

**THE EVOLUTION OF THE HOUSE SPARROW
(*PASSER DOMESTICUS*) IN SOUTHERN AFRICA**

by

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ABSTRACT

The house sparrow, *Passer domesticus*, is one of the most successful invading bird species in the world. It was introduced to southern Africa around 1900 and has since spread through the region. Its dispersal was characterised by an initial slow phase followed by a rapid increase in the rate of spread. Following 50 years of slow spread, the rate of dispersal accelerated to over 80 km/year. The initial slow rate can be attributed to an Allee effect, defined as “a disproportionate reduction in reproduction below a threshold population density due to reduced probability of finding a mate”. The rapid phase involved a combination of long-range jumps (leap-frogging dispersal) and diffusive movement over short distances. Dispersal was significantly faster along railway lines.

Introduction of the house sparrow, *Passer domesticus*, to southern Africa involved unknown numbers of both the *domesticus* race of Europe and *indicus* of Asia, resulting in the establishment of a genetically diverse founder population along coastal South Africa. The birds have undergone significant differentiation since introduction about 100 years ago. Significant sexual size dimorphism was detected among southern African house sparrows, especially in flight structures. Males were larger than females in all characters except tarsus and claw length. Overall body size variation was clinaly ordered with a general increase in size with latitude in conformity with Bergmann's rule. Tarsus length also increased southwards, with the longest tarsi in birds of coastal sites in South Africa and the shortest in Zimbabwe. Patterns of variation in morphological characters paralleled climatic trends, especially minimum temperature and humidity. Beak size and shape of Zimbabwean birds appeared to be under the greatest influence of climatic factors. Shorter and more conically shaped beaks were selected for in females in Zimbabwe. Natural selection was modifying the morphological characters resulting in adaptive radiation in morphology of southern African populations. Few studies of microevolution (change in morphology over a short period) have been conducted in birds and none in invading bird species in the tropics. A founding population comprising both the Asian and the European races of the house sparrow, *P. d. domesticus* and *P. d. indicus* first arrived in Zimbabwe 30 years ago. Because of its recent introduction to Zimbabwe and because of its known potential for rapid adaptation and differentiation elsewhere in its new range, the house sparrow provided the ideal case study in microevolution in tropical Africa. Morphological differentiation in Zimbabwean populations of the house sparrow was analysed to determine temporal variation in local samples and the extent of variation from parent populations of Asia and Europe. Samples collected since arrival in Zimbabwe up to 1980 were compared with those collected from current populations in 1998/1999 to determine local changes over time. The Zimbabwean samples were then contrasted with samples from Asian and European populations to determine the extent of differentiation in the introduced birds of Zimbabwe. Zimbabwean populations had differentiated from their Asian parents in six of the seven morphological characters examined. The greatest differentiation was in beak size and shape for both males and females. Males developed larger beaks and shorter wings than the Asian birds and female beaks became more conical. A large proportion of the potential phenetic diversity of the founding population of both *domesticus* and *indicus* genes had been realised in Zimbabwe.

PREFACE

This study was undertaken at the School of Life and Environmental Sciences, University of Natal Durban under the supervision of Dr R. Slotow. The material used was examined at the Durban Museum and the National Flagship Institution (then Transvaal Museum in Pretoria) both in South Africa as well as the Natural History Museum of Zimbabwe in Bulawayo, Zimbabwe. Locally, Mr. P. Mlilo, Department of Mathematics, National University of Science and Technology, Bulawayo, Zimbabwe rendered some assistance with statistics.

The study represents original work by the author and has not been otherwise submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

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CHAPTER 1 INTRODUCTION

One of the goals of systematics is to detect the evolutionary process at work (James 1970) and introduced species such as the house sparrow, *Passer domesticus*, offer a unique opportunity for the systematic biologist to realise this goal. Populations introduced by humans are isolated from the homogenising effect of flow of genetic and cultural traits from parent populations (Lang & Barlow 1997) and if introduction dates, numbers and origin of the animals are all known an assessment of the impact of micro-evolutionary forces can be made. For this reason the house sparrow has become an interesting subject of study for both zoogeographers and ecologists.

Studies of the introduction and subsequent spread of the house sparrow in its new range in America, Australia and New Zealand have provided useful information in the understanding of invasions and dispersal patterns, as well as hybridisation and formation of subspecies under various selection pressures (Johnston & Klitz 1977, Johnston & Selander 1964, Niethammer 1971, Pizey 1980, Robbins 1973, Summers-Smith 1963 1988). Previously, studies of ecological invasions were conducted mainly on species of agricultural and epidemiological importance (Parker & Reichard 1997). However, numerous species of plants and animals have invaded natural areas resulting in vast range extensions and displacement of local species (Spellerberg 1997). Animal species ranging from insects to mammals were affected. The Argentine Ant, *Iridomyrmex luminis* was taken from Brazil to Louisiana, North America in 1891 as well as to Australia and South Africa, while the Cotton Cushion Scale, *Icerya purchasi* was taken from Australia to California in 1868 (Bryant 1997). The Nile Perch, *Perca niloticus*, a predatory fish was introduced to Lake Victoria in 1962 (Bryant 1997). Mammalian species included the red deer, *Cervus elaphus* and the Himalayan thar, *Hemitragus jemlahicus* both taken to Australia, New Zealand, North America and South Africa; the black rat, *Rattus rattus*, the brown rat, *R. norvegicus*, and the house mouse, *Mus musculus* from south east Asia to all suitable habitats worldwide. Introductions of bird species were more numerous and most resulted in unexpected population explosions and subsequent ecological invasions. In North America alone more than 70 species of birds have been introduced and 28 of these have become established (Veit & Lewis 1996). However, only nine have spread from their point of introduction and among these are two doves, the Rock Dove, *Columba livia* and the Collared Turtle Dove, *Streptopelia decaocto*; the European Starling, *Sturnus vulgaris*, first released in 1880; the House Finch, *Carpodacus mexicanus* in 1940 and the House Sparrow in 1853.

Similarly, invasions by various species occurred in southern Africa in the late nineteenth and early twentieth centuries. Some of the most successful of these introductions were of the Feral Pigeon (Rock Dove), *Columba livia*, brought to Cape Town from Holland in 1652; the European Starling, also brought to Cape Town in 1897 by Cecil J. Rhodes; the Indian Myna, *Acridotheres tristis* released in Durban in 1902 (Brooke et al. 1986) as well as the House Sparrow released in Durban and East London between 1890 and 1930 (Summers-Smith 1963).

According to di Castri (1989), such invasions are true evolutionary processes, more or less like speciation and extinction and they offer opportunities to study the impact of microevolutionary forces on introduced populations. New behaviour is acquired due to genetic changes or cultural learning and the rate of morphological and physiological evolution can be estimated since the time of introduction is usually known (Diamond 1986, Lewin 1987). The house sparrow is ideal for the study of invasions because its introduction and spread are still quite recent and because of its rapid movement across the region it is likely to provide a complete cycle of the diffusion

wave in a short time period (Lang & Barlow 1997, Veit & Lewis 1996). Evolutionary research owes two important findings to the house sparrow: -

- (a) that subspecies are formed much quicker than previously thought if there are strong selection pressures,
- (b) that if barriers of hybridisation are broken sympatric populations can hybridise to form homogenous populations by introgression (Niethammer 1971).

Originally, the house sparrow occupied a largely European and Asian range. However, in the last 150 years it experienced a remarkable range extension, spreading to North America, Australia, New Zealand and in the past 100 years to South America and Africa (Baker 1980, Harwin & Irwin 1966, Johnston & Klitz 1977, Long 1981, Summers-Smith 1963 1990). Introductions of the house sparrow have resulted in an unprecedented expansion to a more or less worldwide distribution (Clement 1991, Long 1981). Arriving in North America in 1853, it occupied the entire continent and within a hundred years there was evidence of differentiation to form new and distinct local populations (Summers-Smith 1963, Johnston & Selander 1964, Robbins 1973). The birds taken to Australia and New Zealand also spread rapidly and colonised the continent within a century (Baker 1980, Bryant 1997, Johnston & Klitz 1977, Pizey 1980). Most of this movement took place during the 19th century coinciding with massive human migration from Europe. In the new colonies Acclimatisation Societies were formed and tasked with the introduction of familiar plant and animal species "to improve their new surroundings" (Bryant, 1997).

In Africa there were no Acclimatisation Societies (Brooke et al. 1986, Winterbottom 1966) and there were therefore, no records of exact dates of arrival or actual numbers of sparrows introduced. However, its introduction and subsequent spread is relatively well documented. Reports of first occurrence in Southern Africa were made by individual observers across the region and summaries of these have been produced. Examples include the classic work of Summers-Smith (1963, 1990) as well as reports by Winterbottom (1959), Harwin & Irwin (1966), Vierke (1970), Niethammer (1971) and most recently the Atlas of southern African birds (Harrison et al. 1997). The sparrow now occurs in many African countries with reports of introduction to Kenya, Mozambique, Senegambia, Somalia, Sudan, South Africa and Zimbabwe, followed by establishment and spread through the continent (Ash & Colston 1981, Harwin & Irwin 1966, Long 1981, Morel 1988, Summers-Smith 1963, 1990).

Recorded dates of first arrival in southern Africa ranged from 1890 to 1957. The earliest record for the nominate race was 1890 in East London with birds from Sweden (Clancey 1964, Gebhart 1944, Summers-Smith 1963). Further releases in East London occurred in 1914 and 1930 (Courtenay-Latimer 1942 1955). Birds originating from Surrey, England, were released in Durban in 1914 but no population was established (Mackworth-Praed & Grant 1963). Other introductions of the nominate race were recorded in Maputo, Mozambique in 1955 with birds from Portugal (Pinto 1959) and in Harare, Zimbabwe in 1957 with European birds of unknown origin (Harwin & Irwin 1966). There were a number of unsuccessful attempts to introduce birds of the *domesticus* race. Some of these were at Cape Town by C. J. Rhodes in 1902 and in Pretoria by Sclater in 1905 (Winterbottom 1966, Brooke et al. 1986). However, even the successful introductions of this race did not spread inland remaining sedentary at centres of inoculation (Crowe & Brooke 1985, Harwin & Irwin 1966, Summers-Smith 1963).

Birds of the Asian race, *indicus*, in turn came as pets of Indian labourers brought to work in sugar cane plantations (Clancey 1964). The birds were mostly abandoned or escaped from aviaries. Various dates of arrival were recorded ranging from 1890 (Brooke et al 1986, Summers-Smith 1963, 1988 1990) to 1893, 1897 (Mackworth-Praed & Grant 1963), 1902

(Gebhart 1944), 1907 and 1930 (Courtenay-Latimer 1955, Harwin & Irwin 1966, Niethammer 1971, Vierke 1970, Winterbottom 1959). Thus, with the introduction of both races, a founding population of high potential genetic diversity was established in coastal South Africa.

The house sparrow has since invaded and established in almost every settlement that offered suitable habitats (Brooke 1997, Harwin and Irwin 1966) and its success is attributable to:

- (1) its close contact with man and urbanisation of both man and the bird (Morel 1988, Niethammer 1971). Although it originally evolved with agricultural man, the bird has since emancipated itself from this entirely agricultural background to a more urbanised lifestyle as a close commensal of man (Johnston & Klitz 1977, Long 1981, Summers-Smith 1963 1988 1990). It is found in cities, villages and farms where there is an abundance of food supplies (Brooke 1997, Clement 1991, Harwin & Irwin 1966, Irwin 1981, Maclean 1993, Summers-Smith 1963). In West Africa, it was observed that even when rainfall was low and seeds and insects were fewer, breeding performance did not seem to be affected as the birds resorted to garden insects and scraps from human waste (Morel 1988). The house sparrow occupies a niche alongside human habitation in both its natural and its introduced range (Voous 1960). Long (1981: 375) describes its habitat as "open forest, wooded country, grasslands, cultivated areas, parks, gardens, cities, towns and everywhere where there is human settlement". This close relationship with humans helped in the spread of the bird due to assisted movement across barriers such as oceans, otherwise impassable to the bird on its own. Also in the new territories, dispersal was fastest along lines of human communication like roads and the railway line (Long 1981).
- (2) fewer rivals in the New World habitats and thus less competition. There are only a few known competitors such as the Tree Sparrow, *P. montanus* in Kabul, Afghanistan (Summers-Smith 1988), the Cape Sparrow, *P. melanurus* in southern Africa (Brooke 1997, Harwin & Irwin 1966) and the Iago Sparrow, *P. iagoensis* in the Cape Verde Islands (Summers-Smith 1984). Congeners, however, are not always a deterrent unless morphologically similar to the invader (Lewin 1987). Thus, in southern Africa although spread of the house sparrow was slow where it met the Cape Sparrow, it did not stop altogether. In Swaziland, for example, while the house sparrow came to occupy in human settlements, the Cape Sparrow was to be found in grasslands and cultivated land near human habitation (Parker 1994).
- (3) new and probably fewer predators, parasites and diseases in new habitats. This may lead to uncontrolled growth of sparrow populations (Bryant 1997). In its original range the house sparrow is known to carry diseases like *ornithosis*, *salmonellosis* or New Castle. However, there is need for more work to establish the exact predators, parasites and diseases of house sparrows in the new range.
- (4) the fact that the house sparrow is an aggressive competitor and tends to displace indigenous species from their nests and from surroundings. It nests in the eaves of buildings, in nests of storks and birds of prey, in mud nests of swallows and house martins, in tunnels of sand martins and bee eaters, holes of woodpeckers, or in nests of swifts (Long 1981, Voous 1960). Elsewhere in its range, it is known to displace the Cliff Swallow *Hirundo spilodera*, the Little Swift *Apus affinis*, the Purple Finch *Carpodacus purpureus*, the Saffron Finch *Sicalis flaveola* and the Ruffous Collared Sparrow *Zonotrichia capensis* (Lewin 1987). In southern Africa, there is evidence that species like the Northern and the Southern Grey-headed Sparrows, *P. griseus* and *P. diffusus*, the Cape Wagtail, *Motacilla capensis* and the European Swallow *Hirundo rustica* may be affected (Brooke 1997, Gillet 1966, Irwin 1981). Similar observations were made in West Africa where in Morocco the Black Wheatear, *Oenanthe leucura* was disturbed at its nest (Tongue 1971) and in Senegambia when the house sparrow became established in the city, the grey headed sparrow was pushed to the outskirts of towns

- and to villages (Morel 1988). Like all exotic species the house sparrow is self-perpetuating and can be a permanent threat to biodiversity even above over-exploitation and habitat loss (Bryant 1997).
- (5) short generation time. Breeding takes place all year round and two to three or more broods are produced per year in Europe. In India three to six broods are produced per year with a peak in February to December, while in Australia breeding occurs mainly in spring, summer and at other times (Kendeigh & Pinowski 1972, Pinowski & Kendeigh 1977, Summers-Smith 1963). In southern Africa breeding is also year round with a peak in September to December (Irwin 1981, Maclean 1993).
 - (6) ready hybridisation with other species, resulting in loss of identity of endemic species (Clement 1991, Gavrillov 1965). In Italy, *P. domesticus* crossed with *P. hispaniolensis* and produced the hybrid *P. italiae* (Niethammer 1971, Summers-Smith 1990) while in Somalia, Ash and Colston (1981) found a hybrid of *P. domesticus* and *P. castanopterus*.
 - (7) the presence of unoccupied niches in the new range together with the high genetic variability of the house sparrow contribute to its high level of adaptability. The Asian race, *P. indicus* is known to breed at altitudes up to 3000m in Iran (Felemban 1997) while the European race, *P. domesticus* as low as 640m below the surface in a coal mine in South Yorkshire, England (Summers-Smith 1988).
 - (8) Ability by both adults and juveniles to disperse long distances to explore new and more favourable habitats for breeding (Benson *et al.* 1971, Brooke *et al.* 1986, Clement 1991, Newton-Howes 1966, Summers-Smith 1963 1990).

The house sparrow has therefore, successfully adapted to new environments and for purposes of survival or in order to maximise reproductive success, modifications have occurred in body size and plumage colour and subsequently morphological differentiation due to natural selection (Baker 1980, Johnston 1969b, Johnston & Selander 1964, Selander & Johnston 1967). When optima differ between males and females then sexual dimorphism results (Monaghan & Metcalfe 1986). Correlations of climate trends with those of body size and shape in house sparrows indicated that variation in morphology across the species range was a function of climatic conditions (Fleischer and Johnston 1984). Observed phenotypic adaptations generally resulted from interaction of genotypes with environmental factors (Boag 1983) and the new phenotypes were therefore, a compromise between many conflicting selection pressures. Mayr (1956) observed that parallels between morphological variation and physiogeographic features could be described by the use of ecogeographic rules and that every exception to an ecogeographical rule was an indication of the conflict between phenotypes and the environment. It can therefore, be assumed that phenotypic variation closely reflects underlying genetic variation (Boag 1983). The first ecogeographic rule termed Bergmann's rule states that races of warm-blooded vertebrates from cooler climates tend to be larger than races of the same species in warmer climates (Mayr 1956, James 1970). Body size in this case has been traditionally represented by wing length. Most evidence for this rule came from temperate latitudes (>20°) and not from tropical areas (Graves 1991). House sparrows tended to conform to this rule in North America (Johnston and Selander 1964 1971, Murphy 1985) but not in Europe and New Zealand (Baker 1980, Johnston 1969b). It is hoped that studies of southern African sparrows will shed more light on the extent to which Bergmann's rule might be applicable to populations in the tropics. Ripley's rule, a modification of Bergmann's rule describes the negative correlation between body size variation and humidity levels. Body size tends to be larger in races in arid areas than those in humid regions (Hamilton 1961). A third rule, Allen's rule relates variation in body shape to temperature stating that length of extremities such as tarsi and beaks is positively correlated with temperature. Thus, birds in warmer sites tend to have longer legs and beaks than in the cooler sites (Mayr 1942 1956; Hamilton 1961).

Identification of the house sparrow

Secondary sexual dimorphism.

Male and female adult birds can be readily distinguished in the field. The adult male bird has more elaborate markings on the head and back as well as a black bib while the female is dull brown with indistinct markings. The two races introduced to southern Africa vary in intensity and extent of plumage coloration and in size of males.

Description of adult female:

Generally, brown with dark streaks at the back, fawny grey below, the bill is horn and paler below. The bold buff eyebrow from the eye to the back is distinctive of the adult female. There is one prominent pale bar on the wing (Pizey 1980, Summers-Smith 1963, Maclean 1993, Brooke 1997, Clement 1991). The immature looks like the female but is paler and lacks the bold eyebrow.

Description of adult male:

The forehead to the centre of nape is grey, while the cheeks and ear coverts are dingy off-white to grey and the sides of the crown and nape are chestnut-brown. The lores are black and extend behind the eye. There is a white post-ocular spot. The mantle and upper back is brown streaked black while the lower back and rump is grey-brown. The flanks and undertail coverts are pale grey or washed buff. The Palearctic group is predominantly grey (not white) on the cheeks, ear covers and underparts while the Oriental group is smaller in size, with small beaks, white cheeks and underparts and the chestnut plumage is more reddish-brown (Clement 1991).

The aim of this study was to understand the evolution of the house sparrow in southern Africa and there were three specific objectives for this work:

- (1) The first was to describe the spread of the sparrow in southern Africa and to analyse the process of spread of the population across the region as well as compute rates of dispersal. The data was also used to assess the generality of the Allee effect.
- (2) The second objective was to examine the extent of morphological variation among local populations and to relate this to the environment. In terms of the predictions of Bergmann's rule, overall body size would be bigger in birds of the cooler parts of the range than those of warmer parts and according to Allen's rule, populations in arid localities would have longer tarsi than in the more humid sites. Beak size and shape, particularly beak depth would vary in relation to food resources, which in turn would be affected by seasonal variation in temperature and humidity.
- (3) The last objective of this study was to assess morphological differentiation in the birds of Zimbabwe in relation to the parent Asian and European parent stocks. In North America, rapid differentiation was observed in just over 100 years. Similarly, a high level of differentiation would be expected in the birds of southern Africa in response to a different set of climatic factors than they were exposed to in the original range in Europe and Asia

The first objective is addressed in Chapter Two where I analyse the pattern of spread inland from the centres of inoculation in coastal South Africa. Estimates of the rates of dispersal as well as possible routes followed are also presented and the generality of the Allee effect examined. In Chapter Three I discuss intraspecific variation in morphology of southern African house sparrows and its relationship to climate. In Chapter Four I examine first, the extent of micro evolution among current populations of house sparrows in southern Africa, particularly in Zimbabwe, since introduction about 100 years ago and then the level of differentiation of these new populations in relation to parent populations of Europe and Asia. The thesis has been written in the form of papers for publication and Chapter Two, the pattern of spread and dispersal rates, has already been accepted for publication in the *Durban Museum Novitates*.

CHAPTER 2

INTRODUCTION OF THE HOUSE SPARROW, *PASSER DOMESTICUS*, IN SOUTHERN AFRICA: DISPERSAL RATES AND THE ALLEE EFFECT

2.1 Abstract

The house sparrow, *Passer domesticus*, is one of the most successful invading bird species in the world. It was introduced to southern Africa around 1900 and has since spread through the region. Its dispersal was characterised by an initial slow phase followed by a rapid increase in the rate of spread. Following 50 years of slow spread, the rate of dispersal accelerated to over 80 km/year. The initial slow rate can be attributed to an Allee effect, defined as “a disproportionate reduction in reproduction below a threshold population density due to reduced probability of finding a mate”. The rapid phase involved a combination of long-range jumps (leap-frogging dispersal) and diffusive movement over short distances. Dispersal was significantly faster along railway lines.

2.2 Introduction

The house sparrow, *Passer domesticus*, is one of the most successful invasive bird species in the world. It was introduced to South Africa at the turn of the century and in less than a hundred years it had colonised all of southern Africa. It represents one of the most important biological invasions in the region (Brooke et al. 1986, Harwin & Irwin 1966, Long 1981, Niethammer 1971, Summers-Smith 1963 & 1990, Vierke 1970). Like the house finch *Carpodacus mexicanus* in North America (Veit & Lewis 1996) the house sparrow offers a unique opportunity for the study of ecological invasions because its introduction and spread are still quite recent, and because of its rapid movement across the region, it is likely to provide a complete cycle of the diffusion wave in a short time period.

Invasive species of southern Africa have been widely reported on (Macdonald et al. 1986, Godfrey 1934, Long 1981, Harwin & Irwin 1966, Vierke 1970, Niethammer 1971, Winterbottom 1966) but no analysis of the dynamics of their spread has been conducted before. One of the special areas identified for consideration under the program on the Ecology of Biological Invasions initiated by the Scientific Committee on the Problems of the Environment (SCOPE) in 1982 was modelling of the invasion process (Drake et al. 1989). This involved the use of models to analyse spatial and temporal spread of populations so as to understand how dispersal affected the evolution, population dynamics and distribution of organisms (Holmes 1993, Lewis & Kareiva 1993, Williamson 1989). The models have evolved from simple diffusion models to more complex integrodifferential equation models. Assumptions of the simple diffusion models included random movement of individuals, finite velocity and uniform trapping rate by the environment. Later, reaction-diffusion models were formulated which incorporated a growth term and dispersal (Hengeveld 1994, Holmes 1993) as well as age-related reproduction, mortality and dispersal (Hengeveld 1994, van den Bosch et al. 1992). More complex range expansion models followed and these incorporated both individual behaviour and biological details such as directed dispersal, density-dependent dispersal, discrete dispersal phases (Parker & Reichard 1997) and Allee effects (Lewis & Kareiva 1993, Veit & Lewis 1996). Veit and Lewis (1996) used ringing recapture data for the house finch in North America to construct an integrodifferential equation model that included discrete reproduction and dispersal events. They also incorporated an Allee effect which they defined as “a disproportionately lowered fecundity below a critical threshold density of abundance” and attributed the slow initial rate of spread in the early stages of invasion of the house finch to this effect. Okubo (1980) observed that the rate of dispersal of populations was slow during the early stages of an invasion. Lewis and Kareiva (1993) later showed that the Allee effect (reduced reproductive success at low densities) could substantially reduce the rate of spread of

an invading organism. One of the limitations of previous models was that they did not incorporate long distance dispersal. Long distance dispersal generates a stochastic zone ahead of the progressing front by creation of new foci (centres) of spread from which additional dispersal fronts can be generated. The actual rate of dispersal can be determined by a few of these long distance dispersal events. Predicted rates of dispersal tended to be lower than the rates observed when this factor was not corrected for (Hengeveld 1994, Okubo 1980, van den Bosch *et. al.* 1992). Veit & Lewis (1996) included long distance dispersal in their model and used it to explain high observed rates of dispersal.

One of the objectives of this work is to describe the spatial and temporal spread of the sparrow in southern Africa. Secondly, we analyse the spread across the region and compute rates of dispersal. Then we use the data to assess the generality of the Allee effect. If an Allee effect is operational, then the spread of the house sparrow should be characterised by an initial slow phase from the time of introduction, followed by a rapid increase in the rate of dispersal. The slow initial phase is attributed to the Allee effect. At this stage because the local population is small there is reduced reproduction and thus reduced numbers of immature birds and the spread is slow. We assume that the proportion of dispersing birds increases with the local population density. If there is no Allee effect we predict a linear pattern of spread from the time of introduction. Finally, we assess the effect of anthropogenic factors on rates of dispersal. Because of its relationship with man, the house sparrow may spread faster to centres located on the railway line or to larger locations with high human populations.

2.3 Materials and Methods

Records of first sightings of the house sparrow were extracted from published and unpublished literature, from personal notes of observers in the region and from Atlases and distribution maps. These were used to compile a list of locations to which the house sparrow spread from 1900 to 1970 when all of southern Africa had been settled. Where more than one record was found, the earliest recorded date was used as the date of first occurrence at the location (Appendix 1). The data were used to draw maps of (1) proposed routes of spread from Durban, and (2) distribution of the sparrow by 1970.

The main inoculation was assumed to have been at Durban with birds of the *indicus* race. There were six records of introduction to Durban, in 1890 (Brooke *et al.* 1986, Summers-Smith 1963, 1990); 1893,1897 (Mackworth- Praed & Grant 1963); 1902 (Gerbhart 1944); 1907 and 1930 (Courtenay-Latimer 1955, Winterbottom 1959), while only three were recorded at East London in 1890 (Clancey 1964, Gebhart 1944, Summers-Smith 1963), 1914 and 1930 (Courtenay-Latimer 1942, 1955) and one each at Maputo and Harare (Pinto 1959, Irwin & Harwin 1966). The birds introduced to East London, Maputo and Harare were all of the *domesticus* race. Observations by previous workers on the house sparrow in southern Africa have shown that only the *indicus* birds from Durban dispersed from the point of inoculation, those of the nominate race remaining relatively sedentary (Harwin & Irwin 1966, Niethammer 1971, Summers-Smith 1963). For purposes of this analysis, therefore, the time course begins in 1900 at Durban.

Data on first records of occurrence (Appendix 1) were used to estimate the rate of invasion of the sparrow in southern Africa by plotting the dispersal distances against time (date). Dispersal distances to 76 locations indicated in Appendix 1 were measured as straight lines from Durban on a 1: 500 000 map of southern Africa. We predicted an exponential (Allee effect) relationship between dispersal distance and time. Following introduction, reproduction would be low due to small population size or low population density resulting in a low density of immature birds and a depressed rate of dispersal. Thereafter there would be an acceleration of the rate of spread

after a threshold density was attained. To test these alternatives we ran a regression analysis and assessed whether an exponential or linear relationship provided the best fit (higher R^2 value). As the dispersal wave advanced from a large expanding focus new (satellite) foci would be established and rapid radiation from the new foci would result in an acceleration of the rate of spread (van den Bosch *et al.* 1992). To assess the effect of new foci set up ahead of the main spread from Durban, data were separated into sets with new centres at Johannesburg and at Grunau, Namibia. Possible dispersal from East London was analysed from data for locations occupied by the sparrow between 1900 and 1955 in the eastern and western Cape Provinces.

When the line of best fit is drawn through data, some points lie above and below the line. Above the line are points settled before the predicted arrival dates and they are represented by positive residuals. Below the line are the points where the spread progressed more slowly than was predicted by the line of best fit and they are negative residuals. This variation is due to the effect of external factors, barriers and corridors. Corridors both divide and connect landscapes and examples include roads, rail, powerlines, streams and mountain ranges (Chapman 1981, Forman & Godron 1986). Dispersal would be faster along corridors (when they act as routes or conduits for movement) and slower across them (when they form barriers). We predicted faster dispersal to centres located on or close to the railway line. Also because of its close relationship with man, there may be a tendency to spread faster to large towns with high human populations and presumably an abundance of resources, particularly food and breeding sites. Therefore, size of towns and proximity to the railway line may influence the rate of spread. The G-test was conducted on data on location size and proximity to the railway line to test their effect on the rate of spread and a distribution map of the positive and negative residuals from the best-fit line of the log transformed data of the spread from Durban through 1970 was done to show distribution of locations settled ahead of the dispersal and those lagging it, respectively.

