.K. 1978. Interspecific territorialism and competition in Acrocephalus warblers as revealed by playback experiments in areas of sympatry and allopatry. Animal Behaviour 26: 1072-1080.

Clancey P.A. 1980. S.A.O.S checklist of Southern African Birds. Southern African Ornithological Society, Johannesburg

Clancey P.A., Brooke, R.K., Crowe, T.M. & Mendelsohn, J.M. 1991. S.A.O.S. checklist of southern African birds: second updating report. Southern African Ornithological Society, Johannesburg.

- Cody, M.L. 1966. A general theory of clutch size. Evolution 20: 174-184.
- Cordero, P.J. 1993. Factors influencing numbers of syntopic House Sparrows and Eurasian Tree Sparrows on farms. Auk 110: 382-385.
- Craig, A.J.F.K. 1983. Molt in southern Africa passerine birds: a review. Ostrich 54: 220-237.
- Craig, A.J.F.K. In press. Southern Grey-headed Sparrow. In: Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, W. & Brown, C.J. (Eds) The atlas of southern African birds.
- Craig, A., Every, B. & Summers-Smith, D. 1987. The spread of the Southern Grey-headed Sparrow in the eastern Cape Province. Annals of the Cape Provincial Museums 16: 191-200.
- Diamond, J.M. 1978. Niche shifts and the rediscovery of interspecific competition. American Scientist 66: 322-331.
- Dowsett, R.J. 1971. The spread of the House Sparrow in Zambia Bulletin of the Zambian Ornithological Society 3 :50-52.

- Dowsett, R.J. & Forbes-Watson, A.D. 1993. Checklist of birds of the Afrotropical and Malagasy regions. Vol 1: Species limits and distribution. Tauraco Press, Liege.
- Elton, C. 1946. Competition and structure in ecological communities. Journal of Animal Ecology 15: 54-68.
- Gill, F.B. 1995. Ornithology. W.H. Freeman, New York.
- Grant, B.R. & Grant, P.R. 1982. Niche shifts and competition in Darwin's finches: Geospiza conirostris and congeners. Evolution 36: 637-657.
- Hall, B.P. & Moreau, R.E. 1970. An atlas of speciation in African passerine birds. British Museum (Natural History), London.
- Harwin, R.M. & Irwin, M.P.S. 1966. The spread of the House Sparrow, Passer domesticus, in south-Central Africa. Arnoldia 2 (24) : 1-17
- Irwin, M.P.S. 1981. The birds of Zimbabwe. Quest Publishing Salisbury, Zimbabwe.
- Kalinowski, R. 1975. Intra- and interspecific aggression in House Finches and House Sparrows. Condor 77: 375-384.

- Lack, D. 1944. Ecological aspects of species formation in passerine birds. Ibis 87: 260-286.
- Lack, D. 1945. The ecology of closely related species with special reference to Cormorant Phalacrocorax carbo and Shag P. aristolelis. Journal of Animal Ecology 14:12-16.
- Lack, D. 1946. Competition for food by birds of prey. Journal of Animal Ecology 15: 123-129.
- Lack, D. 1947. Darwin's finches. Cambridge University Press, Cambridge.
- Long, R.C. 1961. The birds of the Port Herald District. Part II. Ostrich 32: 23-35.
- Long, J.L. 1981. Introduced birds of the world. David & Charles, London.
- Mackworth-Praed, C.W. & Grant, C.H.B. 1960. Birds of Eastern and North-eastern Africa. Vol. 2. Longman, Green & Co, London.
- Mackworth-Praed, C.W. & Grant, C.H.B. 1963. Birds of the southern third of Africa. Vol. 2. Longman, Green & Co, London.

Maclean, G.L. 1985. Roberts' birds of southern Africa. 5th Ed.

John Voelcker Bird Book Fund, Cape Town.

Markus, M. 1960. Some records of the House Sparrow, *Passer domesticus*, in the Orange Free State and Cape Town Province. Ostrich 31: 106

Mathew, K.L. & Naik, R.M. 1985. Interrelation between moulting and breeding in a tropical population of the House Sparrow *Passer domesticus*. Ibis 128 : 260-265.

McGillivray, W.B. 1981. Climatic influence on productivity in the House Sparrow. Wilson Bulletin 93:196-206.

McLachlan, G.R. & Liversidge, R. 1978. Roberts' birds of South Africa. 4th Ed. John Voelcker Bird Book Fund, Cape Town.