Information on the history of railways was obtained from published literature (Croxtton 1982, Siviter 1981) and from the Railway Museum in Bulawayo. A map of distribution of locations by proximity to the railway line was drawn.

Population data for the towns occupied by the sparrow were obtained partly from publications by Horrell (1953) for South Africa and Mapondera (1981) for Zimbabwe and also from the Population Bureau in Pretoria, South Africa and the Central Statistical Office in Harare, Zimbabwe. Locations not represented in the census reports were classified as small on the assumption that small size would have been the reason for their exclusion. As a further check, relative size was obtained by comparison of location signs on atlases; locations of known size were used as reference points and any locations represented by the same sign on the map were allocated to the same size class. Only a few South African locations qualified as large towns by 1950. However, by 1960 there were more large towns in Zimbabwe (Appendix 1). A map of distribution of locations by size was drawn.

Sparrow ringing and recapture data were obtained from Safring (Avian Demography Unit of the University of Cape Town) as well as from published literature (Harwin & Irwin 1966). These were divided into subsets by sex and by age and used to compute average distances moved and to assess the effect of age on propensity to disperse. Although there is evidence of adult movement in the house sparrow, there is a greater tendency for immature birds to leave their natal areas in search of unoccupied breeding sites (Irwin 1981, Johnston & Klitz 1977, Summers-Smith 1963). If immature birds are dispersing more than adult birds then the result is an Allee effect at low population density since a few adults would produce only a few young and thus a low dispersal rate. A G - test was run on the ringing recapture data to assess the effect of age on propensity to disperse.

Birds may spread to sites located close to their home range or they may disperse to sites tens or hundreds of kilometres away. These long range dispersal events (leap-frogging) result in formation of new foci, creating new waves of dispersal ahead of the main front, thus changing the velocity of the dispersal. To test for tendency to disperse over shorter distances, the birds were further separated into long range and short range dispersers and a G - test was run on the data.

Residuals were normally distributed (Kolmogorov-Smirnov test $P > 0.05$) in all cases of parametric analysis.

2.4 Results

Proposed dispersal routes 1 to 5 took the birds from Durban to Johannesburg, eastern Cape Province, Zimbabwe via Francistown (Botswana), Cape Town and to Namibia, respectively (Figure 2.01). The earliest records were made at Pietermaritzburg (1912), Ladysmith (1947), Voksrus (1948), Bethlehem (1949) and Johannesburg (1949), all on the railway line on route 1, and except for Pietermaritzburg they were all more than 200km away from the centre of spread, B. Town size does not seem to have hindered spread to these distant locations because Pietermaritzburg and Johannesburg were the only large towns then. There was therefore, a latent period from 1900 to about 1947 when there was a sudden jump to locations at least 200km away, followed two years later by a report 500km away in Johannesburg. Rapid dispersal over the next 10 years took the birds north through Botswana to Zimbabwe by 1958 (Route 3), south to Cape Town by 1963 (Route 4) and west through the northern Cape Province to Namibia by 1961 (Route 5). Dispersal along route 2 took the *indicus* birds of Durban west through the eastern Cape region towards East London, A (Figure 2.01). The fact that locations in the eastern Cape were all small and off the railway line could account for the cluster of negative residuals in the province (Figure 2.02). The rate of spread in the eastern Cape Province was slower than predicted by the exponential line from Durban. By 1970 the sparrow occupied all of southern Africa (Figure 2.03).

The exponential line gave the best fit on data for dispersal from Durban to the rest of the region ($R^2 = 0.60$, $P < 0.001$) and for the spread inside Namibia ($R^2 = 0.65$, $P = 0.05$). There was a slow initial rate of spread (an Allee effect) followed by rapid acceleration in the rate after 1950 (Figure 2.04). By then some birds had reached Johannesburg about 500 km away from Durban. Both the linear and exponential gave good fits to the dispersal data from Johannesburg. The linear provided the best fit, explaining 68% ($R^2 = 0.68$, $P < 0.001$) of the spread from Johannesburg while the exponential explained 62% ($R^2 = 0.62$, $P < 0.001$). At this stage the rate of dispersal was over 80 km/year and the distribution of positive residuals on routes 3, 4 and 5 shows that occupation along these routes was more rapid than predicted. Dispersal from East London (Figure 2.04b) was linear ($R^2 = 0.53$ $P < 0.001$) at a rate of 44.5 km/year. This could be due to a constant supply of birds from Durban probably merging with spread from East London, albeit on a smaller scale.

Size of location and proximity to the railway line had a significant effect on the rate of spread of sparrows. There was a tendency for birds to spread more to large towns, although the G test was not statistically significant ($G_{(1)} = 0.08$ $P > 0.05$). However, only a few locations qualified as large towns and these were invariably on the railway line (Figure 2.02), while many small towns were located on or near the railway line. The number of towns leading the dispersal on the rail was higher than those lagging it ($G_{(1)} = 5.58$ $P = 0.01$) (Figure 2.02). An analysis of small towns on their own showed that more small towns on the railway led the dispersal and that there were fewer small towns occupied off the railway (Figure 2.02).

Dispersal rates estimated from ringing data were more conservative, with birds reaching an average rate of 14 km/year. Of the 146 recaptured birds, only 33 had dispersed from where they were ringed and 28 (85%) of these were immature while 5 (15 %) were adult birds. Immature birds tended to disperse more than adult birds, ($G_{(1)} = 19.18$, $P = 0.001$) and male birds were more likely to disperse than females ($G_{(1)} = 18.11$, $P = 0.001$) (Table 2.01). However, large proportions of birds of all ages remained sedentary. The generally sedentary nature of the bird was also reported in Europe (Summers-Smith 1963) and North America (Johnston & Klitz 1977). Of 114 sedentary birds, 87 (77 %) were immature and 27 (23 %) were adults. Birds tended to disperse more over distances of less than 10 km ($G_{(1)} = 20.06$, $P = 0.001$) (Table 2.01). Long distance dispersal occurred to distances ranging from 10 km to over 300 km. A female immature bird dispersed to 343 km in 6 months while another immature of unknown sex reached 232 km in 6 years. About 7.4% of the birds in our data set had dispersed to distances over 10 km. In western Europe long distance movement to over 10 km was recorded in 4.4% of the birds recovered (3.2% of adults and 6.7% of immature birds) while in Britain 2.4% of the birds ringed between 1952 and 1954 dispersed to more than 10 km and in Germany only 0.8% were long distance dispersers (Summers-Smith 1963). Figures for house finches in North America show that immature birds dispersed to 329 km while adult birds reached 98 km (Veit & Lewis 1996).

2.5 Discussion

The invasion of southern Africa by the house sparrow was characterised by an initial period of slow spread for about 50 years after introduction followed by rapid expansion and occupation of most of the sub-region in the next 15 years. The pattern of dispersal was exponential with a rapid acceleration of the rate of spread following an initial slow rate. Following introduction around 1900 populations would have remained small with only a few immature birds and thus a low dispersal rate (the Allee effect). Only when a threshold density was reached could the invasion process start.

Until recently, most invasion research was conducted on species of agricultural and epidemiological interest (Parker & Reichard 1997). The study of invaders of natural habitats intensified with the initiation of the program on the Ecology of Biological Invasions by the Scientific Committee on the Problems of the Environment (SCOPE) in 1982 (Macdonald et al. 1986, Drake et al. 1989). Most research on the progression of invasions through space was mainly descriptive with only a few analyses of the dynamics of the spread. Although the introduction and spread of the house sparrow in southern Africa is still quite recent, its invasion was very rapid and is likely to have gone through the complete cycle of the diffusion wave. It is, therefore, well suited for use as a model for analysis of the dynamics of spread in the region.

2.5.1 The mode of dispersal in southern Africa

Dispersal of the house sparrow in southern Africa is consistent with that observed in other invading species such as the house finch and the European starling *Sturnus vulgaris* in North America; the red deer *Cervus elaphus* and Himalayan thar *Hemitragus jemlahicus* in New Zealand as well as the collared dove *Streptopelia decaocto* in Europe (Harwin & Irwin 1966, Long 1981, Veit & Lewis 1996). It is characterised by rapid acceleration of the rate following a slow initial rate of spread. From the time of introduction of the house sparrow in 1900 there was an initial slow phase until 1949, followed by rapid acceleration of the rate to about 85 km/year. In Australia the house sparrow went through a similar slow phase for 60 years, before spreading rapidly as far as the Tropic of Capricorn (Diamond 1986) and in North America it was only after about 50 years before the spread began (Johnston & Selander 1964). Veit and Lewis (1996) observed a depressed rate during the initial stages of the spread of the house finch

in North America followed by a rapid increase to 40km/year. The lag phase was much shorter for the European starling in North America, lasting for only 10 years before the bird spread rapidly from New York to the rest of the continent (van den Bosch *et. al.* 1992). This lag phase has also been observed in the spread of plant species, for example the spread of the weed *Mimosa pigra* in northern Australia (Lonsdale 1993). The slow initial phase is attributed to an Allee effect when the rate of spread is limited by low population numbers as a result of reduced pair formation. At this stage the population comprises mainly adult birds with lots of resources (especially nesting sites) at their disposal. Effective dispersal would only be seen when large numbers of juveniles had to spread due to limited resources at source (Johnston & Klitz 1977). The nine introduced species that spread more than 50km from the point of introduction in North America had been reintroduced and their populations had risen to at least a few hundreds before they spread (Veit & Lewis 1996). Unlike in North America and New Zealand there were no Acclimatisation Societies in southern Africa and therefore, no records of actual numbers released were kept. However, multiple records of introductions suggest repeated releases, which together with natural increases in local populations would have raised the population sizes above the threshold needed for dispersal to commence.

2.5.2 Dispersal rates

Although ringing recovery data tend to give conservative rates of spread (van den Bosch *et. al.* 1992), they offer an estimation of rates when man does not aid dispersal. The rate of dispersal estimated from ringing recovery data of southern African house sparrows was 14 km/year. This is consistent with observations elsewhere in its range. In Utah, North America it spread at a rate of 16 km/year and in Kansas at 12 - 23 km/year (Johnston & Klitz 1977) while in Europe the rate of dispersal was 28 km/year (Summers-Smith 1963). Where it was aided by man the rate accelerated to between 48 km/year and 120 km/year in North America (Johnston & Klitz 1977). In southern Africa the rate of dispersal rose to over 80 km/year by 1960. The acceleration seems to be closely linked to the availability of corridors for easy passage (lines of communication and human settlements).

2.5.3 Long-range dispersal (leap-frogging)

There was a tendency for birds to spread quickly to large distant locations (long range dispersal). Lines of communication tend to eliminate the barrier of distance, resulting in an acceleration of dispersal rates. An analysis of the spread of cholera in the United States in 1832 and in 1866 showed different patterns of spread for the two incidents of the epidemic (Chapman, 1981). The former spread in a distance-related pattern from centre to centre, whereas in 1866 the disease seemed to jump from one city to another and then trickle down the hierarchy. The difference was attributed to the fact that by 1866 the major cities of the eastern United States were linked by rail. The spread of an inherited incompatibility factor in *Drosophila* was speeded up by long distance migration aided by commercial fruit transport (Turelli & Hoffman 1991). Lonsdale (1993) noted that the rate of expansion of *Mimosa pigra* stands in wetlands in Australia was higher than expected for normal wind dispersal, and he concluded that flotation increased the rate of expansion of the weed stands in wetlands. Gould (1969) described such a pattern of spread combining long-range dispersal events to large distant sites with the slower wave front as a composite hierarchical expansion-diffusion.

We have described the invasion of the House Sparrow in Southern Africa as an exponential spread with a depressed initial rate attributable to the Allee effect followed by rapid acceleration of the rate to more than 80km/year. Dispersal was a composite hierarchical expansion-diffusion (Gould 1969) which is a combination of both long-range dispersal events and diffusive movement over short distances. Spread tended to be more rapid along the railway line and to large towns. Similar analyses of other southern African invasions such as the Indian

myna and the European starling would add to our knowledge of the dynamics of invasions in southern Africa.

Table 2.01. Propensity to disperse in southern African house sparrows. Ringed birds recaptured at ringing locations (non dispersers), at locations up to 10 km away (short range dispersers) and over 10 km from ringing locations (long range dispersers).

		Male		Female		Total	
		Adult	immature	Adult	immature	adult	immature
Total ringed		18	80	14	9	41	162
Non dispersers		16	57	11	6	39	129
Dispersers	All	2	23	3	3	2	33
	0-10km	1	14	2	1	1	19
	>10 km	1	9	1	2	1	14

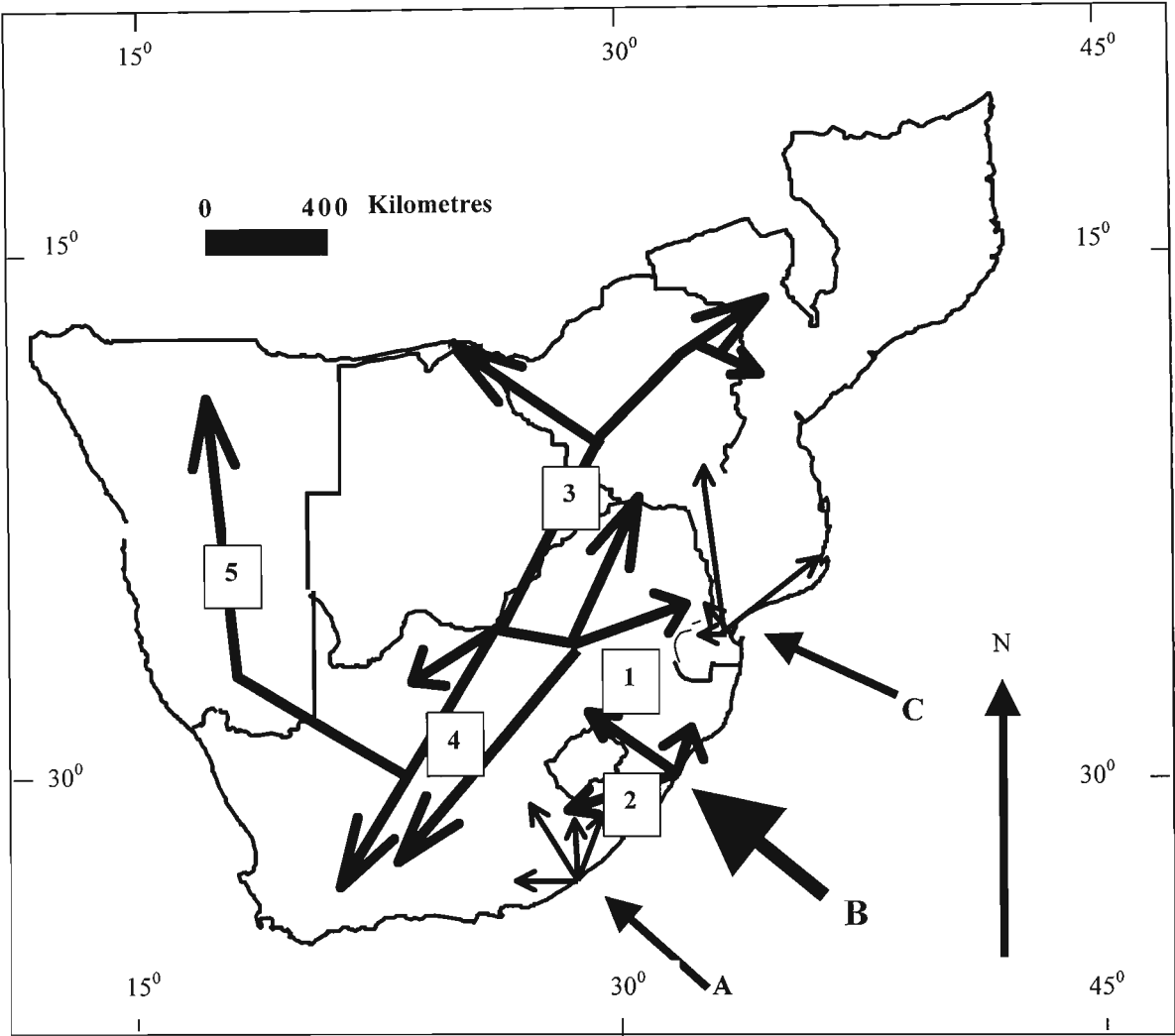


Figure 2.01. Dispersal routes of the house sparrow in southern Africa. Points A, B and C are known points of inoculation with the main introduction at A, Durban in 1900. Numbers refer to proposed routes of dispersal: (1) from Durban to Johannesburg; (2) from Durban to East London; (3) from Johannesburg to Zimbabwe (via Francistown, Botswana); (4) from Johannesburg to Cape Town; (5) from De Aar to Namibia.

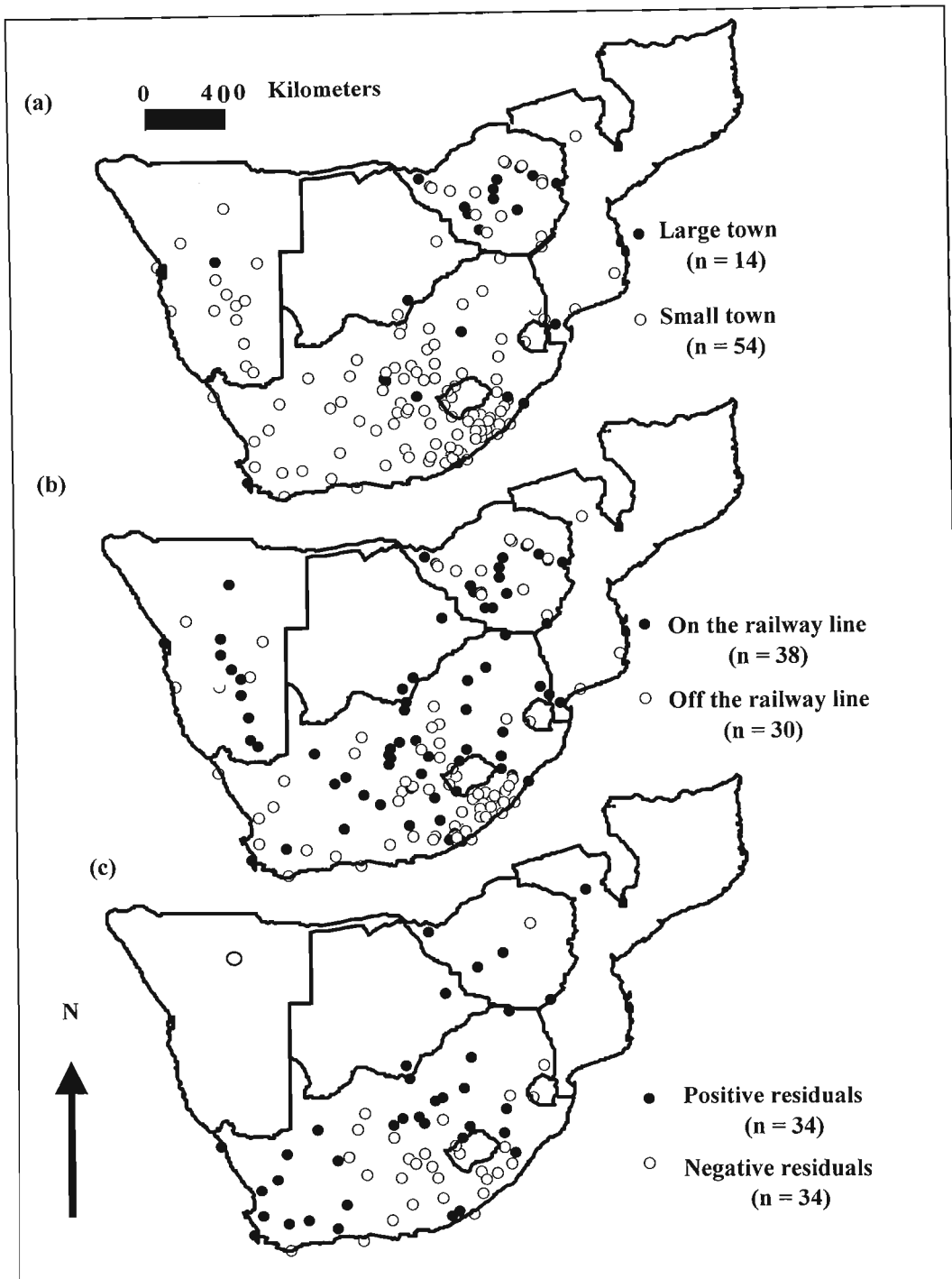


Figure 2.02. Distribution of locations of first reports of the house sparrow in southern Africa. (a) Distribution of locations by size. Solid circles represent large towns and open circles show small towns. (b) Distribution of locations of the house sparrow by proximity to the railway line. Solid circles are locations on the railway line and open circles are those off the railway line. (c) Distribution of positive and negative residuals from the best fit on data for all locations. Solid circles are positive residuals (locations leading the dispersal) and open circles are negative residuals (locations lagging the dispersal).

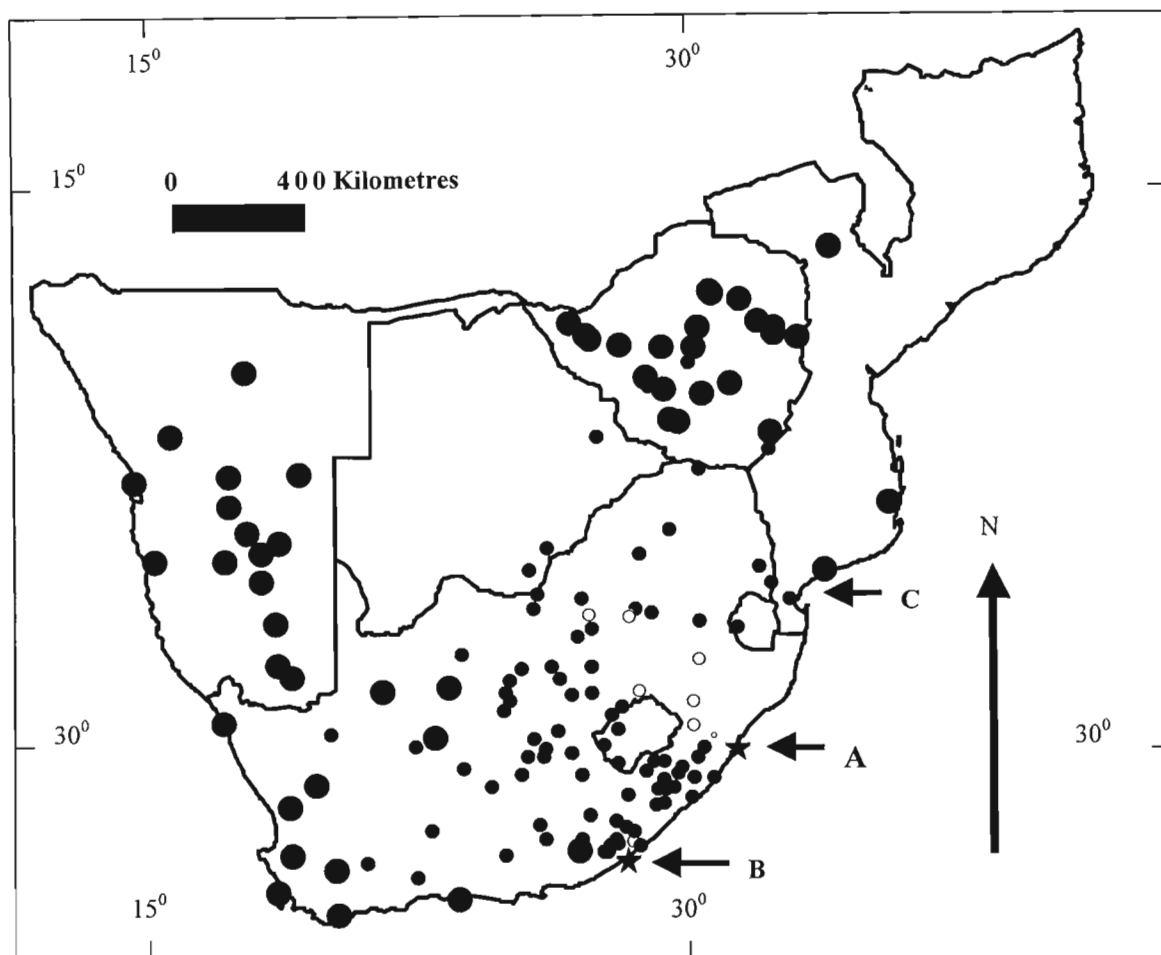


Figure 2.03. The spread of the house sparrow in southern Africa from 1900 through 1970. Centres of inoculation were at Durban (A), East London (B) and Maputo (C). The smallest open circle indicates arrival at Pietermaritzburg (1912) and thereafter circle size increases at 10year intervals starting from 1950 through to 1970.

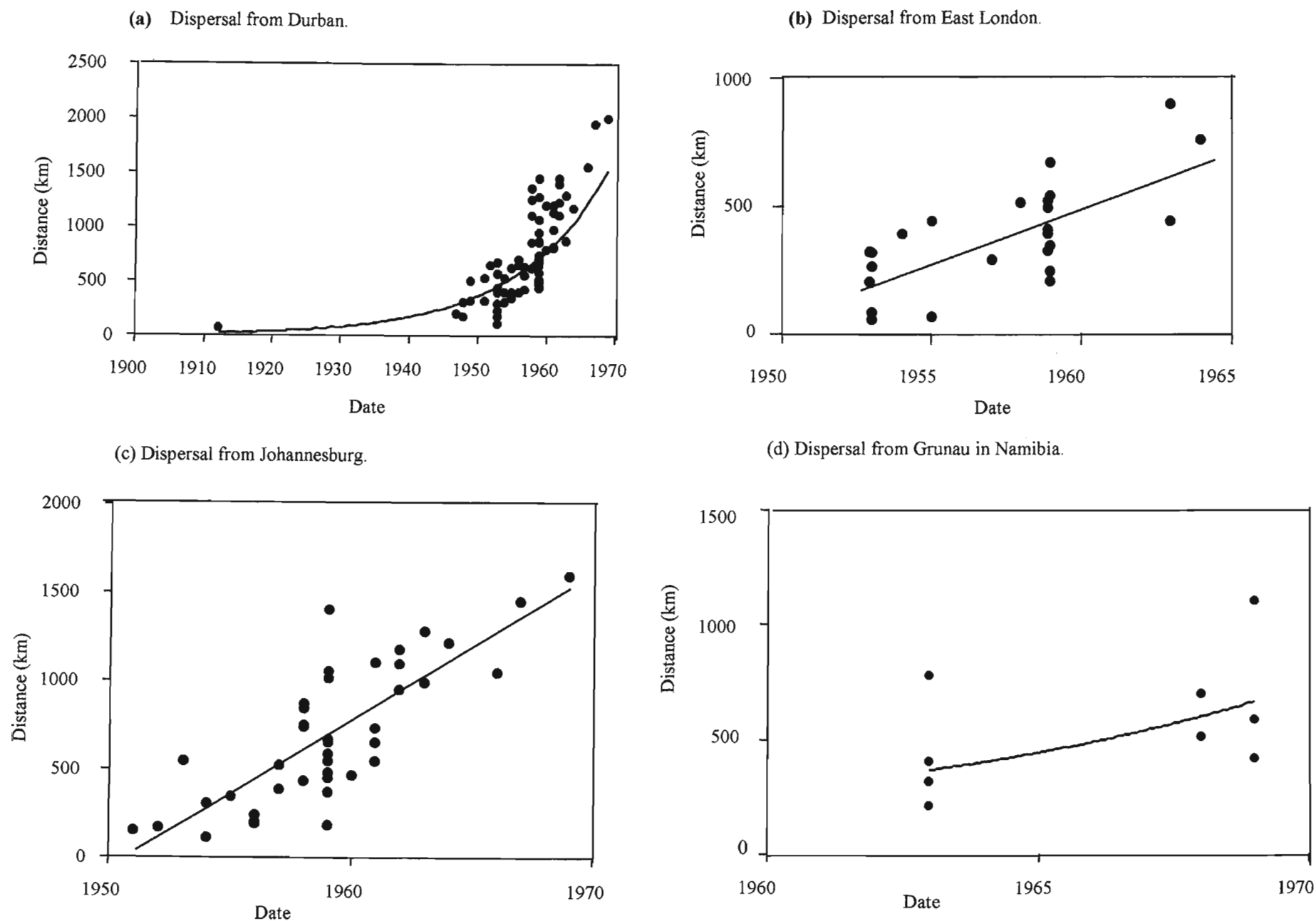


Figure 2.04. Dispersal of the house sparrow through southern Africa. (a) The overall dispersal pattern from Durban through to Namibia and Zimbabwe, (b) the dispersal from East London to the Eastern Cape Province of South Africa, (c) the dispersal after arrival at Johannesburg and (d) is the pattern of dispersal in Namibia.

CHAPTER 3

MORPHOLOGICAL DIFFERENTIATION AND THE EFFECT OF CLIMATE ON SOUTHERN AFRICAN POPULATIONS OF THE HOUSE SPARROW (*PASSER DOMESTICUS*)

3.1 Abstract

Introduction of the house sparrow, *Passer domesticus*, to southern Africa involved unknown numbers of both the *domesticus* race of Europe and *indicus* of Asia, resulting in the establishment of a genetically diverse founder population along coastal South Africa. The birds have undergone significant differentiation since introduction about 100 years ago. Significant sexual size dimorphism was detected among southern African house sparrows, especially in flight structures. Males were larger than females in all characters except tarsus and claw length. Overall body size variation was clinally ordered with a general increase in size with latitude in conformity with Bergmann's rule. Tarsus length decreased southwards, with the shortest tarsi in birds of coastal sites in South Africa and the longest in Zimbabwe. Patterns of variation in morphological characters paralleled climatic trends, especially minimum temperature and humidity. Beak size and shape of Zimbabwean birds appeared to be under the greatest influence of climatic factors. Shorter and more conically shaped beaks were selected for in females in Zimbabwe. Natural selection was modifying the morphological characters resulting in adaptive radiation in morphology of southern African populations.

3.2 Introduction

When two races of the house sparrow, *Passer domesticus domesticus* of Europe and *P. d. indicus*, of Asia were introduced to southern Africa at the end of the 19th century, a founding population of high potential phenetic and genetic variance was created. Thus, a huge base was provided for evolutionary divergence. Although actual numbers of birds introduced were not known, the general time frame and the parent stock involved were well documented (Clancey 1964, Courtney-Latimer 1942 1955, Gebhart 1944, Godfrey 1931, Harwin & Irwin 1966, Macworth-Praed & Grant 1963, Summers-Smith 1963 1988, Vierke 1970, Winterbottom 1959 1966). This provided a strong case for ecologists and evolutionary biologists to study adaptation and differentiation in recently introduced species in the tropics.

Studies of the house sparrow elsewhere in its new range have detected a remarkable adaptive potential. In Australia, New Zealand, North and South America, where birds of the nominate race were introduced, rapid colonisation and differentiation occurred (Baker 1980, Johnston & Klitz 1977, Johnston & Selander 1964 1971, Long 1981, Pizey 1980, Robbins 1973, Selander & Johnston 1967, Summers-Smith 1963 1988). Within 100 years of introduction to North America, significant differentiation had taken place in the invading populations (Johnston & Selander 1964). The house sparrow, like other invading species, has to adapt to a new suite of environmental factors in its new range. This results in behavioural and often morphological and physiological changes (Diamond 1986). These phenotypic adjustments or observed adaptations may be followed by corresponding genetic control, a process termed the Baldwin effect (Boag & Grant 1981, Hamilton 1961). It can be assumed, therefore, that in the long run phenotypic variation closely reflects underlying genetic variation (Boag 1983) and thus morphological measurements can be used to develop and test evolutionary theories. This provides a base for the study of the rate of evolution of invading species, that is, how soon the accompanying morphological and physiological evolution occurs, as well as to what extent the phenotypic variation is genetically based. Such evolutionary changes would normally take thousands of years (Neithammer 1971).

Climatic factors (the environment) influence avian adaptation and success by way of modification

of behavioural and physiological processes (James 1991). Assessments of the effect of environmental factors on morphological variation in house sparrows in North America indicate that selection for optimal size tends to be most intense during winter months. That is, body size variation tends to be affected more by minimum temperatures (Grant 1972 1986, Johnston & Fleischer 1981, Lowther 1977, Rising 1972). In this study I examined morphological variation in relation to environmental factors within and between localities in southern Africa. According to Johnston (1969b), such analyses of local differentiation are in fact studies of adaptation.

Similar work was undertaken on the colonisation and adaptation of the house sparrow in North America, Australia and New Zealand (Baker 1980; James 1970; Johnston & Klitz 1977; Johnston 1969a, 1969b, 1972b, 1973, 1976a, 1976b; Johnston & Selander 1964, 1971, 1972; Selander & Johnston 1967). In New Zealand variation in body size ran contrary to that predicted by Bergmann's rule, which relates to the inverse correlation between intraspecific size variation and environmental temperature (Mayr 1942, 1956, Hamilton 1961, James 1970). There was a tendency to small body size in the cooler southern parts of New Zealand while in the warmer north variation was clinaly ordered and closely paralleled that observed in Europe and at higher latitudes in North America (North of the Dakotas) (Baker 1980, Selander & Johnston 1967). Overall body size was negatively correlated with winter wet bulb temperature (Johnston & Selander 1972). This was consistent with Ripley's rule, a modification of Bergmann's rule, which states that there is a tendency to larger body size in arid areas than in humid regions (Hamilton 1961). Variation in body shape tends to follow Allen's rule (Mayr 1942 1956; Hamilton 1961, Selander & Johnston 1967, Johnston & Selander 1972). Length of extremities is positively correlated with temperature (Allen's rule). In a study of the Cape Sparrow, *Passer melanurus* in southern Africa, Slotow & Goodfriend (1996) observed that tarsi were longer in warmer parts of the range. In nature these selection forces do not operate in isolation and the birds would, therefore be subjected to a combination of ecogeographic rules.

Previous work on the house sparrow in southern Africa focused mainly on the introduction and spread of the bird in the region (Brooke 1997, Brooke *et. al.*1986, Harwin & Irwin 1966). In an abstract presented at a symposium on birds and man, Crowe and Brooke (1985) reported the existence of considerable adaptation by the house sparrow to local conditions in South Africa, especially to ambient temperature and solar radiation. No further work has been done in southern Africa to determine the extent of adaptation and differentiation since introduction.

The current study was conducted to investigate variation in morphological characters of house sparrows in southern Africa. There were two main objectives to this study. The first was to examine the extent of morphological variation in southern African populations of the house sparrow and the second was to determine the relationship between this variation and the environment. I predicted significant geographic variation in body size and shape of the house sparrow across its southern African range. In terms of the predictions of Bergmann's rule the birds of the hot, arid conditions of Zimbabwean in the north should be smaller in body size than those of the cooler South African localities. Therefore, a southward increase in overall body size was predicted for the region. Variation in local temperature and humidity conditions in Zimbabwe and South Africa would affect length of extremities according to Allen's rule so that populations in arid localities would have longer tarsi than those in the more humid sites. Variation in feeding structures would be expected to match trends in general body size variation (Allometry), but as Grant (1986) observed in finches beak size and shape tends to be related to food resources. He noted that beak depth was modified more readily by variation in food resources increasing significantly after severe winter. Seed size and abundance were affected by seasonal variation in temperature and bigger seeds were more readily available to the finches following severe winter temperatures. The house sparrow like the finches is a granivorous bird

although it has become more omnivorous due to its close association with urban man (Summers-Smith 1963).

Morphological data from specimens of house sparrows from southern African localities were analysed to test the following specific predictions:

- (1) A southward increase in overall body size was predicted where birds of the hotter Zimbabwean localities would be smaller overall than the birds of South Africa.
- (2) I predicted a southward decrease in tarsus length with longer tarsi in arid northerly Zimbabwean sites and shorter tarsi in the more mesic South African sites. Further, an east west trend within each country was predicted. In Zimbabwe, longer tarsi were expected in populations of the arid west, in Bulawayo and Hwange than in populations of more humid Harare. Similarly, in South Africa tarsi would be longer in populations of the drier west at Kuruman and shorter in humid coastal localities at East London through to Durban.
- (3) Minimum temperatures tend to be lower in Zimbabwe than in South Africa and this could result in differences in the range of seed size available as food for the birds. Smaller seeds, which are more susceptible to extremes of minimum temperature, would disappear sooner in Zimbabwe and thus, beaks would be bigger relative to body size than in South Africa where a wider range of seed size is expected.

3.3 Materials and Methods

Specimens of the house sparrow were requested from all southern African Museums. Due to differences in local rules and regulations governing loans in the different museums and to the cost and delays in postage, it was not possible to get all the specimens to a central place. Permission was granted to assemble all South African specimens at the National Flagship Institution's Museum of Natural History (then Transvaal Museum) in Pretoria. Zimbabwean specimens were examined at the Natural History Museum of Zimbabwe in Bulawayo, where they are kept. Specimens could not be obtained from Mozambique and Namibia due to problems in communication. There were no house sparrows in the Botswana museum and none collected from Botswana in other local museums.

More than eight hundred specimens were obtained from the Durban Museum, East London Museum, Bloemfontein Museum and the Transvaal Museum, all in South Africa and from the Natural History Museum of Zimbabwe as well as from the British Natural History Museum at Tring and the Bonn Museum. Many were of immature birds and only 380 southern African specimens of adult birds were used in this analysis. Samples were put into population groups based on localities of specimens (Fig. 3.01). Generally, there were fewer specimens of female birds than males in museums (a situation also noted by Grant 1986). Following the method of Johnston and Selander (1971), only samples with a minimum of 5 specimens were used for the analysis. Of the 19 southern African populations sampled, 14 had sufficient males and 9 had sufficient females for statistical analysis (samples from sites 3, 4, 5 and 8 were not used for this analysis).

Specimens were separated according to sex, age and condition. Ageing of the male birds was done according to Johnston and Fleischer (1981), Selander and Johnston (1967) and Summers-Smith (1963). The main characters used in determining male age were pileum colour, extent of skull ossification and clarity of colour on the feathers of the bib and the nape while females were aged mainly on skull ossification and pileum colour.

Six measurements of morphological characters were taken from both male and female adult birds using vernier callipers reading to 0.02mm and one (wing length) was taken with a stopped steel ruler to 0.05mm (Table 3.01). Measurements were taken according to Svensson (1984), Johnston (1969b), Selander and Johnston (1967). Tarsus length was used as an index of body size.

According to Johnston and Selander (1964), tarsus length tends to be a more reliable measure of body size in house sparrows than wing length. Where a single trait is used as an index of body size it is recommended that tarsus length be used (Boag & Grant 1981, Freeman & Jackson 1990). Measurement error was estimated by a repeatability coefficient, r , for four repeated measurements of traits on a small sample of house sparrows. Among its other uses, repeatability can be used to assess the reliability of repeated measurements on the same individual (Barnard 1994, Lessels & Boag 1987) in which case it is calculated as the interclass coefficient from a one way Anova (Sokal & Rohlf 1981).

Environmental data were obtained from the offices and publications of the Meteorological Services Department in Harare, Zimbabwe; the Weather Bureau in Pretoria, South Africa and from Schulze (1965). Eight environmental factors were used as follows: (1) Latitude; (2) Longitude; (3) Absolute maximum temperature (the highest temperature recorded annually); (4) Absolute minimum temperature (the lowest temperature recorded annually); (5) Mean temperature (the sum of absolute maximum and absolute minimum divided by 2); (6) Precipitation (the mean annual rainfall); and (7) Relative humidity (the mean annual relative humidity).

3.3.1 Statistical analysis

Summary statistics for all measurements were calculated with StatGraphics (SGPLUS7.0) software at the School of Life and Environmental Sciences, University of Natal and at the Natural History Museum of Zimbabwe in Bulawayo.

3.3.1.1 Sexual dimorphism

A single way Analysis of Variance (ANOVA) was run on the combined data set to determine sexual size dimorphism. Generally, tarsi and claws were longer in females than in males while all other structures were longer in males than in females (Table 3.02). However, separating the birds of South Africa from those of Zimbabwe revealed different trends in sexual dimorphism. The birds of Zimbabwe were significantly sexually dimorphic in size of all except bill width and depth. Males exceeded females in wing length ($P < 0.001$), tail length ($P < 0.001$) and bill length ($P < 0.05$) while tarsi ($P < 0.05$) and claws ($P < 0.001$) were longer in females than in males. In South Africa sexes differed in 5 characters namely wing length ($P < 0.001$), tail length ($P < 0.01$), bill length ($P < 0.05$), bill width ($P < 0.05$) and bill depth ($P < 0.001$) and males exceeded females in all five. There was no significant difference between tarsus and claw length of males and females although these tended to be longer in females than in males. Thereafter sexes were treated separately and Zimbabwean and South African samples were also separated for subsequent analyses.

Parametric statistics were used because residuals from ANOVA of all characters were normally distributed as determined by the Kolmogorov-Smirnov tests ($P > 0.05$) (Marcus 1993, Sokal & Rohlf 1981).

3.3.1.2 Geographic variation in body size.

The Principal Components Analysis of variation (PCA) was run on the data set for seven morphological characters and the first three principal components extracted. Principal Components Analysis of variation (PCA) is used to describe relationships between morphological characters and to reduce large numbers of characters into a small set of factors (Principal Components). The principal components can then be saved for subsequent use in a regression analysis or other prediction technique like Anova (Freeman & Jackson 1990, Pimentel 1979, Sokal & Rohlf 1981). The Principal Component (PC) with coefficients of the same sign indicates size variation and is known as the growth or general component and this is usually the first Principal Component (PC1). PC1 is therefore, normally considered an index of overall body size

and accounts for 40-60% of total variance (Dunn & Everitt 1982, Niles 1973a b, Pimentel 1979, Rising 1987, Robins & Schnell 1971, Rohwer 1972, Schluter 1984, Zink 1982). Graphs of PC2 and PC3 values on PC1 were drawn to show separation of characters along the principal components. Further, scatterplots of PC2 and PC3 on PC1 were done to see if populations clustered out on any of the axes. Regression of PC1 on environmental factors was run to simulate the way the environment would affect the individual. This way the individual could then be examined over its total character states (Johnston & Selander. 1972).

Since PC1 values accounted for low percentages of variation (28% and 34% for male and female South African birds; 22% and 29% for Zimbabwean males and females, respectively), it was decided to use either tarsus or wing length as an alternative measure of size in southern African populations of the house sparrow. Johnston and Selander (1964) observed that for the house sparrow in North America, tarsus length was a better measure of size than wing length. Further, Freeman and Jackson's (1990) recommended that where a single variable has to be used as an index of body size then tarsus length should be used. To determine whether tarsus length was the better measure of size than wing length in southern African house sparrows, a regression analysis of wing or tarsus on PC1 was performed. The character with the higher R^2 value from the regression was a better measure of size. A value of $R^2 = 16.11\%$ was obtained from the regression of tarsus wing length on PC1 and $R^2 = 6.05\%$ from the regression of wing length on PC1. Thus, tarsus length was used as an index of body size in southern African house sparrows.

3.3.1.3 Single character variation

To determine single character variation, further Manovas were run on wing, claw, tarsus and tail length with each character as the dependent variable, population as an independent variable and time as the covariate. The Scheffe Multiple range tests were performed to determine homogenous sets of populations. An Analysis of covariance (Ancova) was performed on the beak dimensions with bill length, width and depth as dependent variables, population as the independent variable and tarsus as the covariate in order to remove a size effect.

3.3.1.4 Geographic variation in beak size and shape.

To determine geographic variation in beak size and shape independently of body measurements, a further Principal Components Analysis was run on beak dimensions. PC1 values obtained from the Principal Components Analysis of beak dimensions were regressed on tarsus length to factor out the effect of body size on beak size. A Manova was run on the residuals from the regression of PC1 of beaks on tarsus to determine geographic variation in beak size independent of body size. Further, the residuals were regressed on the environmental factors to determine the effect of the environment on beak size independent of body size. When PC1 of beak dimensions is plotted against tarsus length the deviations of individual beak PC1 values from the linear regression line are residuals. It would be expected that beaks would be larger in bigger birds than in smaller ones (Allometry). A deviation from allometry suggests possible adaptive modification of the character that varies independently of body size. The character which varies independently of body size is actually being modified by the environment (Grant 1986).

3.3.1.5 The effect of the environment on morphological characters.

Regression analyses were performed on all morphological characters relative to the eight environmental factors. If there is adaptive radiation in southern African sparrows, patterns of variation in morphological traits should closely parallel variation in environmental factors as predicted. Generally, bigger birds would occur in the cooler parts of the range and size variation would follow climatic clines (Figs 3.02 & 3.03).

3.4 Results

3.4.1 Sexual size dimorphism

There was significant secondary sexual dimorphism in size of house sparrows both in Zimbabwe and in South Africa and the latter birds were bigger on average than their Zimbabwean counterparts. Generally males were larger than females. An exception to this trend was tarsus and claw length (Table 3.02). Tarsi and claws were significantly longer in Zimbabwean females than in their male counterparts. No significant difference was detected between South African male and female tarsi and claws (Fig. 3.04).

Flight characters were significantly dimorphic both in Zimbabwe and in South Africa. Both wings and tails were longer in males than in females. Generally, South African birds had shorter wings and longer tails than Zimbabwean birds (Fig. 3.05).

Sexual dimorphism in beak structures varied between the two countries. South African birds were significantly dimorphic for beak length ($P < 0.05$), width ($P < 0.01$) and depth ($P < 0.001$) while male and female Zimbabwean birds differed only in beak length ($P < 0.05$). In South Africa male beaks were generally larger than female beaks in all dimensions. In Zimbabwe, on the other hand, beaks were significantly longer in males than in females but did not differ significantly in width (Fig. 3.06). Thus, there was significant sexual size dimorphism both in overall size and shape of beaks in South African birds but only in bill length of Zimbabwean birds. Therefore, short, conical beaks increased fitness in females and more robust beaks were selectively advantageous for male birds in southern Africa.

On the whole, therefore, there was significant sexual dimorphism in southern African house sparrows and patterns of dimorphism were different in Zimbabwe and South Africa. Sexes differed in all characters except bill width and depth in Zimbabwe and in all except tarsus and claw in South Africa. Thus, flight structures and bill length appeared to be under the influence of related selection forces in both countries. Generally, in Zimbabwe males had longer tails, wings and bigger beaks than their females, which in turn had small conical beaks. South African males, on the other hand had longer wings and tails and larger beaks overall than the females.

3.4.2 Principal Components Analysis of variation (PCA)

3.4.2.1 Separation of morphological characters on components of variation

Principal Components of all seven morphological characters were extracted for the data matrices of male and female birds separately (Table 3.03). The first three Principal Components accounted for low percentages of the total variance. PC1 accounted for only 28% of the variance in males and 34% in females of South African birds and only 22% and 29% of variation in Zimbabwean males and females, respectively.

PC1 comprised positive coefficients in all South African birds and in Zimbabwean females and was therefore, a measure of overall body size in South African birds generally and in Zimbabwean females only.

In Zimbabwean males however, PC1 consisted of both positive (tail, bill width, wing and tarsus) and negative (claw, bill length and bill depth) coefficients. All characters loaded positively on PC2 (Table 3.03). It appears that PC1 may be a measure of shape more than size and that PC2 may provide the measure of size variation in Zimbabwean males.

Tarsus, tail and wing length separated together in one direction along PC2 while bill depth and length separated together in the opposite direction (Fig. 3.07a). Bill width loaded heavily on PC3

with corresponding negative correlation of tarsus and tail length (Fig. 3.07b). PC3 therefore, described mainly variation in bill width of Zimbabwean males.

Among Zimbabwean females claw and tail separated together in one direction and beak depth and width separated together in the opposite direction along PC2 axis (Fig. 3.08a). PC3 described mainly variation in wing length (Fig. 3.08b).

In South African males, PC2 summarised shape variation, with high negative coefficients for tarsus and claw length and low positive coefficients for wings, tails and all beak dimensions (Fig. 3.09). Tails loaded strongly negatively along the third component of variation in males. Thus, PC3 was mainly variation in tail length. Similarly, PC2 of South African females summarised a negative correlation of tarsus with tail length while beak width and depth were opposed along the axis of the third component (Fig. 3.10).

There was strong covariation of beak dimensions, particularly bill length and depth and they tended to separate together in the opposite direction to tarsus and flight structures. This suggested that beak size and shape may be controlled by genes independent of those that influence tarsus and flight structures (Freeman & Jackson 1990), especially in Zimbabwe.

3.4.2.2 Separation of beaks on components of variation

In a separate Principal Components Analysis of beak dimensions only, PC1 accounted for 44% of variation in Zimbabwean males and 55% in females. In South Africa PC1 explained 55% and 52% of the variation in males and females, respectively.

In Zimbabwean males PC1 of beaks comprised both positive and negative coefficients. Bill length and depth both loaded positively on PC1 while bill width loaded negatively. PC2 comprised a high positive coefficient of bill width and low positive coefficients of bill depth and bill length. PC2 therefore, summarised mainly variation in bill width of Zimbabwean males (Fig. 3.11). On the PC3 axis bill depth was positive while bill length was negative. This axis described opposing effects of bill depth and bill length in Zimbabwean males.

All coefficients of PC1 were positive in Zimbabwean females and PC2 was made up of the positive correlations of bill length and depth on the one hand and the negative correlation of bill width on the other (Fig. 3.12a). On the PC3 axis, bill depth had a strong positive coefficient while bill length and bill width were negative (Fig. 3.12b). Thus, PC3 summarised variation in bill depth.

In South African birds all coefficients of PC1 were positive in both sexes. In males, bill width was strongly negative and bill length positive on PC2 (Fig. 3.13a) while PC3 summarised variation in bill depth (Fig. 3.13b). In females on the other hand, PC2 had low coefficients for all beak dimensions. Bill width was negative on this axis while bill depth was positive and bill length had zero loadings on PC2 (3.14a). Bill length loaded positively on PC3 while bill depth and width separated together with negative coefficients along the PC3 axis (Fig. 3.14b). PC3 was the inverse relationship of bill length and bill depth in South African females.

Thus, PC1 was an index of overall beak size variation in all except Zimbabwean males and PC2 summarised variation in shape of beaks. PC3 summarised opposing effects on bill length and depth in South African females and in all Zimbabwean birds while in South African males PC3 was variation in bill depth.

3.4.3 Geographical variation in size

Analysis of variance of all southern African samples together detected significant geographic

variation in PC1, 2 and 3 of both sexes and in all male characters except wing length as well as all female characters except tarsus and claw length, bill length and bill width. When Zimbabwean and South African samples were separated different trends were revealed.

3.4.3.1 Geographical variation in body size

In the analysis of combined southern African samples significant geographic variation was detected in PC1, 2 and 3 of both sexes ($P < 0.01$) (Table 3.04). On separating the samples, this trend was lost and there was no significant geographic variation in PC1 of both Zimbabwean and South African male birds ($P > 0.05$). PC2 of males ($P < 0.001$) still varied significantly among Zimbabwean and South African populations. PC1 of females was also significantly different among both Zimbabwean ($P < 0.01$) and South African ($P < 0.05$) populations analysed separately (Table 3.04). Since PC1 represents general body size in all except Zimbabwean males, the analyses of variance identified significant interpopulation differences in overall body size of females of both Zimbabwe and South Africa and none in South African males. When PC2 was used as an index of body size in Zimbabwean males then variation in PC2 suggested significant interpopulation variation in overall body size of Zimbabwean males as well.

Although there was considerable overlap on the scatterplot of PC2 on PC1, Zimbabwean males and females tended to cluster out by population (Fig. 3.15a,b). However, there was no obvious separation of South African populations of both sexes on these two axes (Fig. 3.16).

3.4.3.2 Geographic variation in tarsus and claw length

Interpopulation variation was detected in tarsus length of all southern African males together ($P < 0.001$). Female tarsus length did not vary but the residuals of individual tarsus measurements from the mean varied significantly among southern African populations for females ($P < 0.01$) (Table 3.04). Again trends in South Africa and Zimbabwe were different. In Zimbabwe there was no significant variation in both sexes while in South Africa populations differed in male tarsus length ($P < 0.001$) and in the residuals of female tarsus length ($P < 0.01$). According to the Scheffe multiple range test (Fig. 3.17), there was no clear trend in tarsus length of either sex. In males, the shortest tarsi were in mid latitudes at Nylstroom (9) and this population was significantly different from those of high latitude localities at Umtata (17) and East London (18) where the longest tarsi were found. Females in Pretoria had the shortest tarsi and were significantly different from those of Umtata which again with the longest tarsi. Both Zimbabwean males and females had longer tarsi than would be predicted from their geographic position and Durban females had shorter tarsi than expected from the latitudinal trends. Only the males were geographically variable for claw length ($P < 0.05$), with a southward trend similar to that of tarsus length variation.

3.4.3.3 Geographic variation in flight structures

Only wing length of females differed among populations ($P < 0.01$) and tail length varied geographically in both sexes ($P < 0.001$). No differences were detected in wing length in Zimbabwean and South African samples separately for both sexes, although Zimbabwean males generally had longer wings than South African birds of both sexes. Tail length was highly variable in both the combined southern African samples and in the separate Zimbabwean and South African samples. Females ($P < 0.01$) had differentiated more in tail length than males ($P < 0.05$) in both countries. The shortest tails were found in the north in Zimbabwe for both sexes (Fig. 3.18). Males in Harare (1) had the shortest tails and were significantly different from those of Kuruman (11), Bloemfontein (12) and Umtata (17) and females in Harare (1) had significantly shorter tails than those of Pretoria (10), Weenen (13), Durban (15), East London (18) and Port Elizabeth (19). Thus, tails were longest in the south in coastal South African

localities and in the west.

3.4.3.4 Geographic variation in beak dimensions

Sexes differed significantly in beak dimensions among populations across the southern African range. While males had become significantly different in all three beak dimensions ($P < 0.05$), females only differed in beak depth ($P < 0.01$). In separate Zimbabwean and South African samples however, beaks varied differently. Beak length and depth differed significantly among Zimbabwean samples. In Zimbabwean males the greatest variation among populations was in beak depth ($P < 0.001$) and then beak length ($P < 0.05$) while females differed most in beak depth ($P < 0.01$) and then in beak width ($P < 0.05$) (Table 3.04). In South Africa only beak width ($P < 0.05$) and depth ($P < 0.01$) of male birds varied significantly among populations and there was no geographic variation in female beaks. Generally, South African birds had bigger beaks than their Zimbabwean counterparts.

3.4.4 Effect of climate on morphological variation

Trends in variation of temperature and humidity levels followed both latitudinal and longitudinal clines. Due to a tendency to higher absolute maximum temperatures and lower absolute minimum temperatures in Zimbabwe, temperature range values were higher in Zimbabwe than in South Africa (Fig. 3.19). Humidity levels were highest in coastal South African sites decreasing northwards and westwards (Fig. 3.20). The effect of climate on morphological variation in southern African populations of house sparrows was examined against these trends.

3.4.4.1 effect of climate on overall body size

Latitudinal trends in PC1 (body size) were different between the sexes. Whereas PC1 of males was significantly correlated with both latitude and longitude (Fig. 3.21), PC1 of females was only weakly correlated with longitude (Fig. 3.22), decreasing towards the east. In males PC1 increased southwards and varied inversely with longitude. If PC1 is used as an index of overall body size variation then the regression identified a clinal increase in size of males from low latitudes to higher latitudes in conformity with the predictions of Bergmann's rule. Males were also bigger in the drier west, again in agreement with Ripley's observations that birds tend to be bigger in the more arid parts of the range.

There was no statistically significant variation in PC1 of females along either latitude or longitude, although PC1 values tended to be lower at higher longitudes (Fig. 3.22). Thus, body size of female birds decreased clinally eastwards also in conformity with Ripley's rule. Similar trends had been observed in North America where average size of house sparrows increased with latitude and hence with decreasing temperature (Grant 1986, Johnston & Klitz 1977, Summers-Smith 1988). Patterns of variation were only secondarily related to latitude and topography but primarily to temperature and moisture (James 1970).

Analysis of the association between climate and body size in southern African samples detected a close correlation between overall size of birds and temperature and humidity variables. Generally, PC1 varied directly with absolute minimum temperature and inversely with absolute maximum temperature, temperature range and precipitation. Because climatic conditions were different between Zimbabwe and South Africa regressions differed. PC1 of Zimbabwean male birds was positively correlated with absolute minimum temperature (Regression: $F_{1,96} = 7.82$ $R^2 = 7.53$, $P < 0.01$) and precipitation (Regression: $F_{1,96} = 5.06$ $R^2 = 5.01$, $P < 0.05$) but regressed negatively on absolute maximum temperature (Regression: $F_{1,96} = 7.63$ $R^2 = 7.37$, $P < 0.01$), mean temperature (Regression: $F_{1,96} = 5.89$ $R^2 = 5.78$, $P < 0.05$) and temperature range (Regression: $F_{1,96} = 7.99$ $R^2 = 7.68$, $P < 0.01$). Thus, (PC1) of males was smaller in the more

arid lowlying locations with relatively higher maximum temperatures, lower minimum temperatures and wider temperature ranges. However, since PC1 comprised negative and positive coefficients it could not be used as an index of body size variation. Since PC2 of males had all positive coefficients it might provide a better measure of variation in size of male Zimbabwean birds. PC2 changed inversely with minimum temperature ($F_{1,96} = 21.45$, $R^2 = 18.26$, $P = 0.001$) and precipitation ($F_{1,96} = 21.45$, $R^2 = 18.26$, $P = 0.001$) but increased with maximum temperature ($F_{1,96} = 17.20$, $R^2 = 15.19$, $P = 0.001$), mean temperature ($F_{1,96} = 13.03$, $R^2 = 11.95$, $P = 0.001$) and with temperature range ($F_{1,96} = 19.95$, $R^2 = 17.21$, $P = 0.001$). If PC2 is an index of body size variation in Zimbabwean males then male birds were larger in cooler sites and in more arid ones in Zimbabwe in conformity with the predictions of both Bergmann and Ripley. Since PC values did not seem to provide a reliable index for Zimbabwean males, tarsus length was preferred as a measure of body size variation.