Murphy, E.C. 1978 Seasonal variation in reproductive output of House Sparrow: the determination of clutch size. Ecology 59: 1189-1199.

Murray, B.G. Jr. 1988. Interspecific territoriality in *Acrocephalus*: a critical review. Ornis Scandinavica 19:309-313.

- Orians, G.H. & Willson M.F. 1964. Interspecific territories of birds. Ecology 45: 736-745.
- Payne, R.B. 1969. Overlap of molting and breeding schedules in a collection of African birds. Condor 71 : 140-145.
- Payne, R.B. 1972. Mechanism and control of molt. In: FarMer, D.S. & King, J.R. (eds), Avian Biology. Vol. 2 :103-155. Academic Press; New York.
- Payne, R.B. & Payne, K. 1967. House Sparrows reach the Zambezi river in Mozambique. Ostrich 38 : 283-284.
- Penry, E.H. 1978. The House Sparrow: A successful opportunist? Bulletin of the Zambian Ornithological Society. 10(1): 25-27
- Pocock, T.N. 1966. Contributions to the osteology of African birds. Proceedings of the 2nd Pan-African Ornithological Congress. Ostrich supplement 6: 83-94.
- Pomeroy, D.E. 1993. Song in the lives of three common birds in Uganda. Proceedings of the VIII Pan-African Ornithological Congress 447-452.
- Pulliam, H.R. 1983. Ecological community theory and the co-existence of sparrows. Ecology 64: 45-52.

Pulliam, H.R. 1985. Foraging efficiency, resource partitioning, and the co-existence of sparrow species. Ecology 66: 1829-1836.

Pulliam, H.R. & Scott, G.S. 1977. The use of space by wintering sparrows. Ecology 54: 1393-1399.

Sclater, W.L. 1930. *Systema Avium Aethiopicarum*. Vol. 2: 305-992. Taylor & Francis, London.

Seel, D.C. 1968a. Clutch-size, incubation and hatching success in the House Sparrow and the Tree sparrow Passer spp at Oxford. Ibis 110: 270-282.

Seel D.C. 1968b. Breeding seasons of the House Sparrow and Tree Sparrow. Ibis 110: 129-144.

Seel, D. C. 1969. Food, feeding rates and body temperature in the nestling House Sparrow, Passer domesticus at Oxford. Ibis 111: 36-49.

Sibley, C.G, Ahlquist. J.E. & Monroe B.L. Jr 1988. A classification of the living birds of the world based on DNA-DNA hybridization studies. Auk 105: 409-423.

Sibley, C.G. & Monroe, B.L. 1990. Distribution and taxonomy of birds of the world. Yale University Press, New Haven & London

- Siegfried, W.R. 1972. Breeding success and reproductive potential in the Cape Sparrow, Passer melanurus. In: Kendeigh, S.C. & Pinowski, J. (Eds). Productivity, population dynamics and systematics of granivorous birds 167-179. Polish Scientific Publishers, Warsaw.
- Summers-Smith, J.D. 1963. The House Sparrow. Collins, London.
- Summers-Smith, J.D. 1984. The sparrows of the Cape Verde islands. Ostrich 55: 141-146.
- Summers-Smith, J.D. 1988. The sparrows. T & AD Poyser, Calton.
- Thompson, P.M, & Lawton, J.H. 1983. Seed size diversity, bird species diversity and interspecific competition. Ornis Scandinavica 14: 327-336.
- Uys, C.J. 1962. The House Sparrow, Passer domesticus, at Grunau. Ostrich 33: 39.
- Veiga, J.P. 1990. A comparative study of reproductive adaptations in House and Tree Sparrows. Auk 107: 45-59.
- Vernon, C.J. 1962. Passerinae at Francistown, Bechuanaland Protectorate. Ostrich 33: 339-340.

White, C.M.N. 1963. A revised checklist of African flycatchers, weavers and waxbills. Government Printer, Lusaka.

Wiens, J.A. 1977. On competition and variable environments. American Scientist 65: 590-597.

Winterbottom, J.M. 1966. Some alien birds in South Africa. Bokmakierie 18 : 61-62.

Winterbottom, J. M. 1971. A preliminary checklist of the birds of South West Africa. South West Africa Scientific Society, Windhoek.

Wittenberger, J.F. 1982. Factors affecting how male and female Bobolinks apportion parental investment. Condor 84: 22-39.