PC1 of Zimbabwean females on the other hand, responded strongly to climatic changes (all regressions significant at $P < 0.001$). PC1 increased with maximum temperature, temperature range and mean temperature but decreased as minimum temperature, precipitation and relative humidity increased (All regressions: $F_{1,61} = 13.77$ $R^2 = 20.94$, $P < 0.001$). PC1 of Zimbabwean females provided an index of body size variation. Hence, female body size was larger in birds at arid sites and at low minimum temperatures.

Body size of Zimbabwean birds was therefore, subject to selective pressures associated with temperature and humidity levels. Generally, minimum temperatures and humidity levels increased with altitude in Zimbabwe (Meteorological Services of Zimbabwe, unpubl.) and maximum temperatures were higher at low altitudes such that low lying sites often had below zero minimum temperatures and high maximum temperatures. This would result in a large temperature range between the hottest and the coolest months of the year. Body size was probably being modified for survival at both extremes of temperature in which case temperature range would be more significant than just maximum and minimum temperatures independently.

In South Africa, PC1 had no significant relationship with climatic factors suggesting that the birds were not undergoing adaptive changes in overall body size. However, individual morphological characters were responding to climatic variation.

3. 4. 4. 2 *Effect of climate on tarsus length*

While wing length has traditionally been considered the morphological character that provides the best measure of size in birds, Johnston and Selander (1964) found that for house sparrows, tarsus length provided a better measure of body size. In keeping with this observation regressions of tarsus length with climate were used to reassess cause and effect relationships in southern African house sparrows.

Generally, tarsus length varied weakly clinally on latitude and longitude. Male tarsi increased clinally southwards and westwards (Fig. 3.23) while female tarsi did not change significantly with either latitude or longitude (Fig. 3.24). However, the longest female tarsi were still in the south.

No significant relationship was detected between tarsus and climate in Zimbabwean birds of both sexes. In South African birds, tarsi only varied inversely with maximum temperature in both males (Regression: $F_{1,132} = 7.83$ $R^2 = 5.94$, $P < 0.01$) and females (Regression: $F_{1,81} = 10.15$ $R^2 = 11.51$, $P < 0.01$).

Tarsus length was therefore, under selection forces related to absolute maximum temperature in

South Africa with long tarsi in the south at lower maximum temperatures and also in the west.

Claw length was also closely correlated with both temperature and humidity, especially in Zimbabwe. In Zimbabwean males, claw length regressed positively on mean temperature (Regression: $F_{1,96} = 4.35$ $R^2 = 4.09$, $P < 0.01$) and on temperature range (Regression: $F_{1,96} = 5.50$ $R^2 = 5.12$, $P < 0.01$). It varied inversely on minimum temperature (Regression: $F_{1,96} = 7.84$ $R^2 = 7.14$), precipitation (Regression: $F_{1,96} = 10.46$ $R^2 = 9.30$, $P < 0.01$) and relative humidity (Regression: $F_{1,96} = 7.54$ $R^2 = 6.89$, $P < 0.01$). Claw length of females also regressed positively on mean temperature ($F_{1,61} = 6.52$ $R^2 = 9.65$, $P < 0.01$) and temperature range (Regression: $F_{1,61} = 6.52$ $R^2 = 9.65$, $P < 0.01$) and inversely on minimum temperature (Regression: $F_{1,96} = 7.84$ $R^2 = 7.14$), precipitation (Regression: $F_{1,61} = 6.52$ $R^2 = 9.65$, $P < 0.01$) and relative humidity (Regression: $F_{1,61} = 6.52$ $R^2 = 9.65$, $P < 0.01$).

In South Africa claw length varied inversely with maximum temperature in males only (Regression: $F_{1,132} = 4.35$ $R^2 = 3.36$, $P < 0.05$). No relationship was detected between female claws and climate.

Thus, in Zimbabwe both males and females had longer claws in the more arid sites with low absolute minimum temperatures and in South African males, claws like tarsi, tended to be longer in the south at sites with low absolute maximum temperatures.

3. 4. 4. 3 *Effect of climate on flight characters*

There was no obvious latitudinal or longitudinal pattern of variation in wing length (Fig. 3.25) but tail length increased southwards and westwards in both male and female birds (Fig. 3.26). Again a strong correlation was detected between tail length and temperature as well as humidity. In Zimbabwe, tail length regressed more strongly on climate in females than in males. In males it only varied inversely with precipitation (Regression: $F_{1,96} = 3.80$, $R^2 = 3.87$, $P < 0.05$) while in females it was positively correlated with both mean temperature and temperature range (Regression: $F_{1,61} = 16.97$, $R^2 = 24.61$, $P < 0.001$) and varied negatively on precipitation and relative humidity (Regression: $F_{1,61} = 16.97$, $R^2 = 24.61$, $P < 0.001$). In South Africa there was greater sexual dimorphism in tail length response to climate. In male birds, tails responded to humidity variables, changing inversely with both precipitation (Regression: $F_{1,132} = 5.72$, $R^2 = 4.52$, $P < 0.01$) and relative humidity (Regression: $F_{1,132} = 3.80$, $R^2 = 3.04$, $P < 0.01$). In females on the other hand, tails were shorter at lower minimum temperature (Regression: $F_{1,81} = 6.48$, $R^2 = 7.76$, $P < 0.01$) and at high temperature ranges (Regression: $F_{1,81} = 6.21$, $R^2 = 7.46$, $P < 0.01$).

While wings did not seem to vary with climate in the southern African range, male tails were under selection forces related to humidity and female tails responded to both temperature and humidity variables. Both in Zimbabwe and South Africa, males in the more arid sites had longer tails and females in warmer sites had longer tails.

3. 4. 4. 4 *Effect of climate on beak shape and size*

Only bill length and bill depth varied significantly with latitude and longitude (Fig. 3.27 & 3.28). Bill length increased clinally southwards and there was a corresponding decrease in bill depth, especially in females. Along longitude, beaks became shorter and deeper towards the east. In Zimbabwe, these latitudinal and longitudinal trends were closely matched with climatic variation but not in South Africa.

In Zimbabwean males, bill length and bill depth responded similarly to climatic variation. Both were positively correlated with absolute maximum temperature (Regression: length $F_{1,96} =$

10.20, $R^2 = 9.17$, $P < 0.01$; depth $F_{1, 96} = 29.93$, $R^2 = 22.86$, $P < 0.001$), temperature range (Regression: length $F_{1, 96} = 9.43$, $R^2 = 8.54$, $P < 0.01$; depth $F_{1, 96} = 32.72$, $R^2 = 24.47$, $P < 0.001$) and mean temperature (Regression: length $F_{1, 96} = 4.71$, $R^2 = 4.46$, $P < 0.05$; depth $F_{1, 96} = 26.23$, $R^2 = 20.62$, $P < 0.001$) and regressed negatively on absolute minimum temperature (Regression: length $F_{1, 96} = 8.06$, $R^2 = 7.39$, $P < 0.01$; depth $F_{1, 96} = 32.73$, $R^2 = 24.48$, $P < 0.001$) and precipitation (Regression: length $F_{1, 96} = 5.12$, $R^2 = 4.82$, $P < 0.05$; depth $F_{1, 96} = 20.30$, $R^2 = 16.74$, $P < 0.001$). In females, bill length was the most variable, increasing with absolute maximum temperature (Regression: $F_{1, 61} = 10.20$, $R^2 = 9.17$, $P < 0.01$), temperature range and mean temperature (Regression: $F_{1, 61} = 17.73$, $R^2 = 22.52$, $P < 0.001$) but decreasing as absolute minimum temperature (Regression: $F_{1, 61} = 8.06$, $R^2 = 7.39$, $P < 0.01$), precipitation and relative humidity (Regression: $F_{1, 61} = 17.73$, $R^2 = 22.52$, $P < 0.001$) increased. Beak depth of female birds only regressed positively on absolute maximum temperature (Regression: $F_{1, 61} = 29.92$, $R^2 = 22.86$, $P < 0.001$) and negatively on absolute minimum temperatures (Regression: $F_{1, 61} = 32.73$, $R^2 = 24.48$, $P < 0.001$).

In South Africa, only male beak width regressed positively on precipitation (Regression: $F_{1, 132} = 5.00$, $R^2 = 3.96$, $P < 0.05$).

Overall, beaks were longer and thinner in the south and the west of the southern African range. In Zimbabwe, males and females in the more arid, warmer sites had longer, broader beaks. South African males had wider beaks in moist sites.

3.5 Discussion

The house sparrow, *Passer domesticus*, has undergone significant morphological differentiation since introduction to southern Africa between 1890 and 1930. Different patterns of sexual dimorphism were detected between the birds of Zimbabwe and South Africa. Five of the seven characters examined were sexually dimorphic in both Zimbabwe and South Africa. In Zimbabwe only beak width and depth were similar between the sexes and in South Africa only tarsus and claw were not dimorphic. Single character variation was clinaly ordered with a general increase in size with latitude. The close correlation of the patterns of variation in morphological characters with climatic trends was attributed to natural selection resulting in adaptive radiation in southern African populations.

Single character sexual size dimorphism was greater among the birds of Zimbabwe. Flight structures were particularly strongly dimorphic in both countries. Also there was stronger correlation of morphological characters with climate in Zimbabwean birds than in South Africa and different sexes responded differently to climatic variation suggesting that different selective forces might be in operation in the two countries and between the sexes. Morphological characters were generally bigger in males than in females except tarsus and claw length. In North America, male birds were larger than females (Johnston & Selander 1972, Rising 1972) and in Europe males were as much as 4-6% larger than females (Johnston 1969b). Similarly flight characters were strongly sexually dimorphic in Europe and North America (Johnston 1973, Johnston & Klitz 1977, Selander & Johnston 1967). Reexamination of data gathered by Bumpus in 1898 on sparrows killed in a storm in North America reaffirmed his observation that sexual dimorphism was accentuated by overwinter mortality (Buttemer 1992, Johnston & Selander 1973c, Johnston *et. al.* 1972). Further work by Fleischer and Johnston (1984) focused on the influence of winter conditions on physiology, ecology and behaviour of sparrows. They concluded that severe winters resulted in modification of size distribution in a population. Increasing severity of winter climate results in larger males, but smaller (less variables) females. Thus, small size in males and large size in females lowered survival fitness. Changes in size may be due to a combination of physiological, behavioural, and ecological pressures.

Since minimum temperatures in South Africa were generally higher than in Zimbabwe and maximum temperature was higher in Zimbabwe than in South Africa the birds of Zimbabwe would be subjected to higher annual changes in temperature. This could result in fluctuations in sex ratios and character size dimorphism similar to the "Bumpus effect" of North America and would explain the higher sexual dimorphism in Zimbabwe. Such strong sexual dimorphism would persist if there was ecological partitioning of the habitat along sexual lines (Smouse 1971). Maintenance of sexual dimorphism in size is largely genetic in birds and fighting for feeding rights could be responsible for mortality patterns resulting in modification of size distribution (Johnston and Fleischer 1981).

Further separation of sexes on beak size and shape in southern African sparrows strengthens the argument for ecological partitioning. The tendency towards short, conical beaks in females and relatively longer, broad beaks in males in arid lowlying areas in Zimbabwe is in conformity with Grant's (1986) observations on the relationship between size and shape of beaks with food resources. In Galapagos finches, beak size and shape, especially beak depth was modified rapidly in response to environmental changes (Grant 1986). Previously, Boag and Grant (1981) had demonstrated a direct response to variation in climate. After a dry season nestling survival decreased, more female ground finches, *Geospiza fortis* died and large birds tended to survive more. Because seed abundance decreased following low rainfall and smaller seeds disappeared faster, the birds had to adjust to taking large seeds. This resulted in modification of beak size and shape, especially beak depth. Similarly in southern Africa, selection would favour broader beaks where seeds were bigger and less abundant, such as would be the situation in Zimbabwe where minimum temperatures and precipitation were generally low.

In North America, the house sparrow had differentiated significantly within 100 years of introduction and several studies of morphological variation focused on the influence of climatic conditions on size (Johnston & Fleischer 1981, Johnston & Selander 1964 1971 1972, Selander & Johnston 1967). In all cases, there was a strong negative regression of body size on temperature, especially winter temperatures, consistent with the adaptive predictions of Bergmann's rule (Mayr 1942 1956). In Europe and Asia body size was positively correlated with latitude in Oriental populations but not in Palaearctic groups and there was also a general increase in size from west to east (Johnston 1969a b, Summers-Smith 1988). Grant also showed that average size in birds increased with latitude, hence decreasing temperature (Grant 1986). Although such patterns were related to latitude and topography, James (1970) argued that they were primarily attributable to temperature and moisture. Average body size variation as measured by Principal Component 1 was not significantly different among southern African populations except in Zimbabwean females where there was a strong negative regression with minimum temperature. Zimbabwean females were in concurrence with Bergmann's rule and with my predictions for body size variation in southern Africa.

Tarsus length was then used as an alternative measure of size according to Freeman and Jackson's (1990) recommendations and also since Johnston and Selander (1964) observed that for the house sparrow in North America, tarsus length was a better measure of size than wing length. Tarsus length varied geographically in males, with a general southward increase in size and a negative regression on temperature variables, especially in South African birds. Thus tarsi were longer in birds of the coastal sites in the south. However, in the south, birds of the drier areas in the west had longer tarsi than in more humid sites. This pattern was in concurrence with Allen's rule on adaptation for shorter extremities in cooler, more humid parts of the range (Mayr 1942). According to Slotow and Goodfriend (1996) long legs conferred a selective advantage in the Cape Sparrow, *Passer melanurus*, in arid areas possibly because they

promoted increased convective heat loss.

If natural selection is maintaining the clines of character variation observed in sparrows, then the genetic and nongenetic components of phenotypic variation must covary (James 1970). Future work should determine whether phenotypic adjustments to the environment have become genetically controlled; establish the persistence or otherwise of *domesticus* and *indicus* genes and determine to what extent the evolutionary potential of the house sparrow has been realised in southern Africa.

An analysis of morphological variation in house sparrow populations of southern Africa was successfully conducted and it was established that there was significant sexual size dimorphism in southern African house sparrows and that patterns of dimorphism were different in Zimbabwe and South Africa. Long tarsi, short tails and short, conical beaks conferred a fitness advantage in females and long wings and more robust beaks were selectively advantageous for males. Overall body size was clinaly ordered, increasing with latitude in conformity with Bergmann's rule. There was no clear trend in tarsus and wing length variation in either sex, although the tarsi were longer and wings shorter in mesic sites at high latitudes. Tail length was highly variable and females had differentiated more in tail length than males in both countries. The shortest tails were found in the north in Zimbabwe. Tail length was under selection forces related to humidity and temperature. Short, conical beaks increased fitness in more arid conditions in Zimbabwe and more robust beaks were selectively advantageous for birds in high precipitation areas of South Africa. Thus, southern African birds, particularly those in Zimbabwe, were undergoing adaptive radiation.

Table 3.01. Description of morphological characters examined for the analysis southern African populations of the house sparrow, *Passer domesticus*. (Bill length measurements were taken according to Johnston (1969b), Selander & Johnston (1967). All other measurements according to Svensson (1984)).

Character	Description of character
Wing length	Maximum length of wing: primaries flattened and straightened.
Tarsus length	Length from notch at the back of the intertarsal joint to the lower edge of the last scale before the toes diverge.
Claw length	The chord on top of the claw from the tip to the edge of the skin.
Tail length	From the point of insertion of retrix of naturally folded tail.
Bill length	From the tip of the beak to the anterior edge of the nostril.
Bill depth	From the top of the maxilla to the bottom of the mandible at the proximal end of the nostril.
Bill width	Width of mandibles at the proximal end of the nostril.

Table 3.02. Sexual size dimorphism in morphological characters of southern African house sparrows.

Character	Analysis of Variance ¹			South Africa		
	F. ratio	Combined samples Mean±s.e. males females	of Zimbabwe Mean±s.e. males females	F. ratio	males females	Mean±s.e. males females
Wing length	95.93***	75.2±0.1 72.8±0.2	87.57*** 75.8±0.2 73.3±0.2	34.61***	74.6±0.2 72.5±0.3	
Tarsus length	0.65	17.48±0.06 17.55±0.07	4.74* 17.27±0.07 17.53±0.09	0.40	17.66±0.07 17.58±0.10	
Claw length	12.71***	6.38±0.03 6.58±0.04	17.65*** 6.19±0.04 6.48±0.05	3.38	6.54±0.05 6.68±0.06	
Tail length	12.83***	58.6±0.3 56.6±0.4	27.68*** 55.9±0.3 53.2±0.4	6.65**	60.7±0.5 58.8±0.6	
Bill length	8.24**	8.66±0.03 8.51±0.04	3.85* 8.56±0.04 8.42±0.05	4.61*	8.75±0.05 8.59±0.06	
Bill width	0.80	5.96±0.02 5.92±0.03	1.79 5.91±0.03 5.98±0.04	6.82**	6.05±0.04 5.82±0.05	
Bill depth	5.75*	7.51±0.03 7.41±0.03	0.72 7.50±0.03 7.55±0.04	12.08***	7.52±0.04 7.32±0.04	

¹One way ANOVA.

Sexual size dimorphism statistically significant at *P<0.05; **P<0.01; ***P<0.001.

Number of specimens (Zimbabwe males =103, females =63, South Africa males = 133, females = 81).

Mean±s.e. denotes the mean value plus or minus the standard deviation.

Table 3.03. Principal component weights of seven morphological characters of southern African house sparrows.

Character	sex	Components of Variance					
		South Africa			Zimbabwe		
		Principal Component weight			Principal component weight		
		1	2	3	1	2	3
Wing length	M	0.40	0.26	-0.20	0.46	0.32	0.29
	F	0.46	0.16	0.08	0.27	0.13	-0.81
Tarsus length	M	0.28	-0.54	-0.27	0.31	0.24	-0.31
	F	0.32	-0.63	-0.06	0.35	0.11	-0.02
Claw length	M	0.20	-0.74	0.13	-0.13	0.54	-0.01
	F	0.33	-0.30	-0.24	0.14	0.63	0.39
Tail length	M	0.15	0.06	-0.82	0.41	0.41	-0.48
	F	0.23	0.69	-0.23	0.40	0.47	-0.19
Bill length	M	0.45	0.28	0.10	-0.48	0.33	-0.31
	F	0.54	0.03	0.10	0.52	0.0	0.32
Bill width	M	0.47	0.05	0.44	0.07	0.38	0.70
	F	0.31	0.05	-0.63	0.35	-0.45	-0.09
Bill depth	M	0.52	0.07	0.01	-0.52	0.36	0.07
	F	0.36	0.09	0.69	0.49	-0.38	0.23

Percentage of variance accounted for by principal component 1: South African males 28%, females 34%; Zimbabwean males 22%, females 29%. Total variance accounted for by PC1, 2, 3: South African males 59%, females 65%; Zimbabwean males 57%, females 63%.

Table 3.04. Geographic variation in morphological characters of Southern African house sparrows.

Character	sex	Combined samples		Analysis of variance		Zimbabwe	
		d.f.	F ratio	d.f.	F ratio	d.f.	F ratio
Wing length	M	226	1.28	124	0.54	101	1.97
	F	129	3.09**	66	2.05	62	0.01
Tarsus length	M	225	4.94***	123	5.33***	101	1.00
	F	129	1.90	66	2.22	62	0.02
Claw	M	226	5.22***	124	2.29*	101	5.36**
	F	128	1.58	65	1.34	62	0.01
Tail	M	219	6.69***	120	2.32*	98	1.32
	F	119	14.21***	65	5.76***	53	8.82**
Bill	M	221	1.96*	120	1.02	100	2.60*
	F	127	1.75	64	0.81	62	1.82
Bill width	M	222	3.04***	120	2.33*	101	0.75
	F	128	1.40	65	0.86	62	2.84*
Bill depth	M	220	4.62***	119	2.69**	100	11.90***
	F	128	2.84**	65	1.69	62	8.07*
Tarsus Residuals	M	226	1.53	124	1.50	101	0.09
	F	129	2.80**	66	3.76**	62	0.05
PC1	M	211	5.93***	114	1.48	96	2.64*
	F	116	2.81**	62	2.38*	53	6.63**
PC2	M	211	6.55***	114	3.60***	96	9.04***
	F	116	7.57***	62	2.89**	53	0.02
PC3	M	211	2.22**	114	3.75***	96	1.55
	F	116	2.80**	62	1.24	53	0.53
Residuals of beaks	M	218	4.19***	118	2.23*	99	10.13***
PC1 on tarsus	F	127	2.76**	64	1.30	62	7.74**

¹MANOVA with population as a factor and time as a covariant.

Significant inter-population variation at *P<0.05; **P<0.01; ***P<0.001.

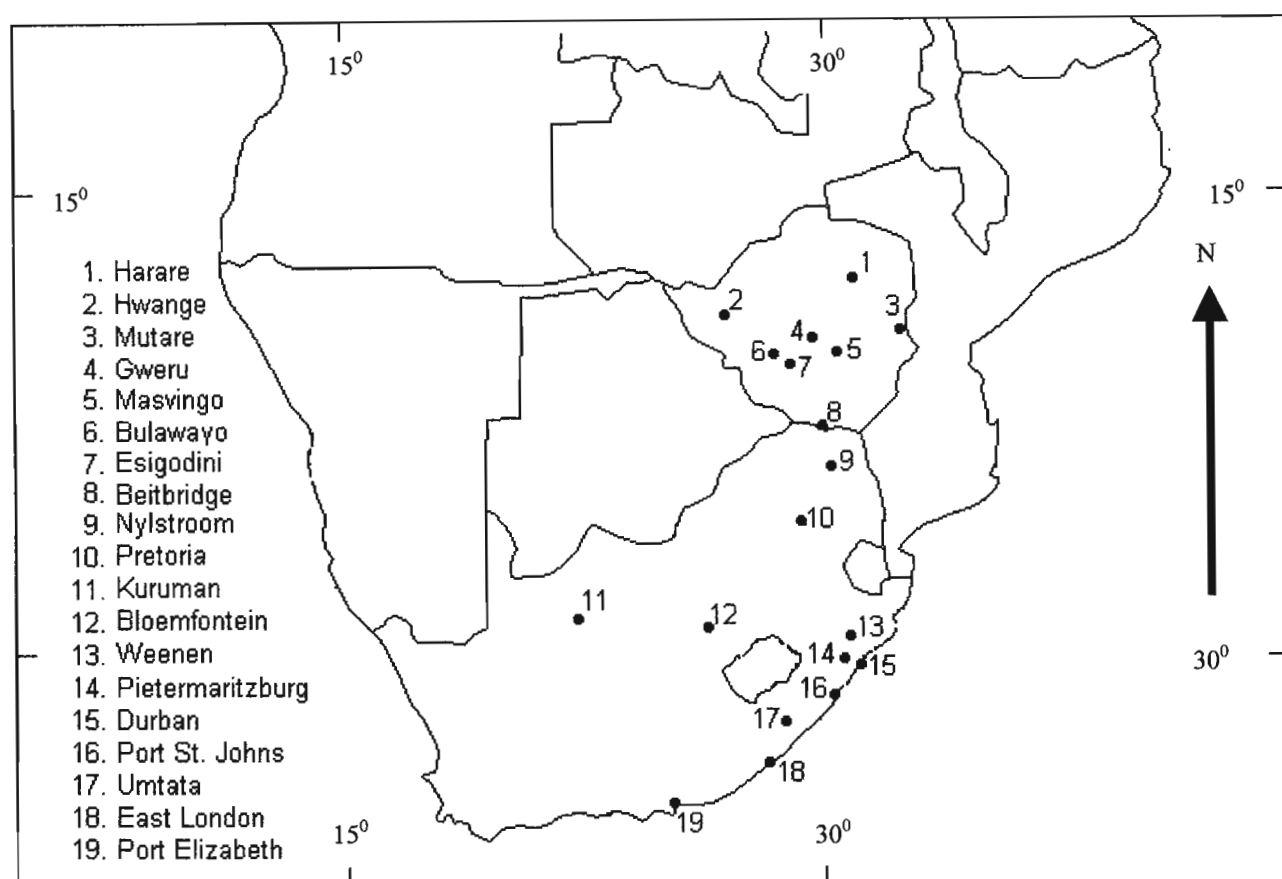


Figure 3.01. Localities from which samples of the house sparrow were taken for this study. The house sparrow was introduced to Durban (15) in 1890, East London (18) in 1930 and Harare (1) in 1957.

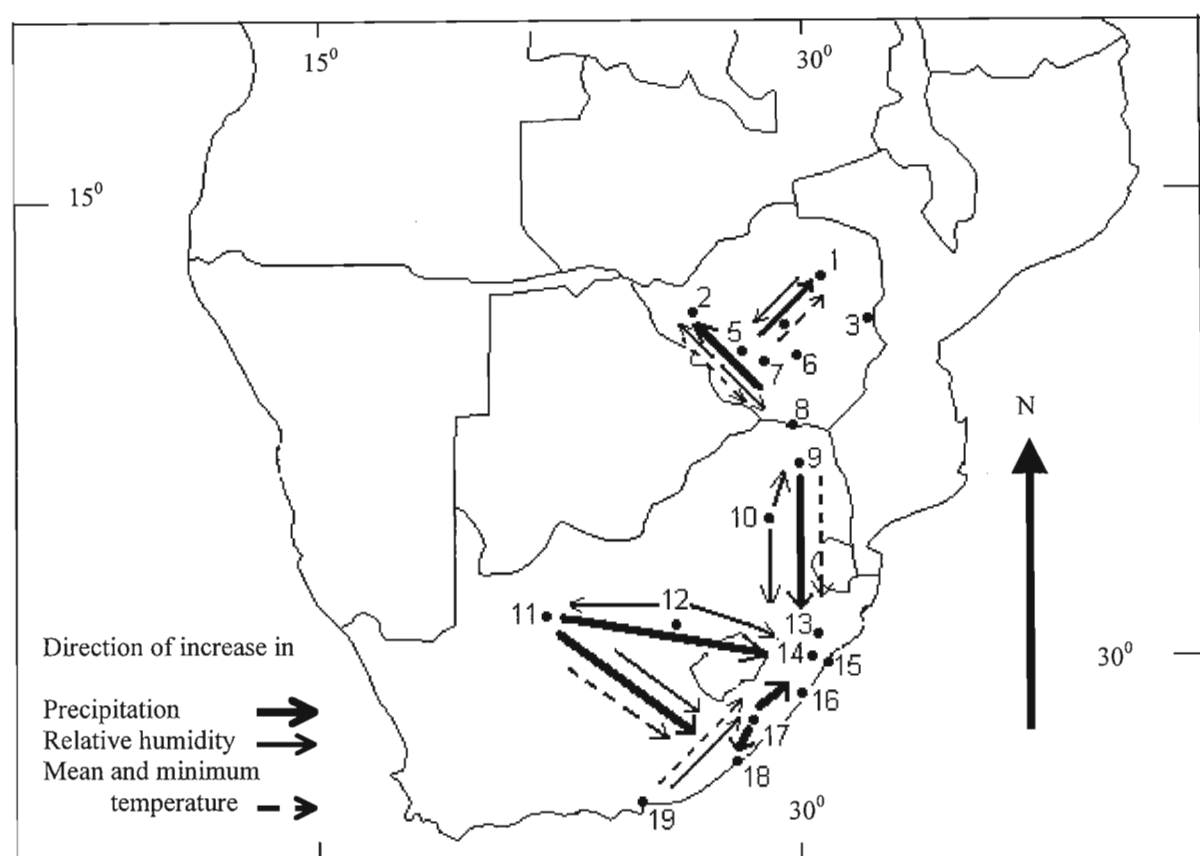


Figure 3.02. Trends in variation of the climatic factors used in the analysis of morphological variation in the house sparrow in southern Africa.

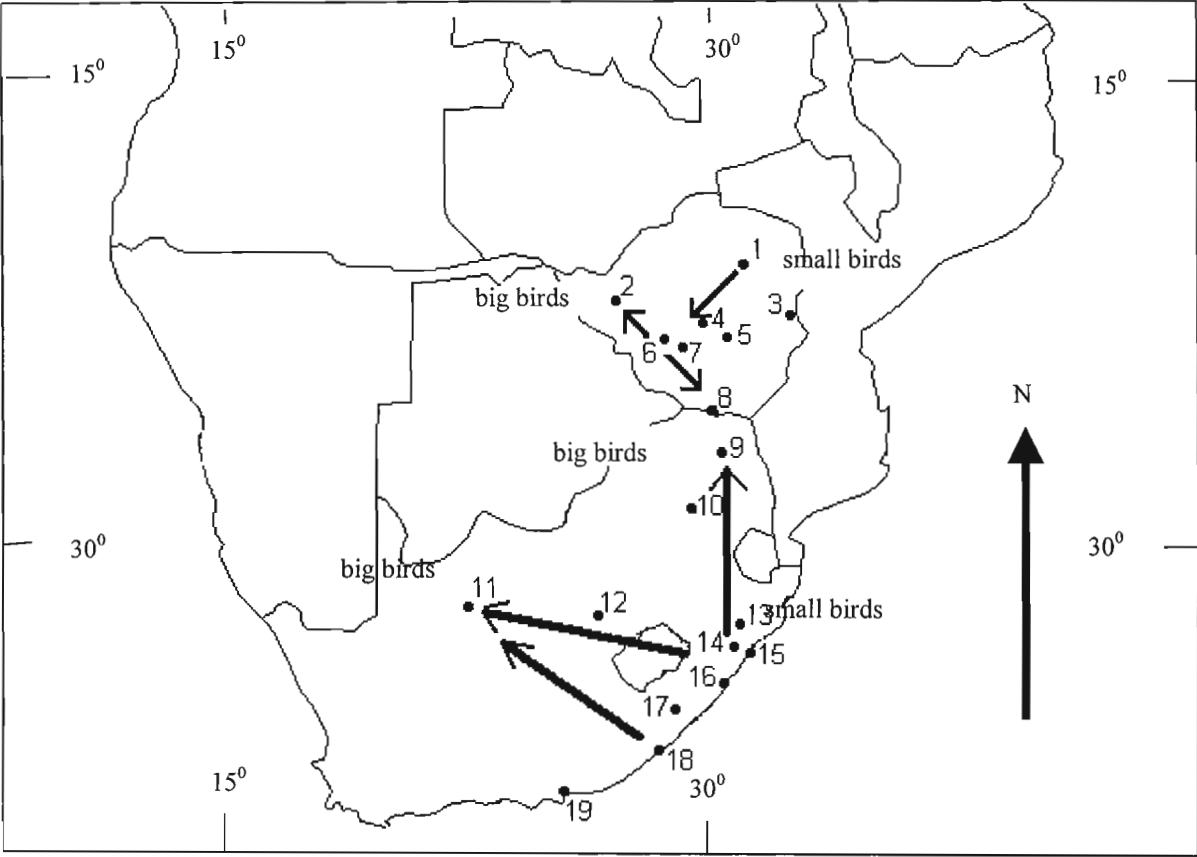


Figure 3.03 Predicted variation in size of southern African house sparrows, based on trends in climatic variation.

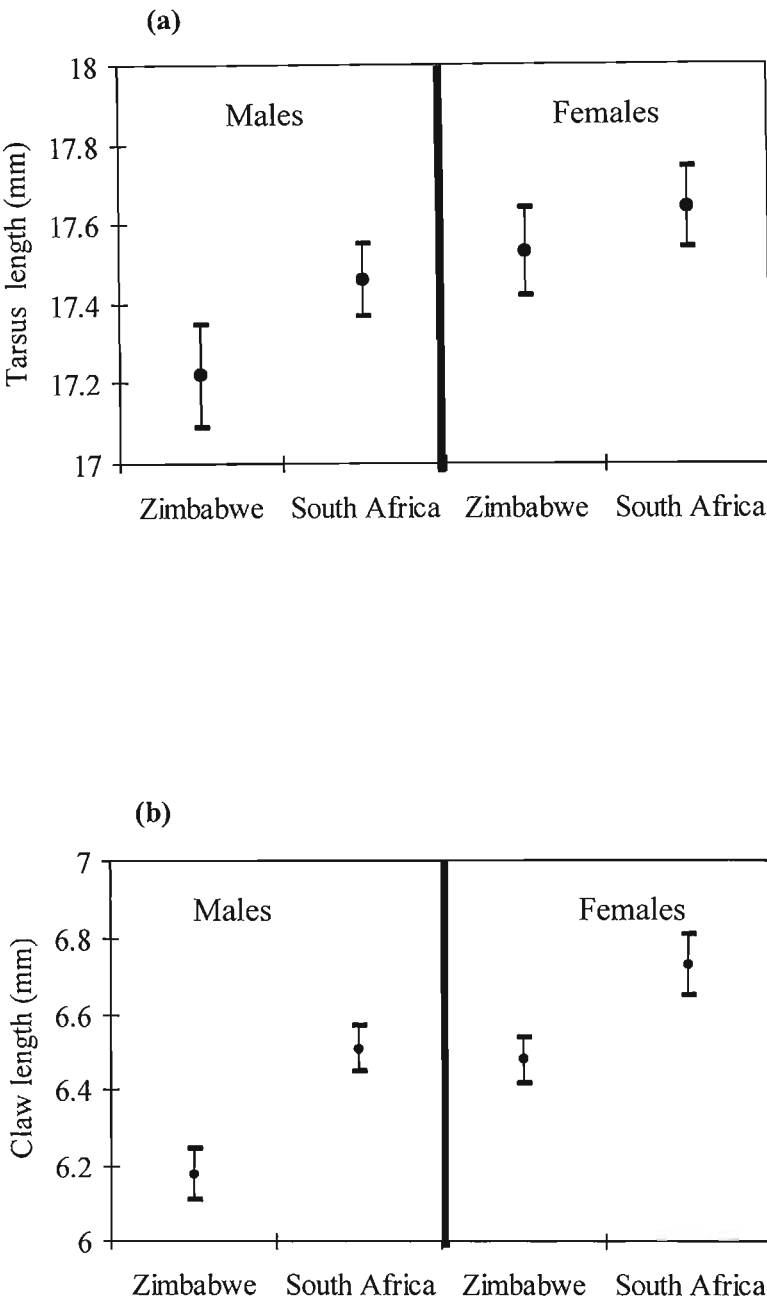


Figure 3.04. Mean values \pm standard error of (a) tarsus length and (b) claw length of Zimbabwean and South African house sparrows.

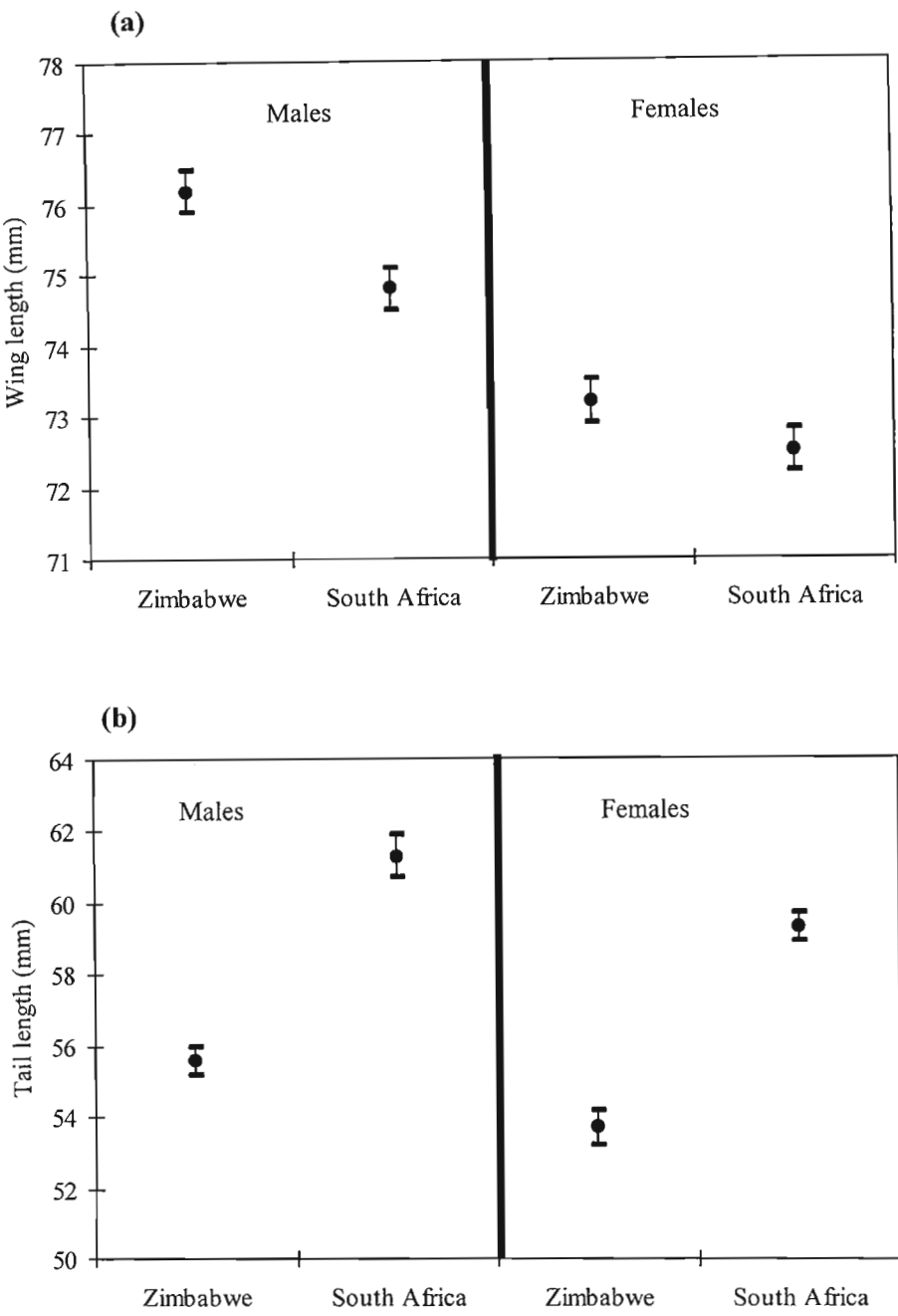


Figure 3.05. Mean values \pm standard error of (a) wing length and (b) tail length of Zimbabwean and South African house sparrows.

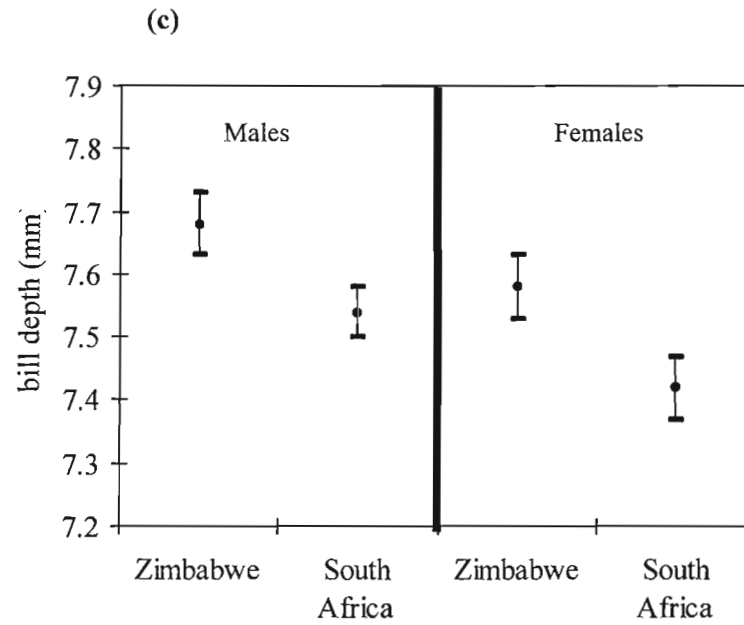
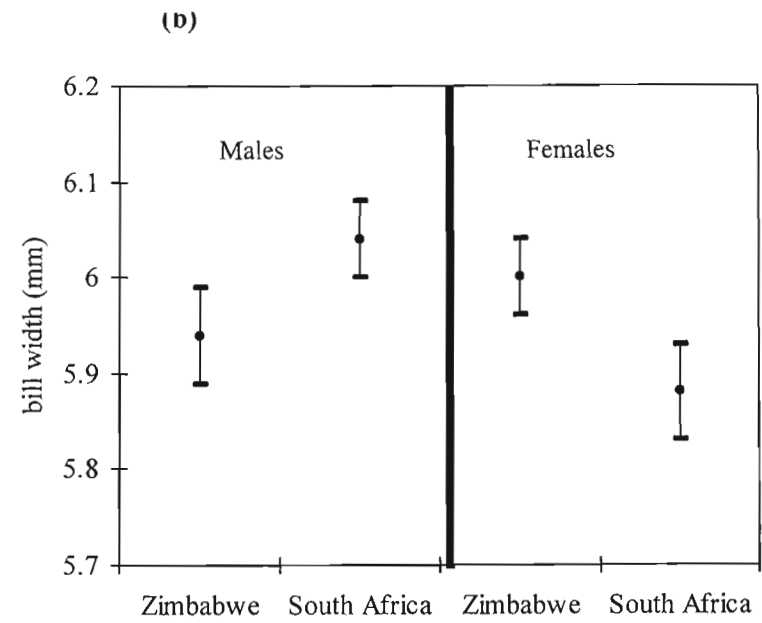
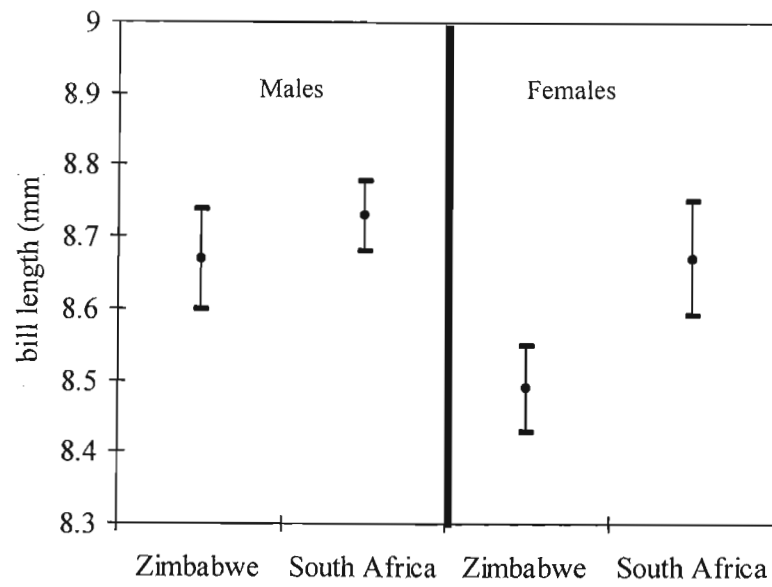


Figure 3.06. Mean values \pm standard error of (a) bill length, (b) bill width and (c) bill depth of Zimbabwean and South African house sparrows.

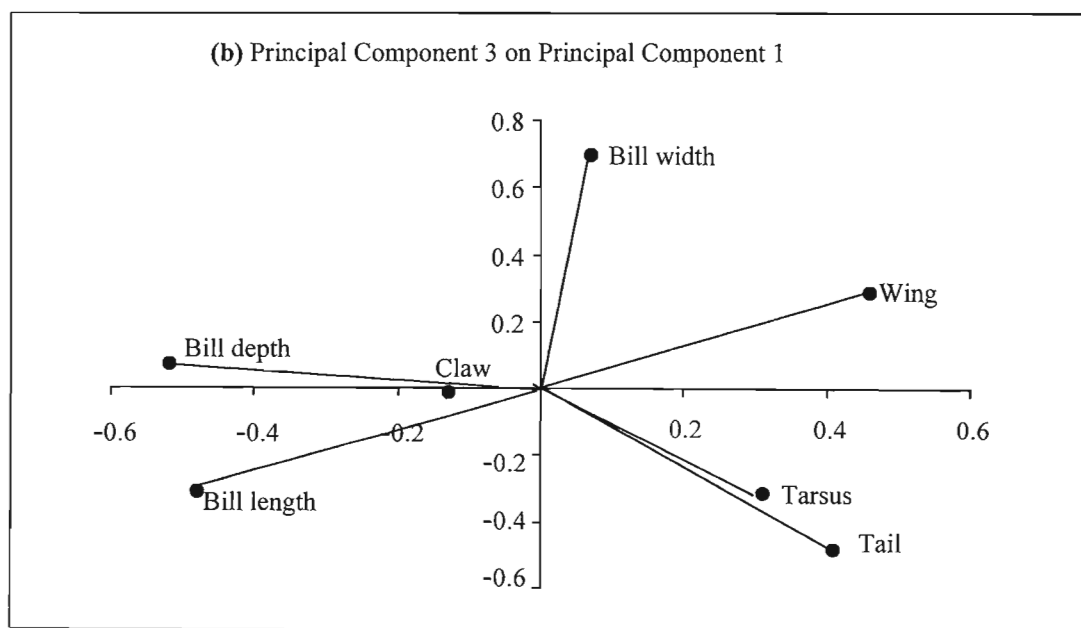
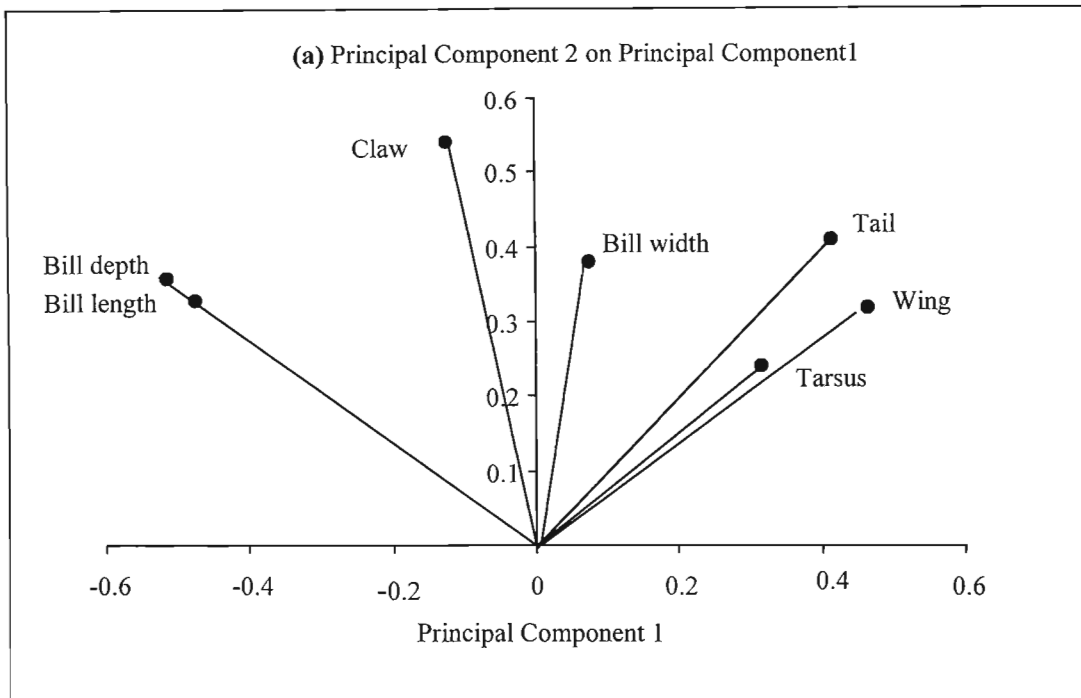


Figure 3.07. Separation of morphological characters of male Zimbabwean house sparrows along the first three principal components of variation.

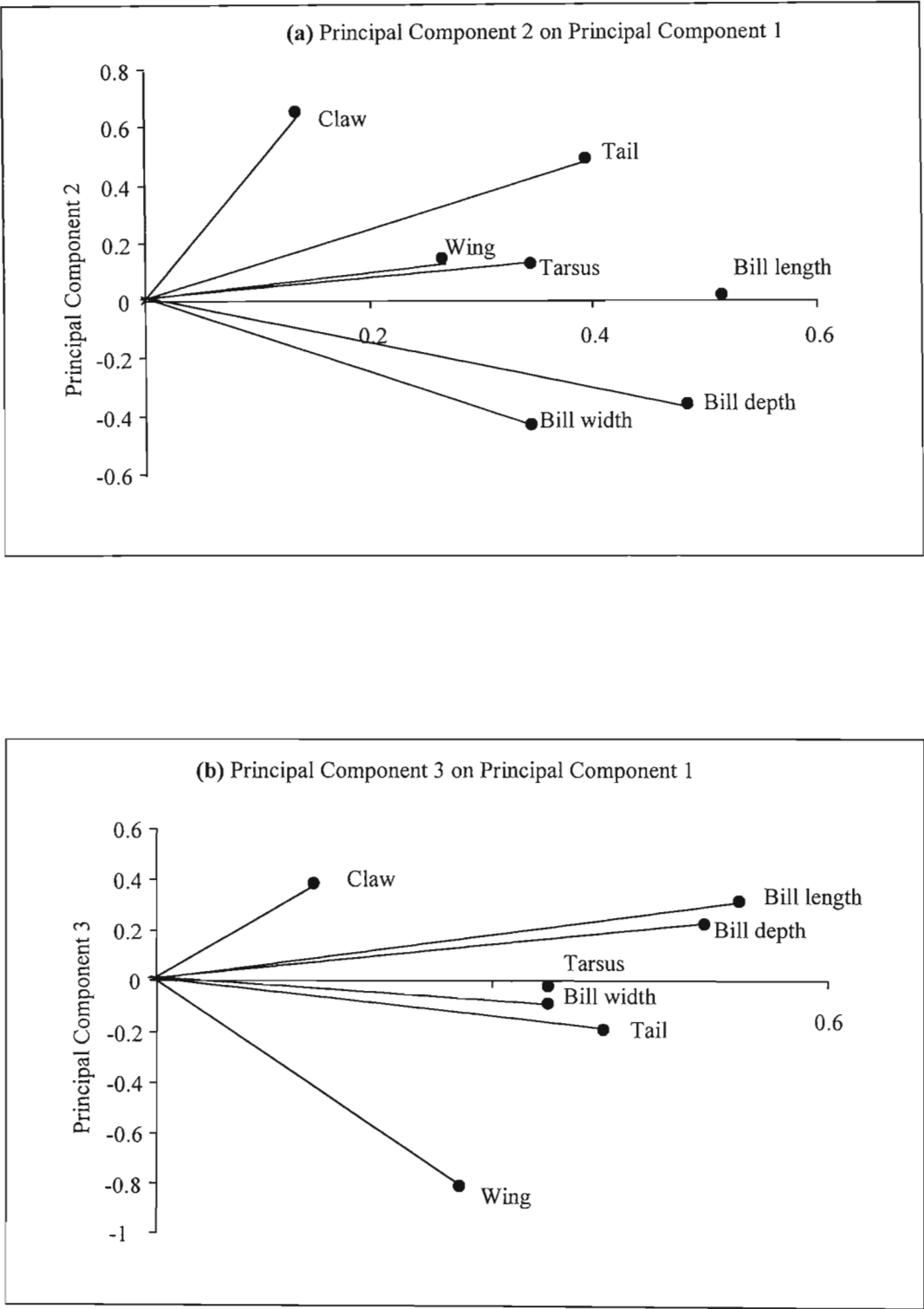


Figure 3.08. Separation of morphological characters of female Zimbabwean house sparrows along the first three principal components of variation.

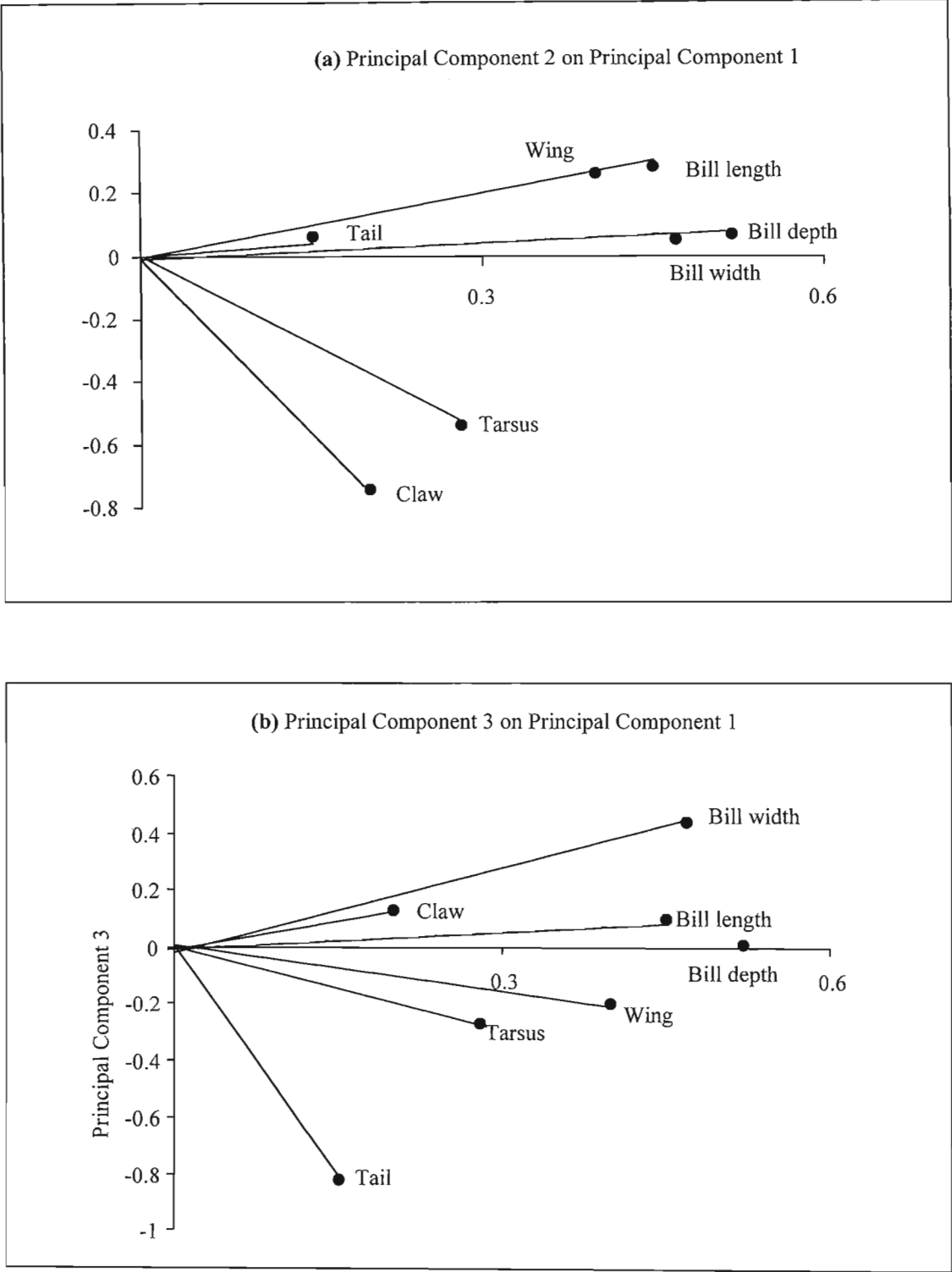


Figure 3.09. Separation of morphological characters of male South African house sparrows along the first three principal components of variation.

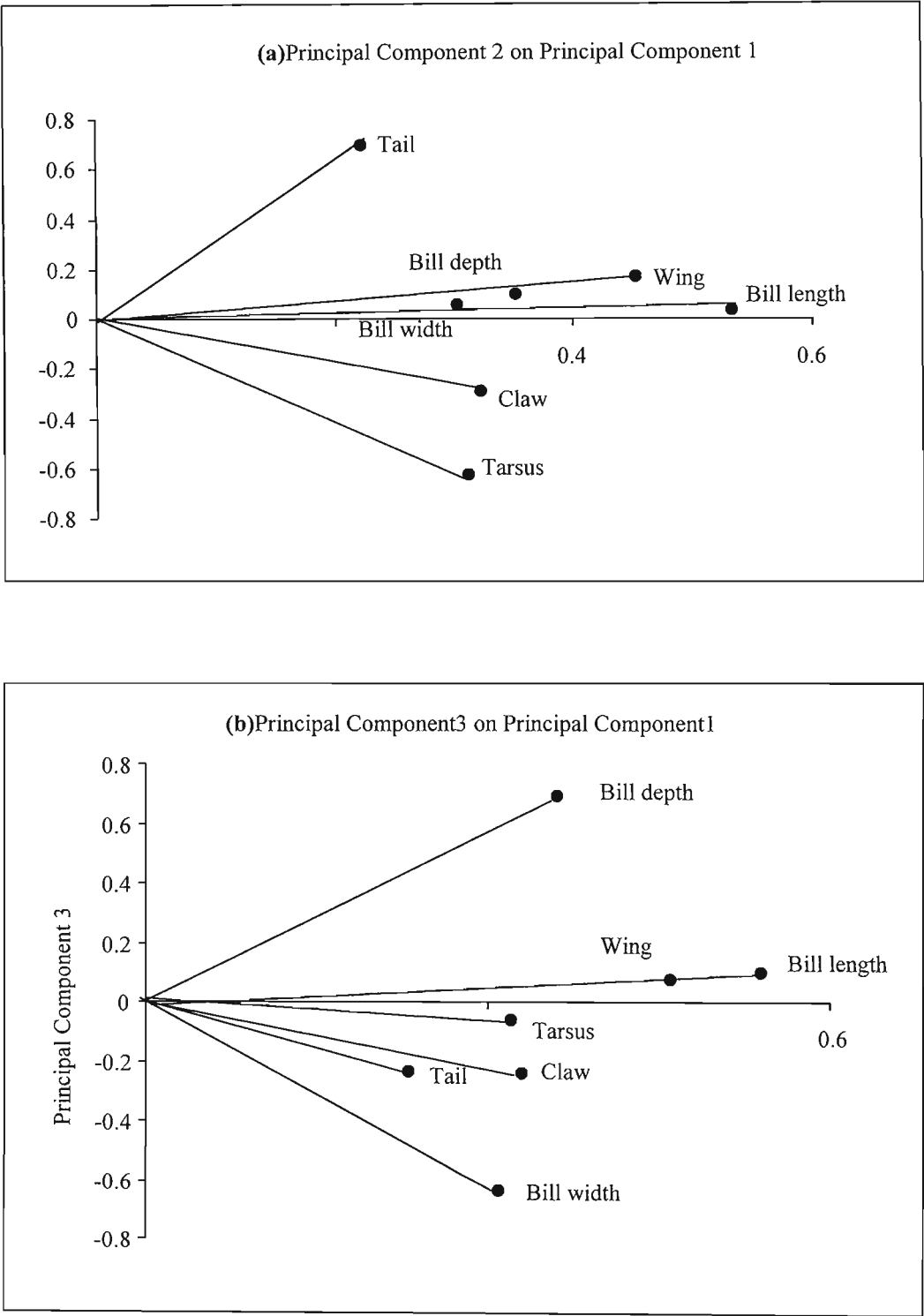


Figure 3.10. Separation of morphological characters of South African female house sparrows along the first three principal components of variation.

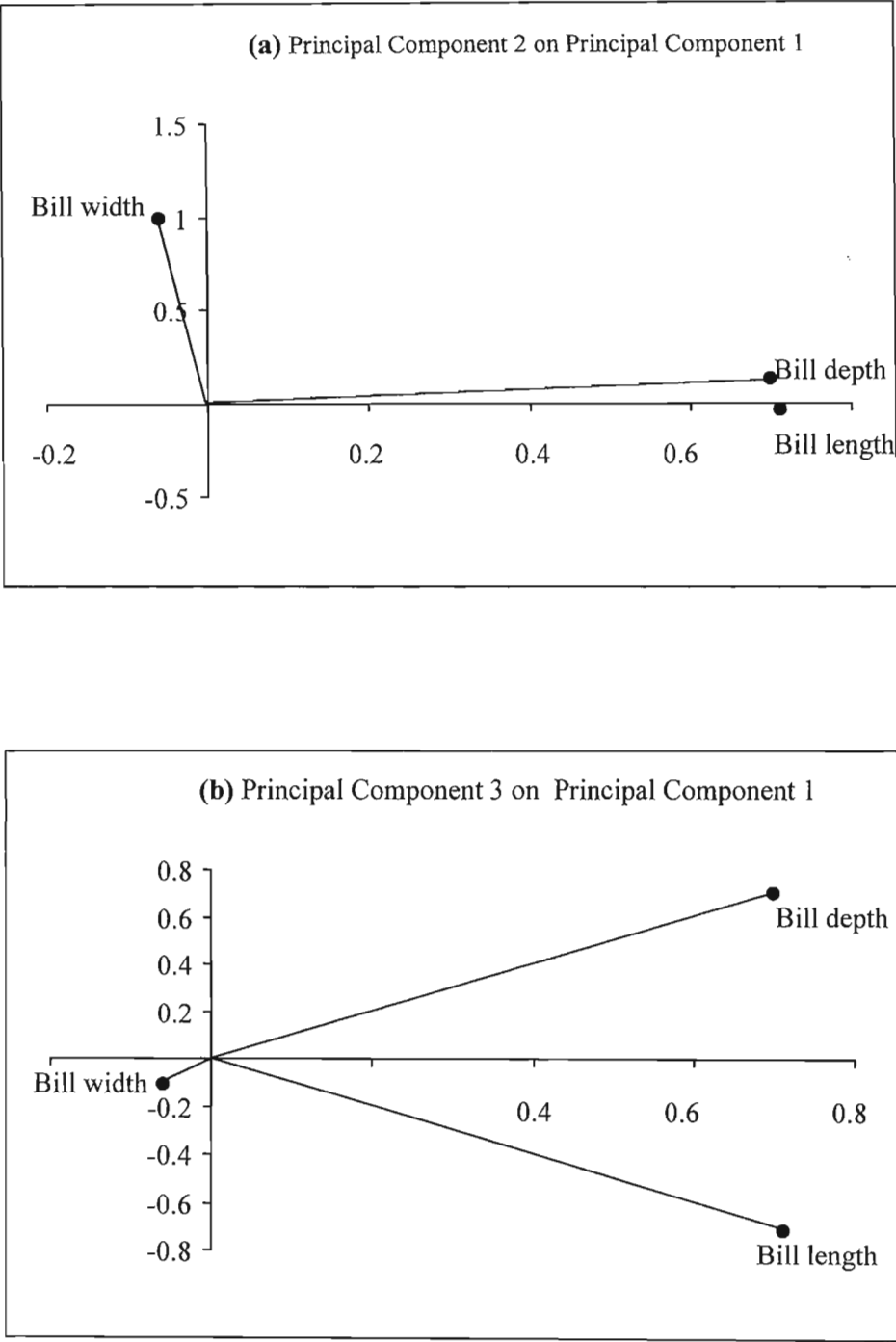


Figure 3.11. Separation of beak dimensions of male Zimbabwean house sparrows along the first three principal components of variation.

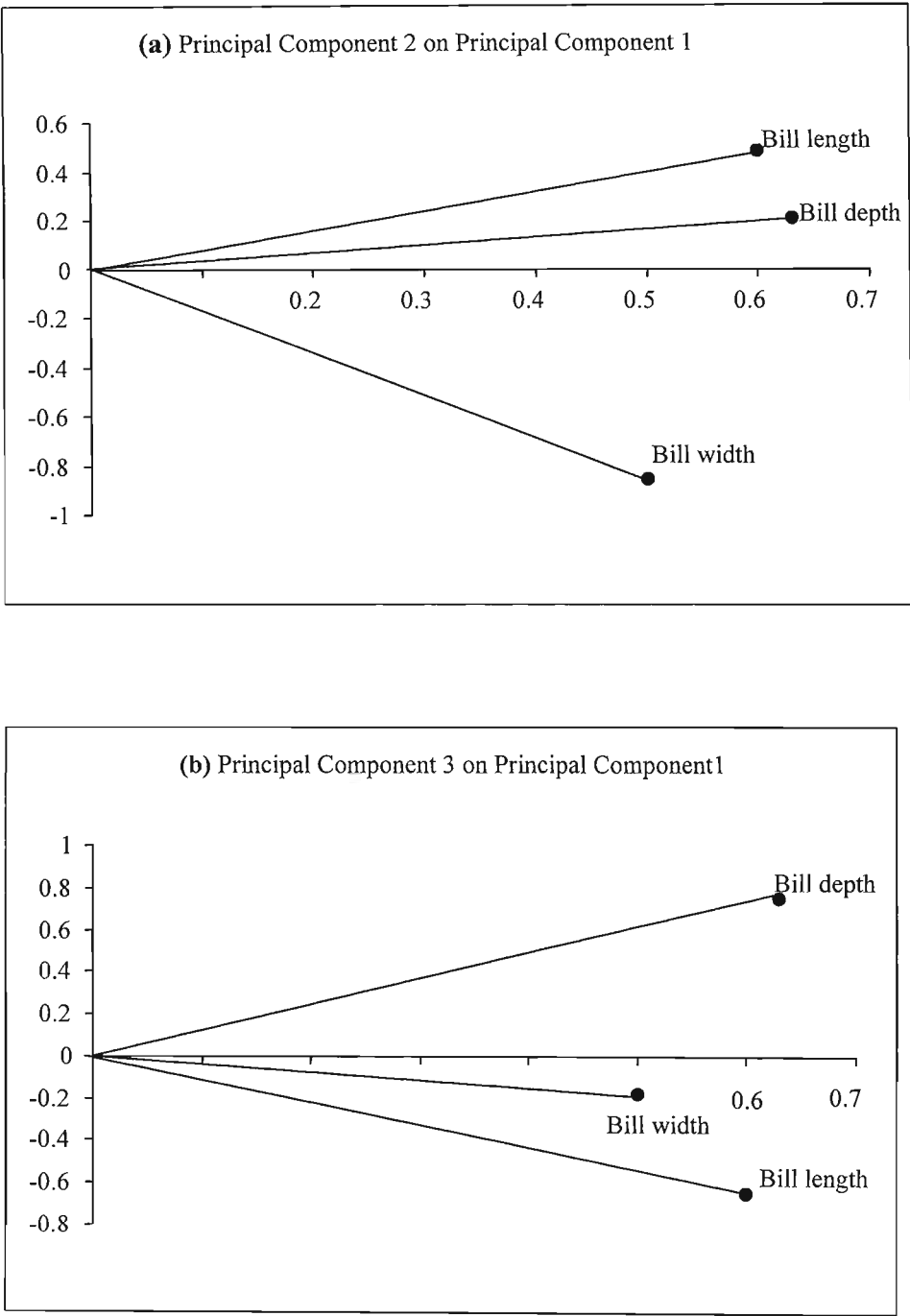


Figure 3.12. Separation of beak dimensions of female Zimbabwean house sparrows along the first three principal components of variation.

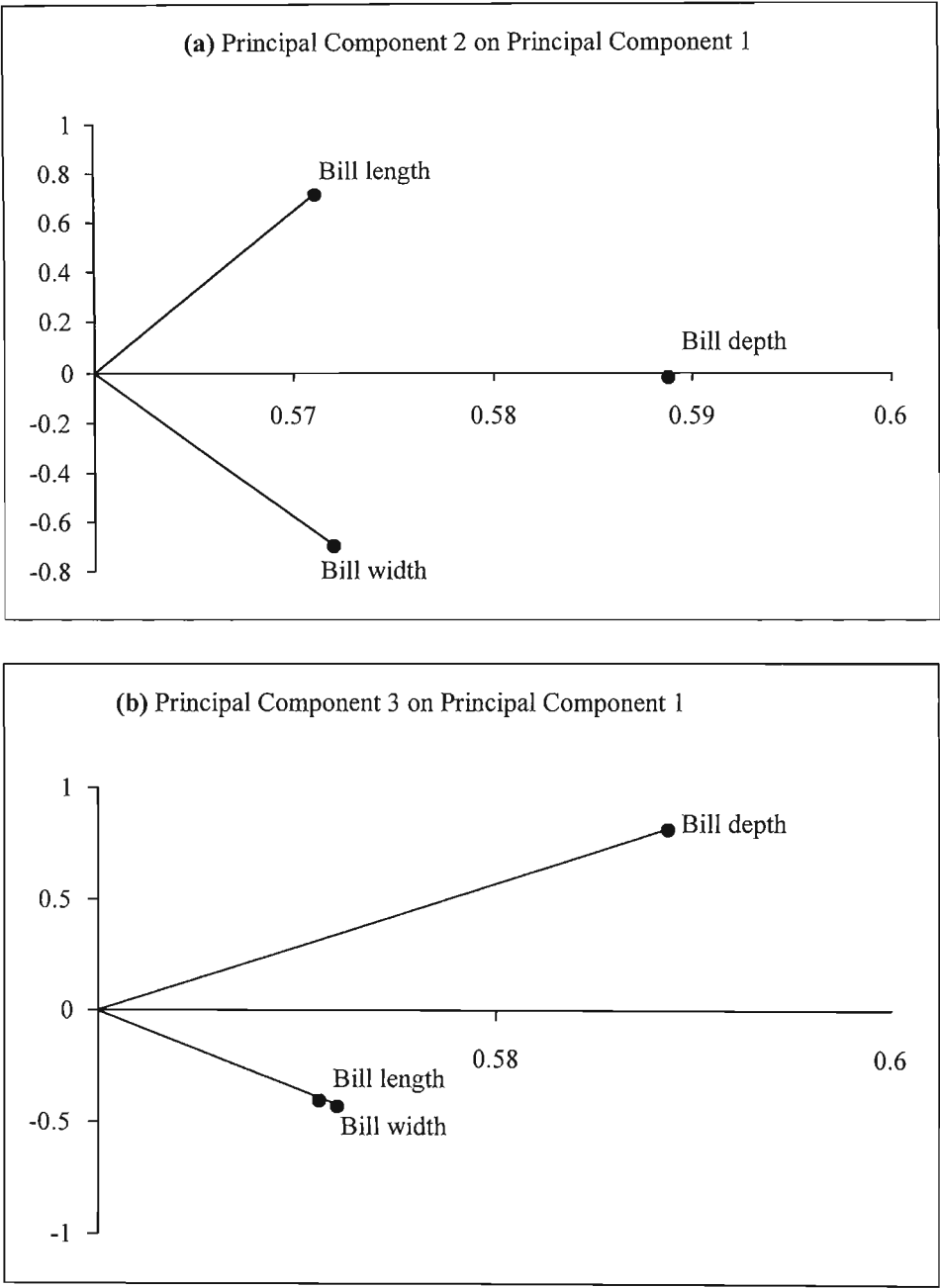


Figure 3.13. Separation of beak dimensions of male South African house sparrows along the first three principal components of variation.

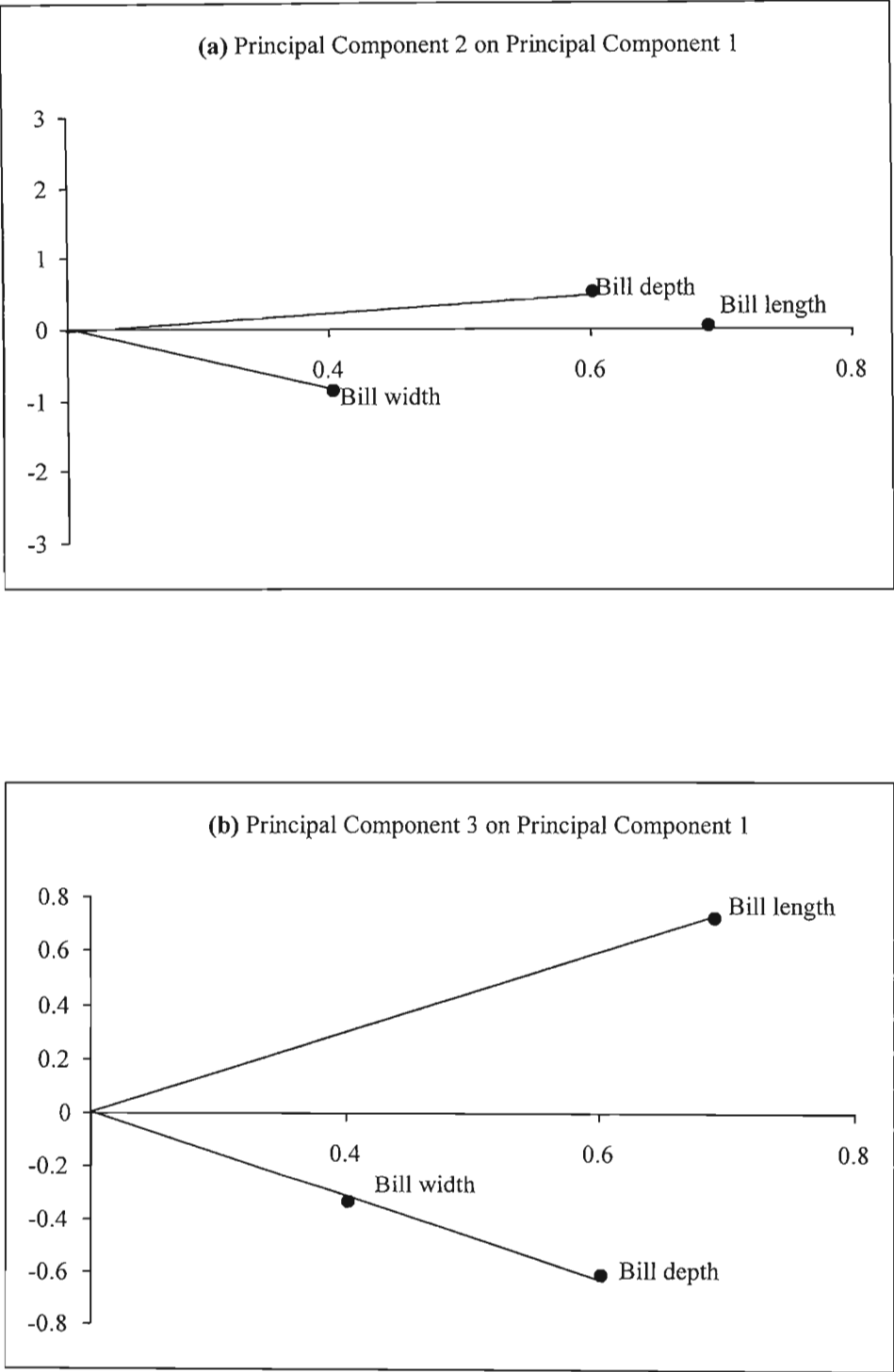


Figure 3.14. Separation of beak dimensions of female South African house sparrows along the first three principal components of variation.

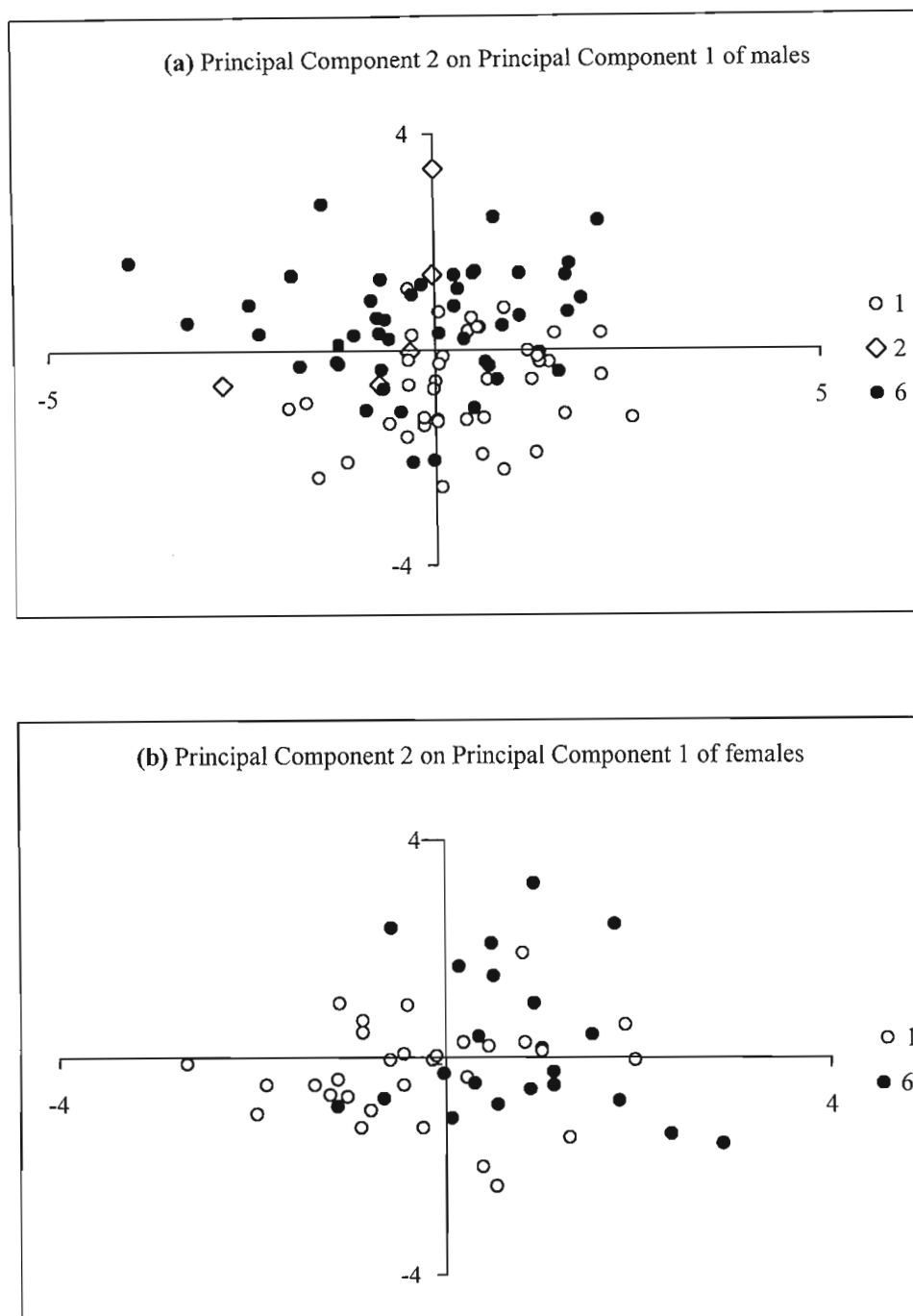


Figure 3.15. Separation of Zimbabwean populations of house sparrows on the axes of the first two principal components of variation. (a) separation of males and (b) separation of females along Principal Components 1 and 2. Numbers refer to population numbers.

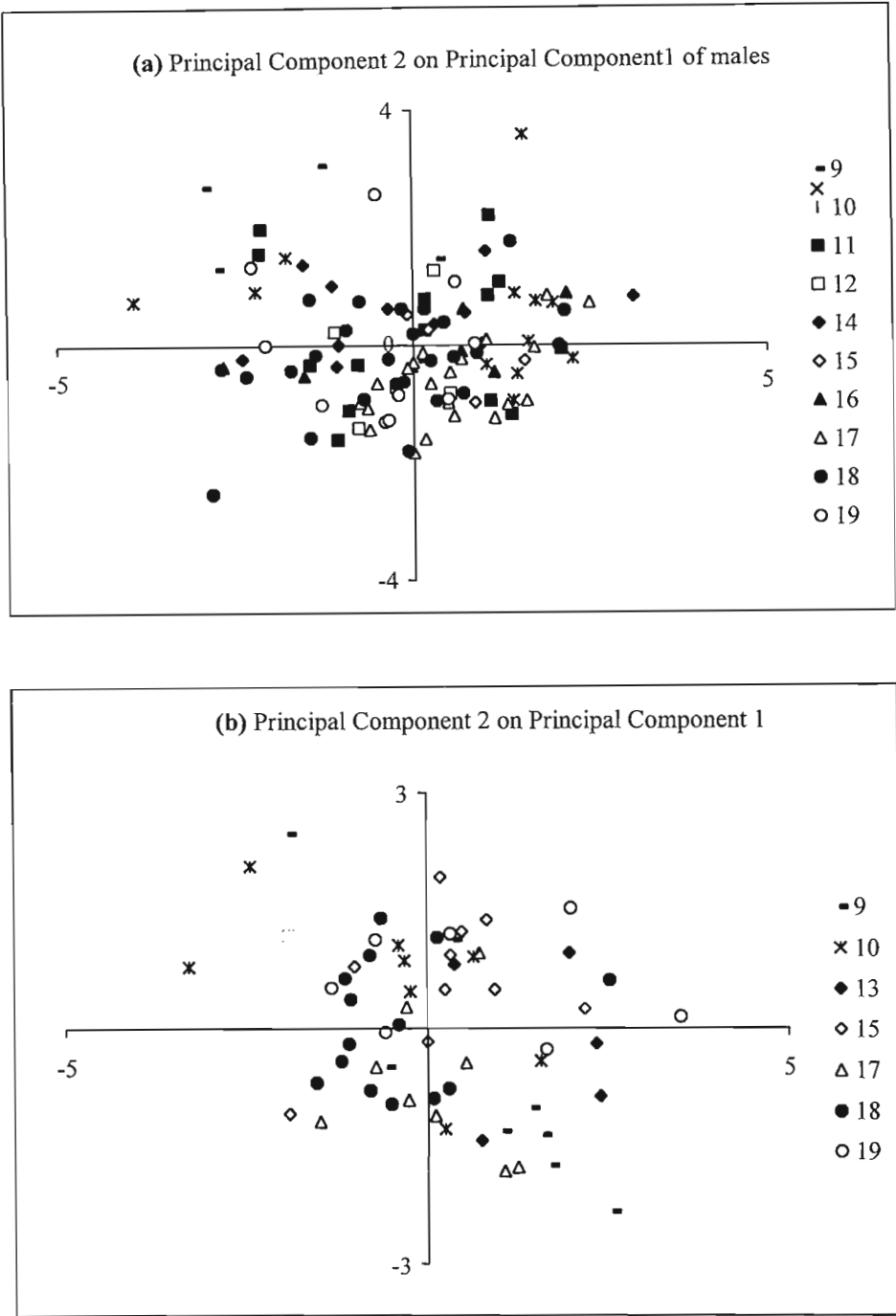


Figure 3.16. Separation of Zimbabwean populations of house sparrows on the axes of the first two principal components of variation. (a) separation of males and (b) separation of females along Principal Components 1 and 2. Numbers refer to population numbers.

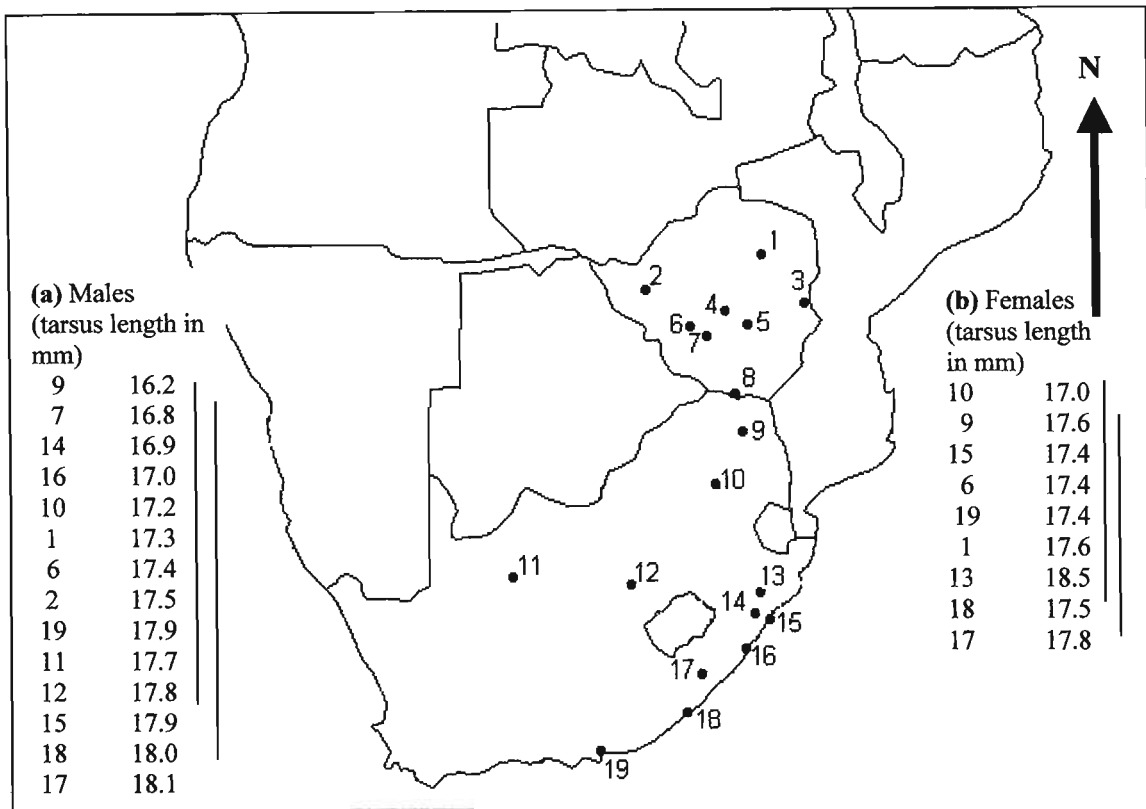


Figure 3.17. Geographic variation in tarsus length of (a) male and (b) female house sparrows in southern Africa. Vertical lines denote homogenous subsets derived from the Scheffe multiple range analysis. Figures refer to population numbers and ranked means of tarsus length, respectively. For females the Scheffe test was not significant for tarsus length but was significant for residuals of tarsus measurements from the means. Actual tarsus means are given here but ranking of females is based on residuals.

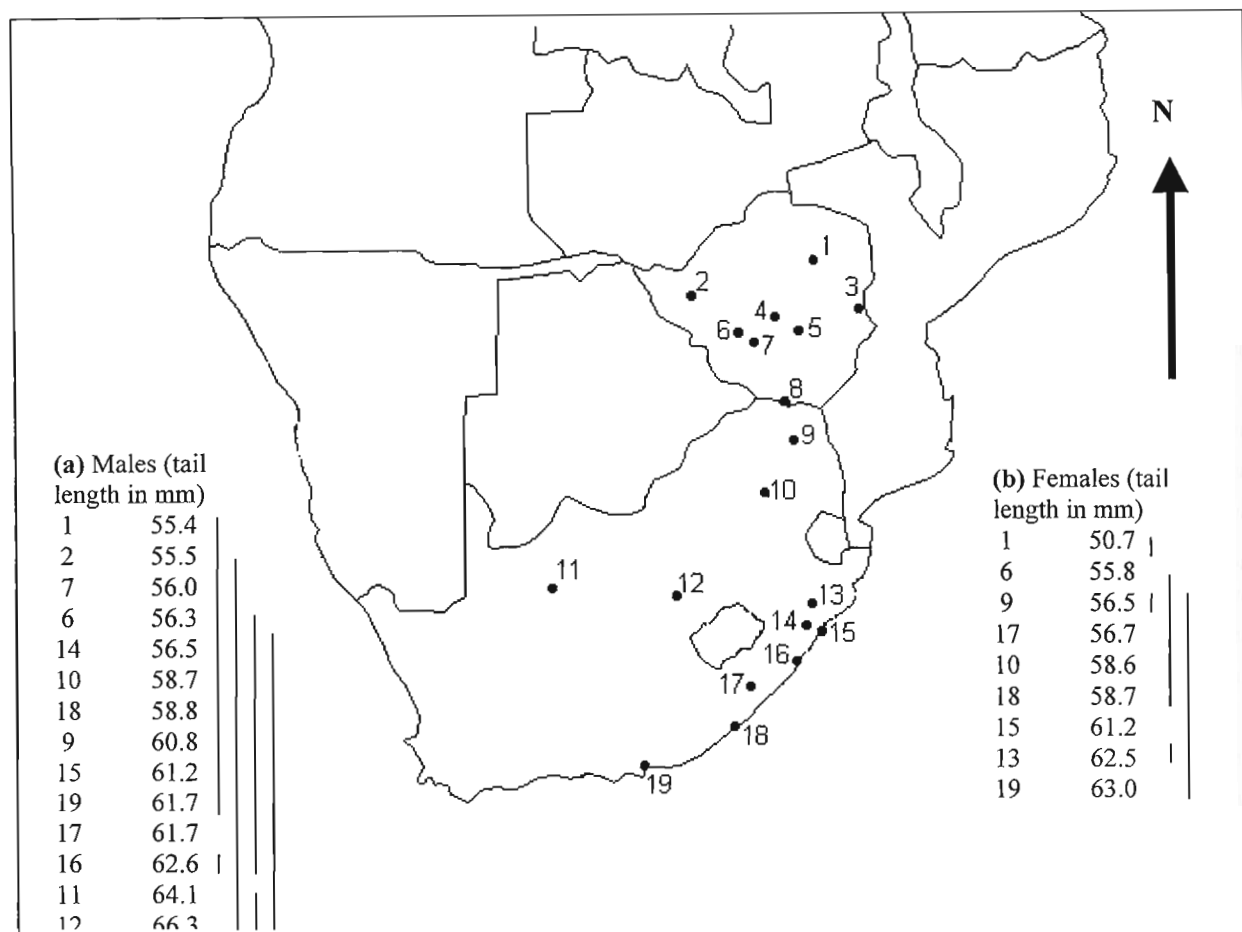


Figure 3.18. Geographic variation in tail length of (a) male and (b) female house sparrows in southern Africa. Vertical lines denote homogenous subsets derived from the Scheffe multiple range analysis. Figures refer to population numbers and ranked means of tarsus length, respectively.

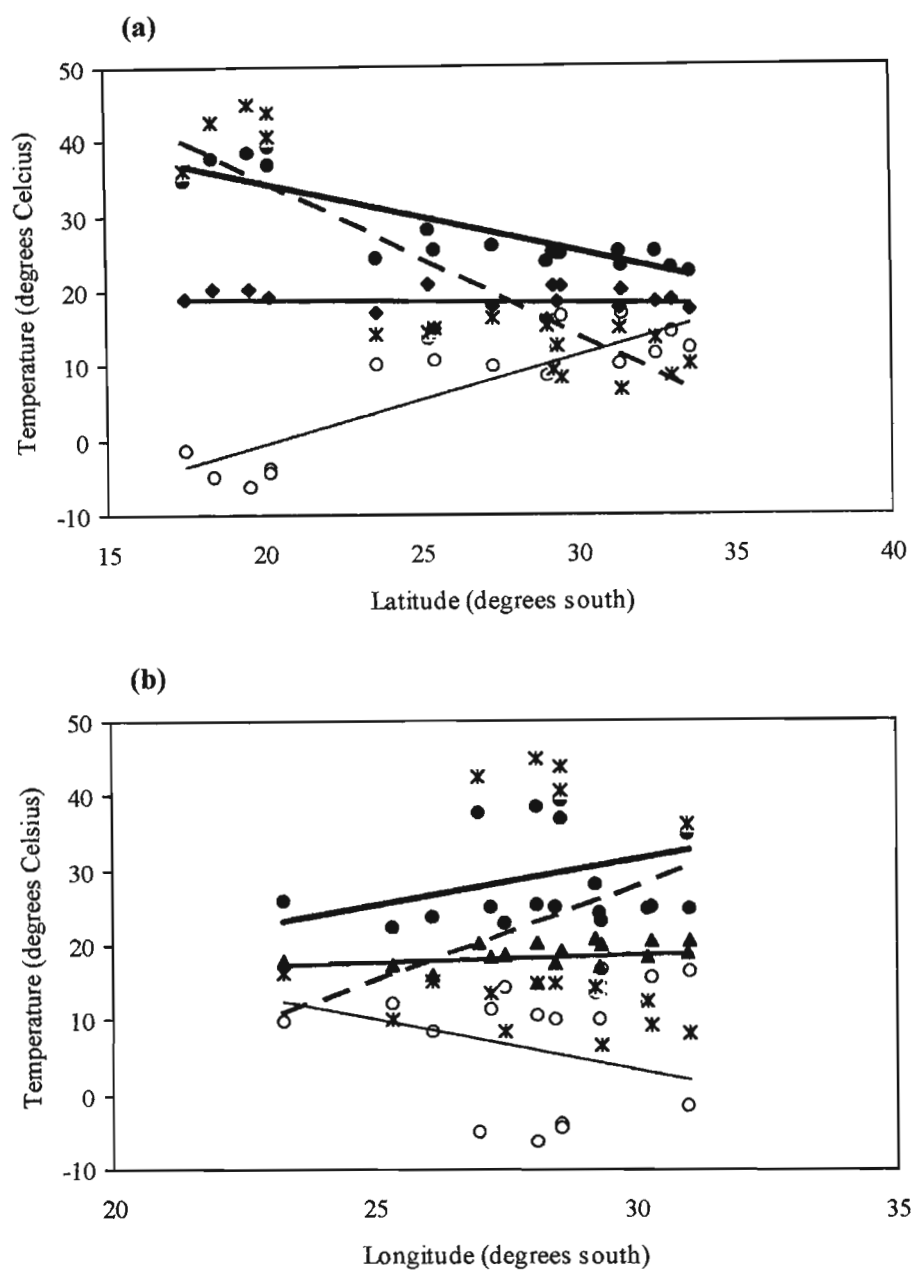


Figure 3.19. Geographic trends in temperature in the southern African range of the house sparrow. (a) Latitudinal trends and (b) longitudinal trends in absolute maximum (——), absolute minimum (—), mean temperature (---) and in temperature range (.....).

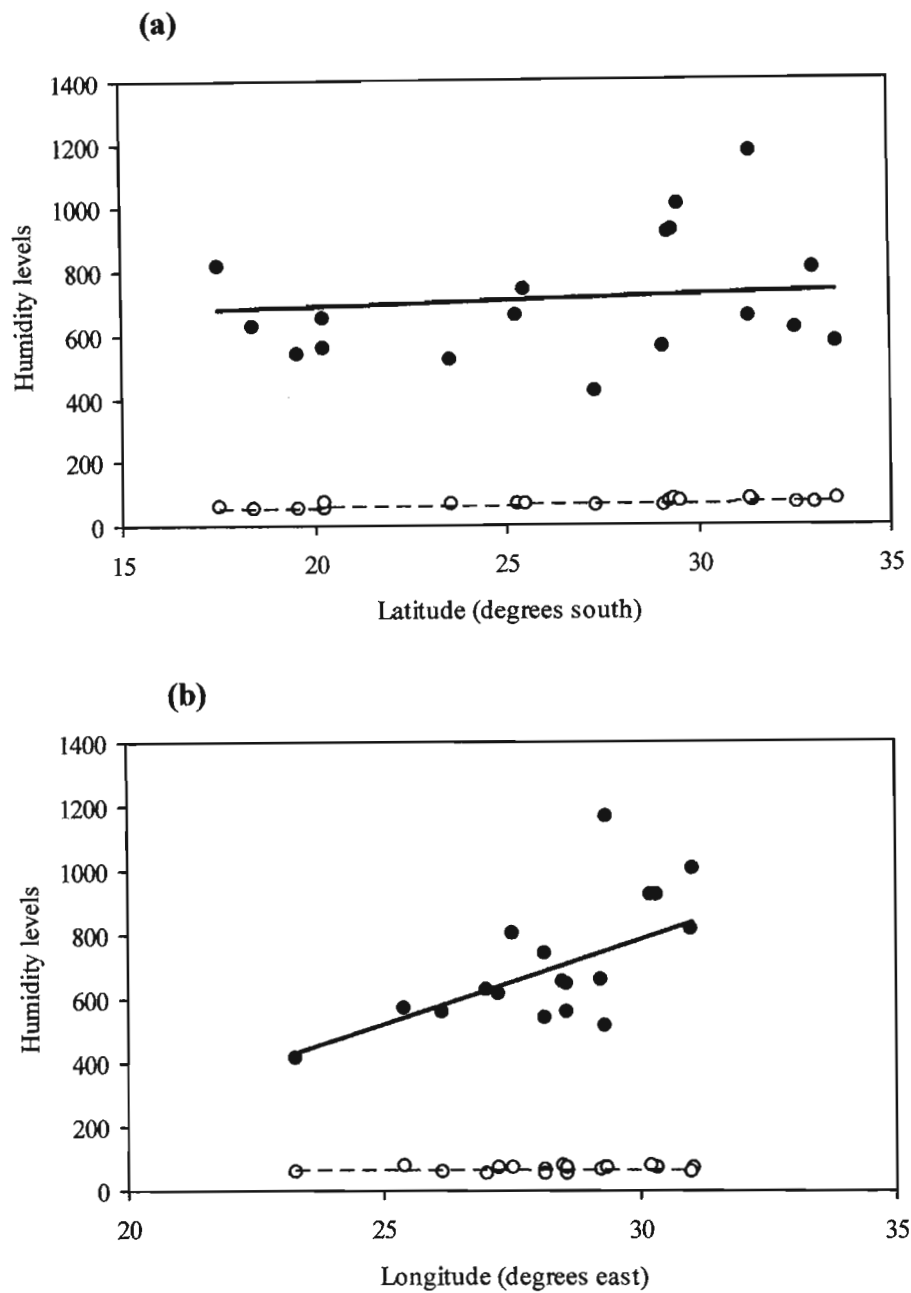


Figure 3.20. Geographic trends in humidity levels in the southern African range of the house sparrow. (a) Latitudinal trends and (b) longitudinal trends in precipitation (——) measured in millimetres and relative humidity (-----) measured as a percentage.

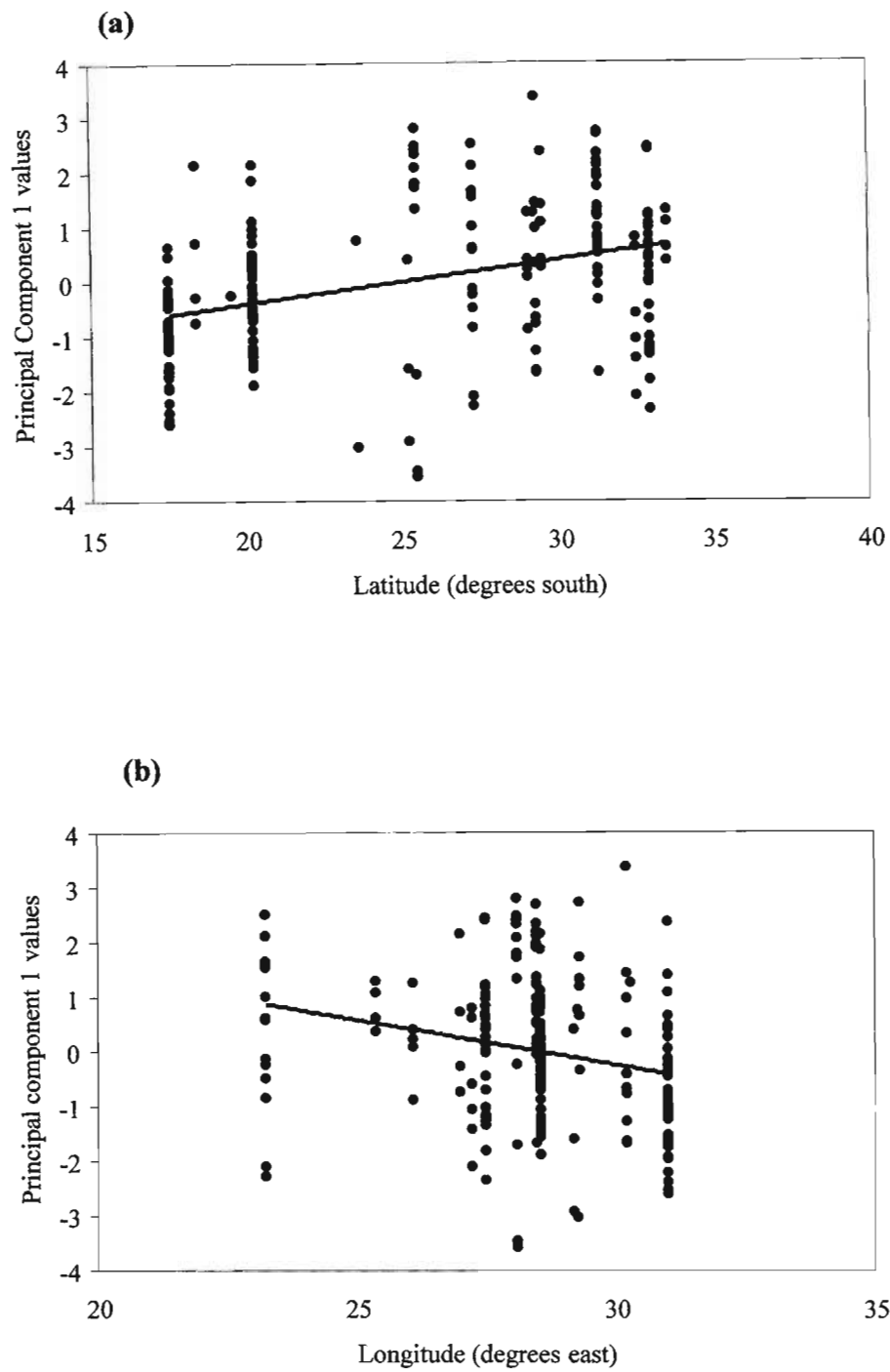


Figure 3.21. Geographic variation in overall body size (Principal Component 1) of male southern African house sparrows along latitude and longitude.

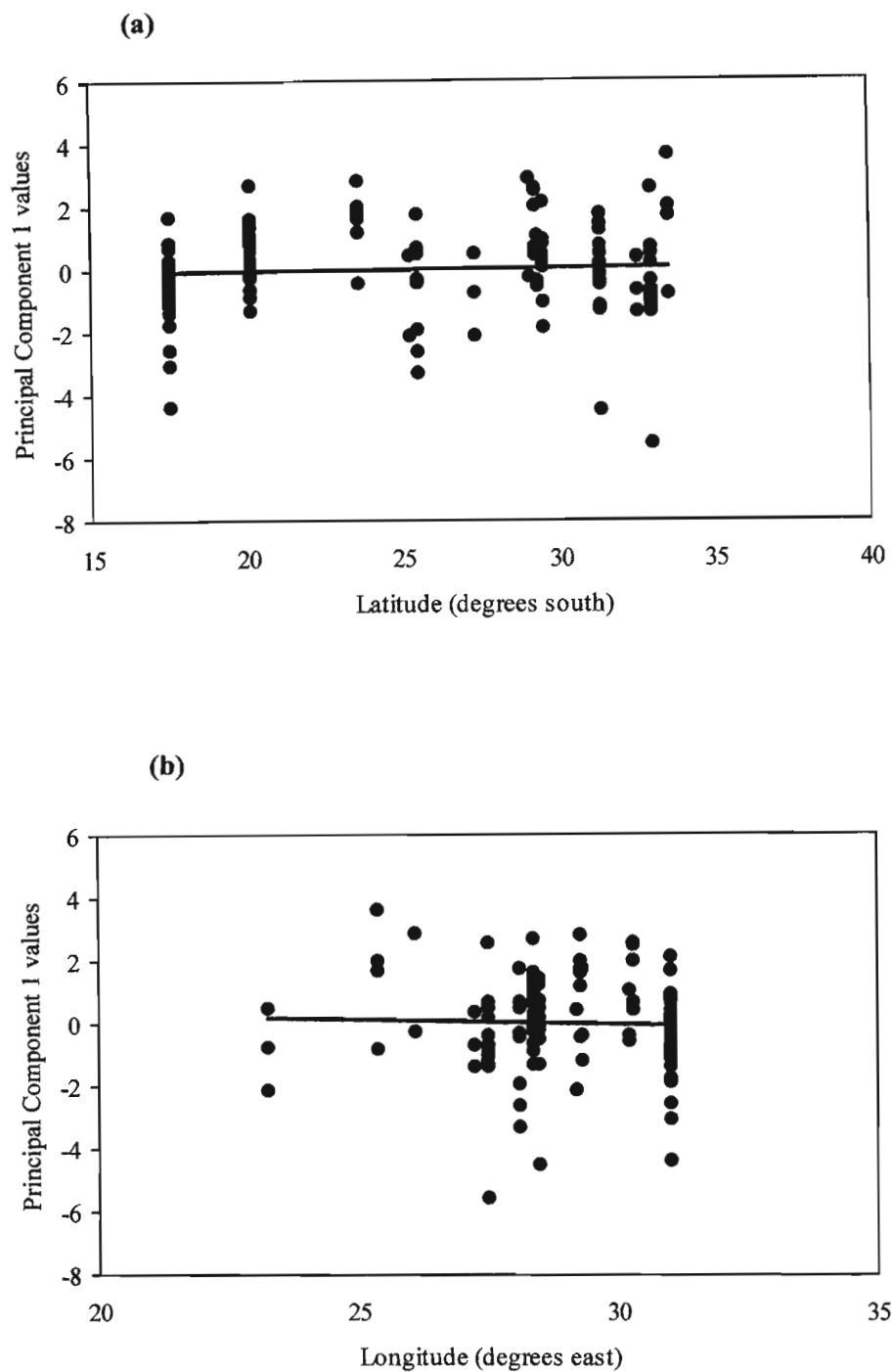


Figure 3.22. Geographic variation in overall body size (Principal Component 1) of female southern African house sparrows along latitude and longitude.

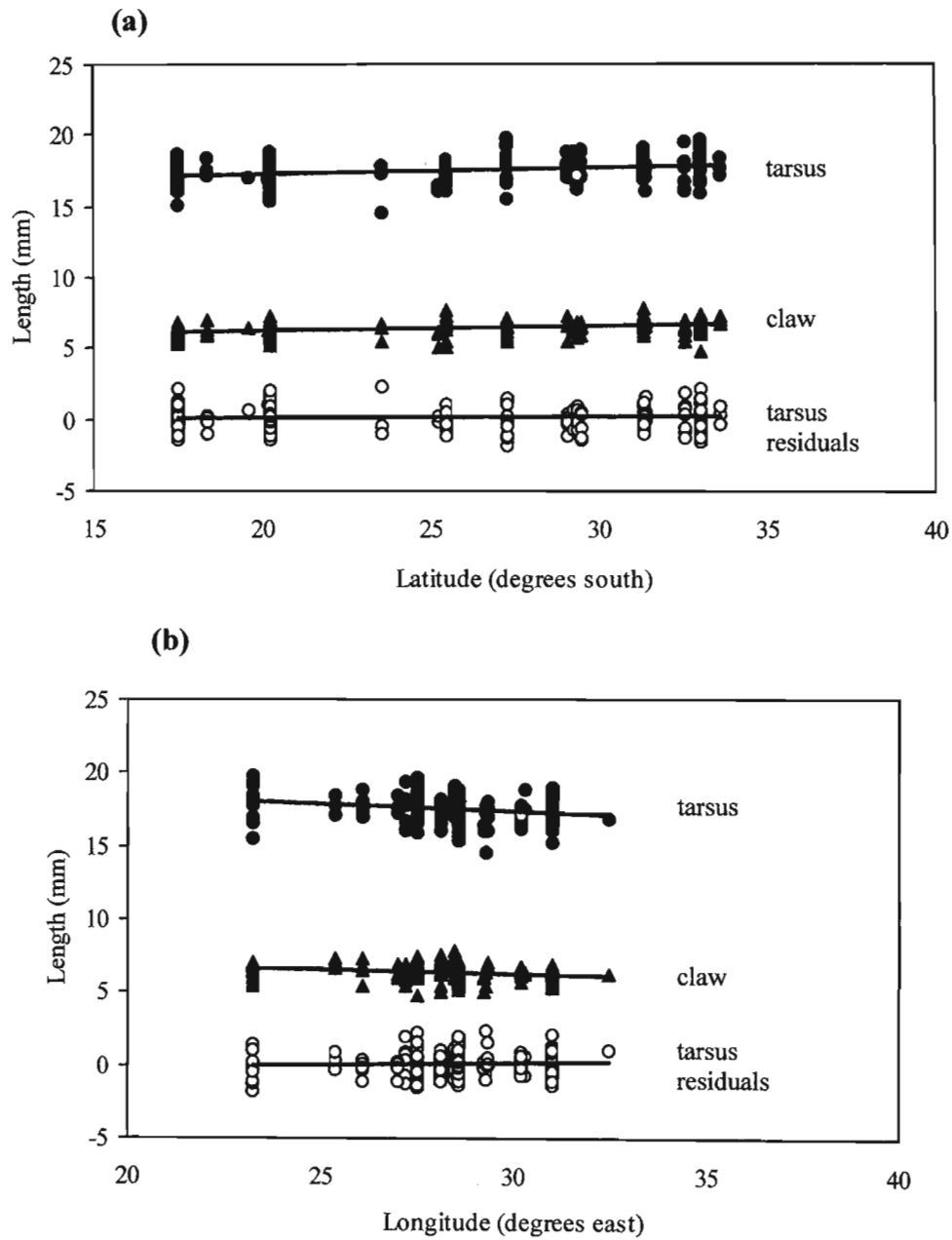


Figure 3.23. Variation in tarsus and claw length of male house sparrows along (a) latitude and (b) longitude in southern Africa.

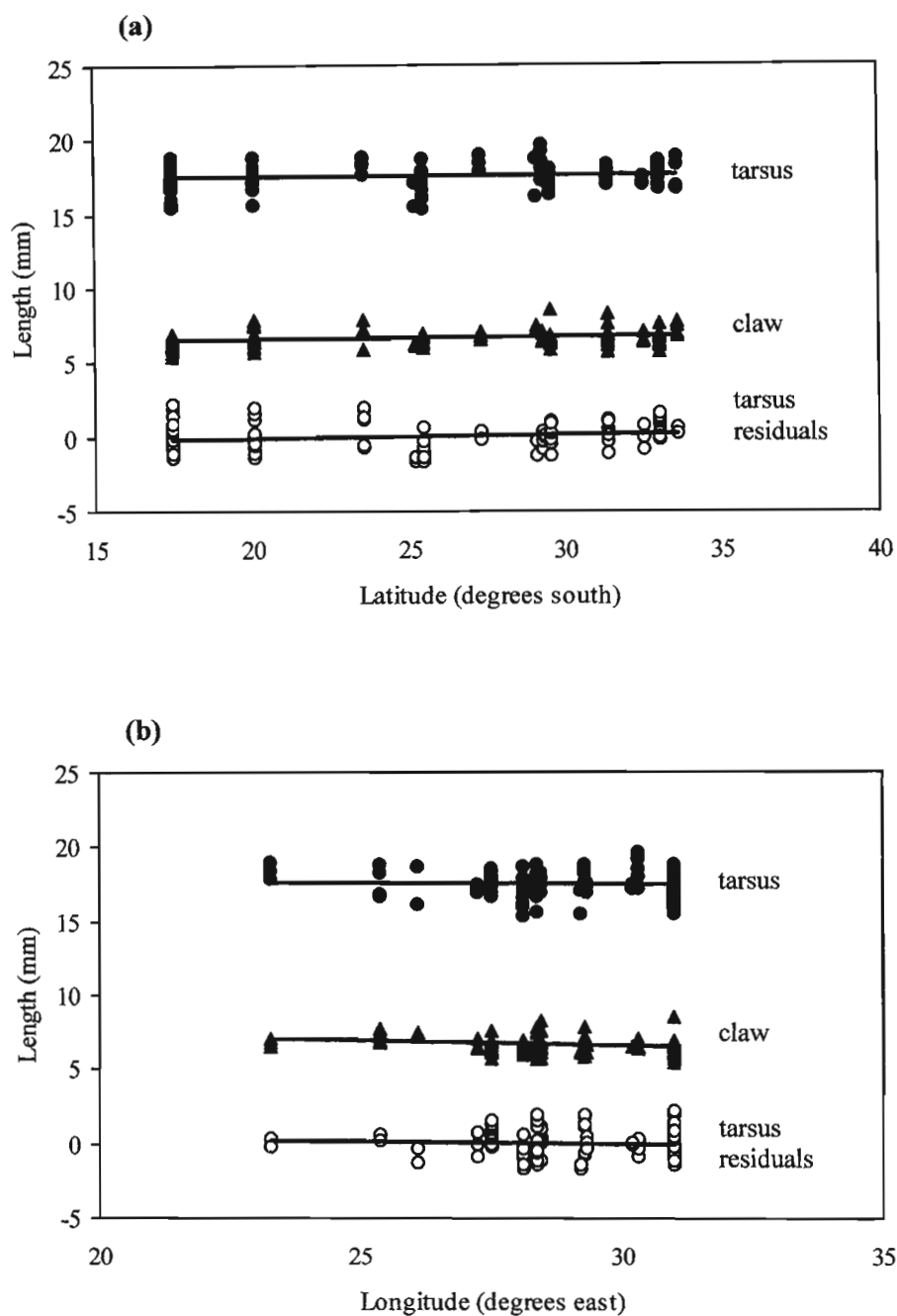


Figure 3.24. Variation in tarsus and claw length of female house sparrows along (a) latitude and (b) longitude in southern Africa.

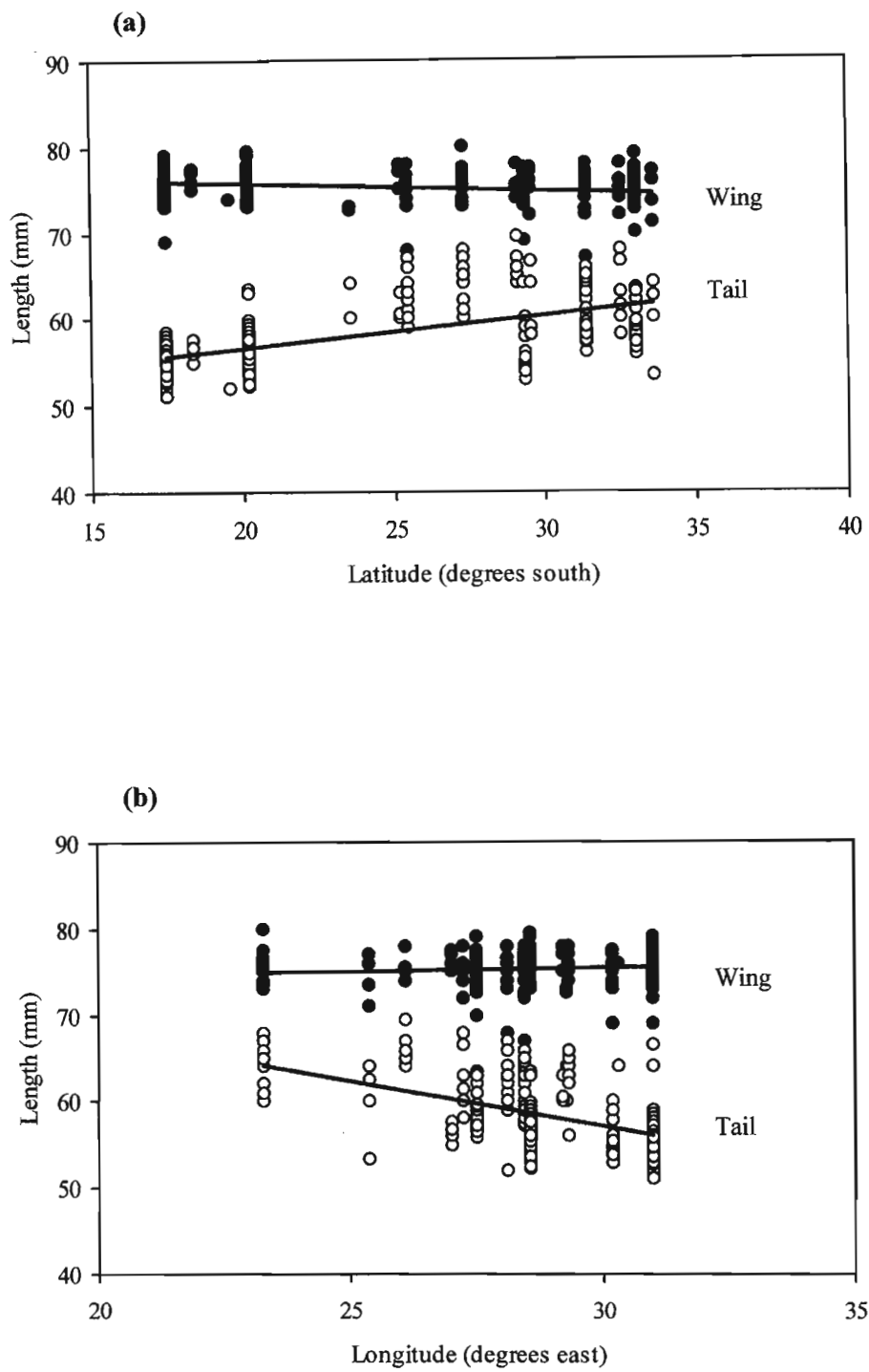


Figure 3.25. Variation in flight structures of male house sparrows along (a) latitude and (b) longitude in southern Africa.

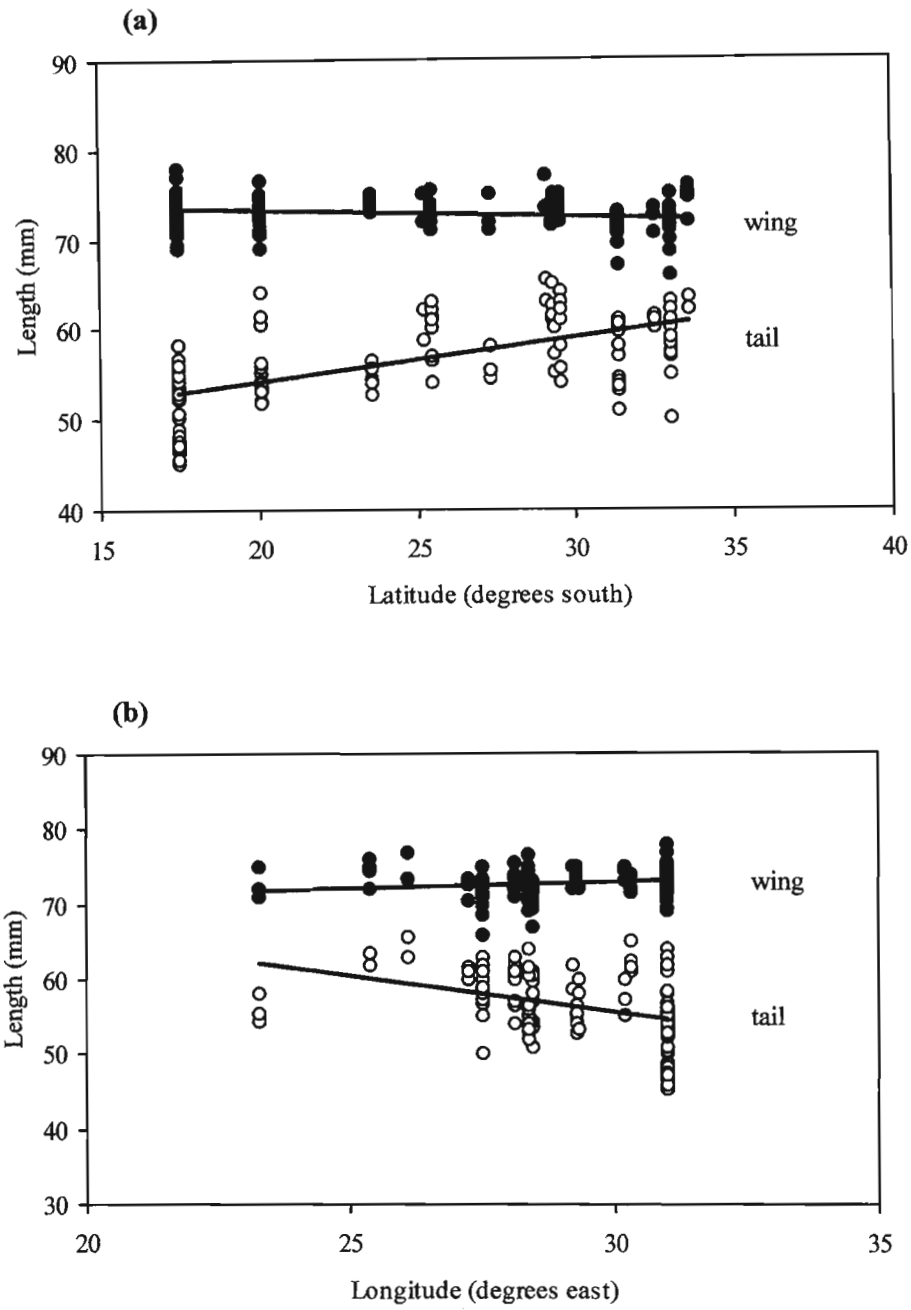


Figure 3.26. Variation in flight structures of female house sparrows along (a) latitude and (b) longitude in southern Africa.

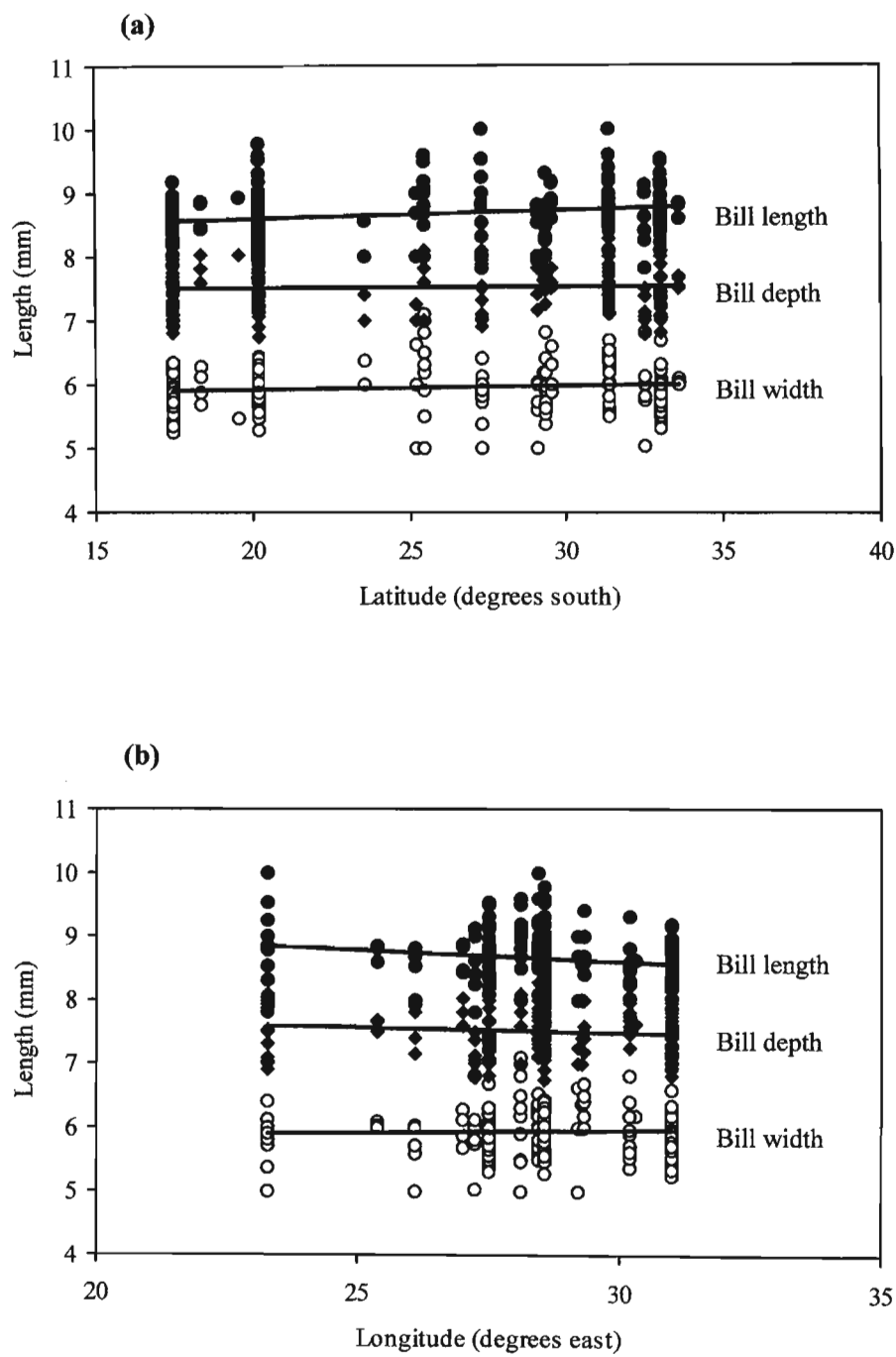


Figure 3.27. Variation in beaks of male house sparrows along (a) latitude and (b) longitude in southern Africa.

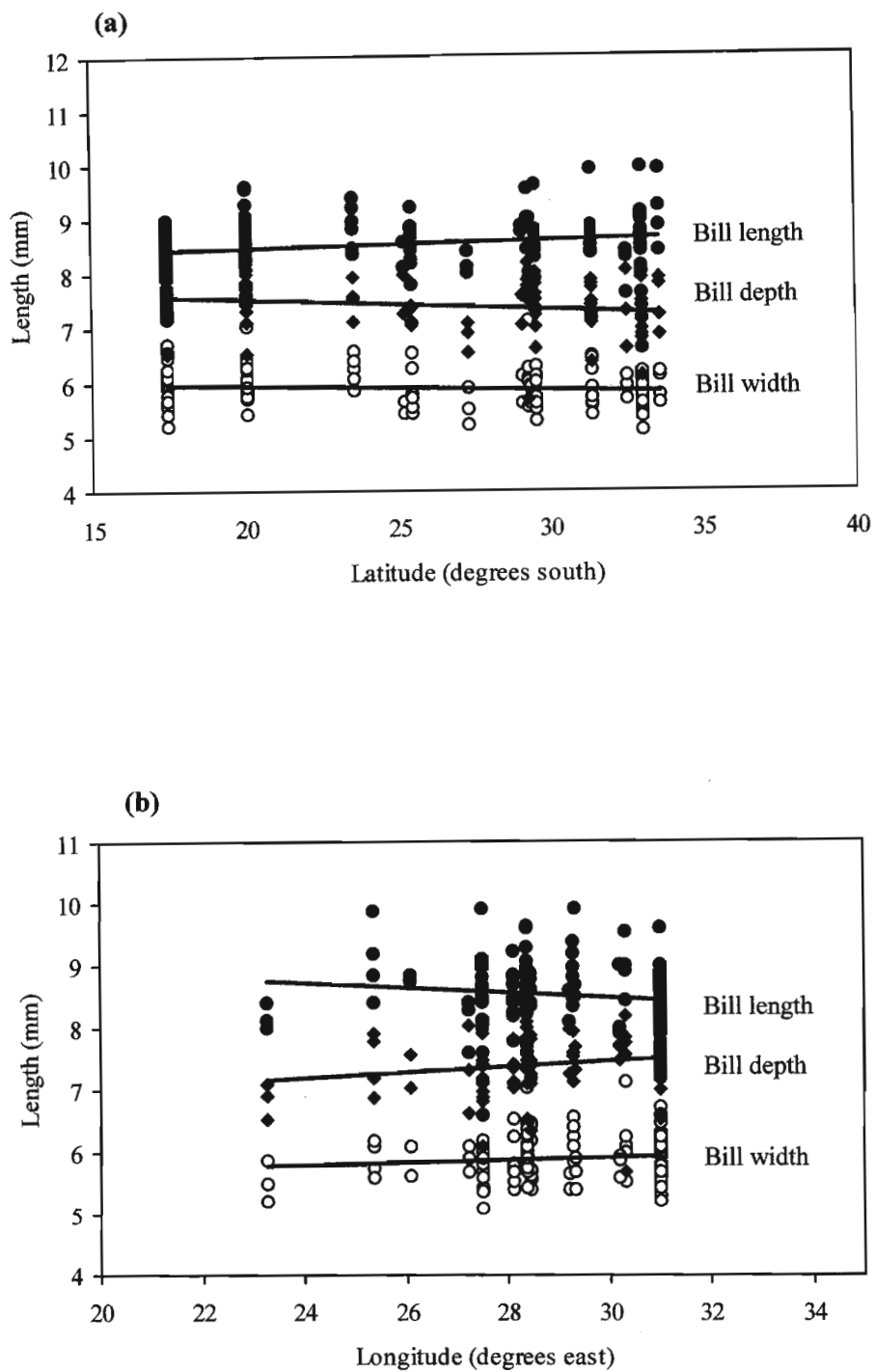


Figure 3.28. Variation in beaks of female southern African house sparrows along (a) latitude and (b) longitude.

CHAPTER 4

MICROEVOLUTION IN THE HOUSE SPARROW, *PASSER DOMESTICUS*, IN SOUTHERN AFRICA: MORPHOLOGICAL DIFFERENTIATION OF ZIMBABWEAN POPULATIONS IN RELATION TO PARENT POPULATIONS OF ASIA AND EUROPE

4.1 Abstract

Few studies of microevolution (change in morphology over a short period) have been conducted in birds and none on invading bird species in the tropics. Invading species can provide empirical data on micro-evolutionary changes in species in new habitats. The house sparrow, *Passer domesticus*, was introduced to southern Africa over 100 years ago and reached Zimbabwe just over 40 years back. Elsewhere in its new range, it has undergone rapid adaptation and differentiation. The house sparrow, therefore, provides an ideal case study in microevolution in tropical Africa. Samples taken from Zimbabwean populations of the house sparrow were analysed to establish temporal variation in local samples and to determine the extent of variation from parent populations of Asia and Europe. Samples collected since arrival in Zimbabwe up to 1980 were compared with those collected from current populations in 1998/1999 to determine local changes over time. The Zimbabwean samples were then contrasted with samples from Asian and European populations to determine the extent of differentiation in the introduced birds of Zimbabwe. Zimbabwean populations had differentiated from their Asian parents in all the seven morphological characters examined. The greatest differentiation was in beak size and shape for both males and females. Males developed larger beaks and shorter wings than the Asian birds and female beaks became more conical. The potential phenetic diversity of the founding population of both *domesticus* and *indicus* genes has been realised in Zimbabwe and one of the questions that now needs to be addressed is whether the phenetic changes observed have been accompanied by genetic adjustments.

4.2 Introduction

Evolutionary research owes one of its most important findings to the house sparrow, *Passer domesticus*. That is, that if there is strong selection pressure subspecies can be formed much quicker than the thousands of years normally expected for avian species (Niethammer 1971). In *P. domesticus*, morphological changes have been observed to occur within a hundred years of introduction to new habitats (Johnston & Selander 1964, 1972, Johnston 1969b, 1973). This is because this species has a high potential for adaptive radiation and differentiation even after short periods of time following introduction (Johnston & Selander 1964, 1972, Johnston 1969b, 1973). According to Mayr (1956), such changes in organic diversity (that is, adaptive radiation and speciation) are an important component of evolution. Adaptation occurs in response to various selection forces in operation in the new habitats, resulting in phenotypic and subsequently genetic modifications (Boag & Grant 1981).

A few studies have been conducted on introduced bird species in the new world and important information obtained on the evolutionary changes that take place in invading species in their new habitats. Boag and Grant (1981) and Grant (1986) established that in Darwin's finches in the Galapagos beak size, particularly beak depth was modified rapidly in response to climatic changes. They noted that following a dry season, large birds survived into the following year and because seed abundance was reduced and seed size ratios were skewed towards larger seeds, birds had to adapt to taking large seeds. A corresponding change in beak morphology was observed.

Invasions of the New World by the house sparrow have created what Baker (1980: 638) refers to as "experiments in nature" or according to Johnston and Selander (1971: 1) a "developing case history of adaptation and differentiation". Throughout the new range, where studies have been conducted, the birds have developed significant interlocality differences in size within short periods of time, becoming distinguishable from parent stocks in just over 100 generations in North America (Baker 1980, Johnston & Selander 1964). Further, the interlocality differentiation was similar in the new range to that in English ancestral populations. Characters were similarly covariant in Europe and America suggesting that differentiation was moulded by natural selection. South American populations on the other hand, were more constrained phenetically than North American ones probably due to the founder effect. Only twenty pairs of house sparrows are known to have been brought to Buenos Aires in 1872 (Johnston & Selander 1973b).

In New Zealand, a small founding population of 110 birds was introduced between 1862 and 1871. Baker (1980) showed that both males and females had undergone significant interlocality differences in size and shape in just over 100 years of introduction, although to a lesser extent than in North American populations. Possible reasons for the restricted variability in New Zealand birds were the founder effect as well as the relatively more homogenous environment in New Zealand (Baker 1980).

According to Fleischer & Johnston (1982), winter climate was the major factor for mortality and selection on size in North American house sparrows. Generally, males tended to be larger and females smaller following selection suggesting sexual differences in response to selection for optimal body size and proportions. Sexual selection favoured bigger size in males while selection for small size in females was attributed to reproductive constraints (Fleischer & Johnston, 1982).

While the North American and New Zealand inoculum came mainly from England, the southern African birds derived from populations of both *P. d. indicus* (brought to Durban from Asia) and *P. d. domesticus* (brought to East London from Europe and England) between 1890 and 1930. The birds of Durban (*indicus*) spread northwards and entered Zimbabwe about 40 years ago (Harwin & Irwin 1966, Niethammer 1971, Summers-Smith 1963). This was one of the three main sources of the founding population of Zimbabwe. The second source was direct introduction of European birds (*domesticus*) to Harare around 1957 (Harwin & Irwin 1966) and the third involved releases in Bulawayo of captive birds of an unspecified subspecies (Harrap, unpubl. notes). Thus, the initial population of Zimbabwean house sparrows was highly phenetically and genetically variable and had a high potential for divergence. Since dates of introduction and origin of populations are known, analysis of morphometric trends in Zimbabwean populations could provide insights into the microevolutionary forces at work in the tropical conditions.

The main objective of this study was to assess the extent to which the potential for divergence had been realised in Zimbabwean birds. Samples of local and exotic populations were compared to determine if Zimbabwean birds had differentiated from the parent Asian and European populations. If Zimbabwean birds descended from Asian and/or European populations a measure of their similarity or dissimilarity to these parent stocks can provide an index to the degree of differentiation in size. The following specific predictions were tested: that (1) there was interlocality and temporal variation in birds of Zimbabwe; (2) tarsus length had increased in birds of hot arid conditions in Zimbabwe; (3) house sparrows in Zimbabwe had become significantly different from Asian and European birds in general body size and (4) beaks had become shorter and deeper in Zimbabwean birds as an adaptation for seasonal variation in seed

size and abundance resulting from the effects of the hot arid, environmental conditions in the new range.

4.3 Materials and Methods

4.3.1 Sampling procedures

Samples of house sparrows comprising 91 males and 28 females were collected from seven Zimbabwean cities (sites 1 to 6 and site 8 in Fig. 3.01) between May and December 1998 and in March 1999. Mist netting was the most successful method although various locally made traps were tried in each city. Fewer females were caught in nets and it was not possible to mount nets for more than 3 days in one locality, as birds became wary and difficult to catch. The birds were made into study skins and incorporated into the collections in the Natural History Museum of Zimbabwe in Bulawayo.

Specimens were aged by both plumage colour and condition of the skull according to Selander and Johnston (1967). Young birds (6 - 7 months old) had soft skulls completely unossified while birds older than 17 months had fully ossified skulls and were classified as adults. Only the adult birds were used and sexes were treated separately in the analysis. Seven morphological characters were measured according to Table 3.01 and the data from the 1998/1999 samples were pooled with data from specimens collected in Zimbabwe by 1980. Parametric tests were used because all characters were normally distributed at $P > 0.05$ as determined by the Kolmogorov-Smirnov test.

4.3.2 Geographic and temporal variation in Zimbabwean populations

An analysis of covariance (ANCOVA) was carried out to determine geographic variation in Zimbabwean populations. Only site 1 (Harare) and site 2 (Bulawayo) had large enough pre 1980 samples for use in the analysis. Each character was assessed in turn with period as the independent variable, where four period levels represented (a) Harare by 1980 (b) Harare in 1998 (c) Bulawayo by 1980 and (d) Bulawayo in 1998 and time was used as the covariate. In this case "time" was represented by ten year intervals based on date of collection of the specimens, such that specimens collected between 1961 and 1970 were put together in the 1970 category. A five yearly analysis would have been preferred but adequate sample sizes could not be obtained.

4.3.3 Differentiation in Zimbabwe in relation to Asian and European populations

An analysis of interpopulation variability can be used to assess the degree of differentiation among populations. This can be achieved by (a) comparing interpopulation variances from ANOVAS and (b) examining ranges of the means of individual characters among the populations concerned. The best comparison of the introduced populations of Zimbabwe with parent stock would have been achieved with European birds taken between 1955 and 1960 (the introduction period to Zimbabwe). However, since representative samples of these could not be obtained, only those that were available were used. These samples of "parent populations" would be phenetically different from the actual populations from which the inoculations were derived. However, such differences were presumed to be minimal, particularly since past work has proved that there was little or no temporal variation over periods of 35 to 100 years in European populations (Johnston 1969a, Johnston and Selander 1971).

4.3.3.1 Interpopulation variances from ANOVAS

Analysis of Covariance (ANCOVA) was conducted to determine variation between the birds collected in Zimbabwe by 1980, extant populations of Zimbabwe represented by the 1998 samples and the samples from parent populations of Asia and Europe. Each morphological character was assessed in turn, with time period as the independent variable, where four time

period levels represented a) Asia b) Europe c) Zimbabwe then (pre-1980 samples) and d) Zimbabwe now (1998 samples). The differences between the populations could result from one of two causes. On the one hand the differences could be the result of the effects of weather around the time that the samples were collected. For example if dry conditions produce larger and harder seeds, and wet seasons produce a wider variety of seed sizes, then the weather could produce differences say in beak size according to the range of sizes of seeds available. On the other hand the changes could be real evolutionary adaptations in time. To determine whether climate alone was not the cause of the changes in Zimbabwean birds an ANOVA was conducted on the climatic variables with time (pre1970, 1980, 1998) as the independent variable.

4.3.3.2 Ranges of means of individual characters

The ranges were obtained as differences between maximum mean character states and minimum mean character states for the samples. Character mean ranges were used instead of the standard error because they give an indication of the variation available for selection to act on and for the interpretation of the changes from the parent stock. The range therefore, gives a measure of realised variability for the character concerned.

4.4 Results

4.4.1 Geographic and temporal variation in Zimbabwean populations

There were significant differences in patterns of temporal variation in size of all morphological characters between the populations of Harare and Bulawayo. Tarsus length increased between 1970 and 1998 in Harare males and in Bulawayo females but decreased in Harare females (Fig 4.01a). There was no significant change in tarsus length of Bulawayo males. Claws also showed variable trends between the sexes and between the two populations (Fig. 4.01b). Claws were similar in males of both Harare and Bulawayo in 1970 and Harare birds had not changed by 1998 but claw length increased in males of Bulawayo. In females claws changed in opposing directions in the two populations. While claw length decreased in Harare females, there was a marked increase in females in Bulawayo.

Generally, wings became shorter in males and longer in females. The greatest change in wing length was in Harare males, which by 1998 had the shortest wings (Fig. 4.02a). Tails were initially shorter in Harare than in Bulawayo in both sexes. Tail length then increased in males and females of Harare and decreased in males of Bulawayo between 1970 and 1998. Tails remained unchanged in females of Bulawayo (Fig. 4.02b). Thus, tails became longer in all Harare birds and shorter in Bulawayo males over time. Selection seemed to favour longer tails and shorter wings in the north at Harare than in the south at Bulawayo.

Beak size and shape were modified differently in males and females of both Harare and Bulawayo. Beak length and width increased in males of both cities and in females of Harare (Fig. 4.03). In Bulawayo beak width increased but bill length decreased in females. Beak depth was similar in males of both populations in 1970 and it increased over time in both populations with the biggest change in beak depth in Harare males between 1980 and 1998. On average, beaks became longer, wider and deeper in all Harare birds and in Bulawayo males and became shorter in females in Bulawayo. Generally, beaks had become more conical in shape in Zimbabwean birds. These changes were not likely to have been allometric since they were not correlated with changes in tarsus or wing length. The comparison of trends in females was limited by lack of Harare specimens for 1970 and Bulawayo specimens for 1980.

In summary therefore, male birds in Harare had acquired longer tarsi and tails, bigger beaks and shorter wings while males in Bulawayo had longer claws, bigger beaks and shorter wings and

tails. In females of Harare, tarsi and claws became shorter while wings and tails got longer and beaks became bigger. In Bulawayo females, longer tarsi, claws and wings as well as shorter conical beaks were selected for but tails showed no obvious response to the selection forces in operation there. The two populations were thus responding to different selective regimes determined by local conditions.

4.4.3 Differentiation from Asian and European populations

4.4.3.1 Interpopulation variances from ANOVAS

The results of the Anova in Table 4.01 indicate that all seven characters assessed differed between the introduced populations of Zimbabwe and parent populations of Europe and that three characters (tail length, beak width and beak depth) differed significantly for both sexes between Zimbabwean and Asian populations (Table 4.01). In addition, Zimbabwean and Asian males differed in wing, tarsus and beak length. There was no significant difference in female wing, tarsus and bill length and none in claws of either sex of Zimbabwean and Asian birds. Thus, Zimbabwean males had differentiated from their ancestral population in all characters except claw length while females differentiated in only three traits; tail length, beak width and beak depth.

4.4.3.2 Mean ranges of individual morphological characters

Comparison of the ranges of means also revealed high levels of differentiation in both sexes of the introduced populations (Figs. 4.04 - 4.06). By 1998 Zimbabwean birds of both sexes had character mean ranges equal to or larger than those of six characters of Asian birds but only four of European populations. In males, all except tarsus length had mean ranges equal to or greater than in Asian birds and the mean ranges of wing length and beak depth were equal to those of European birds. Zimbabwean females exceeded Asian females in the mean ranges of all except beak length and they exceeded European females in the mean ranges of claw length, wing length, beak width and beak depth.

Tarsus length of male birds in pre 1980 samples of Zimbabwe was shorter than in both Asian and European males and in females it was similar to that of Asian birds but shorter than in birds of Europe. By 1998, tarsus length was similar in Zimbabwe and Asian birds but still shorter than in European samples in both sexes (Fig. 4.04a). Claw length did not change over time in Zimbabwean birds, remaining shorter than in both Asian and European birds (Fig 4.04b). Thus, selection tended to favour long tarsi in Zimbabwean birds.

On the other hand, selection favoured reduction in flight structures (Fig. 4.05). In 1980, wings were longer in Zimbabwe than in birds of Asian origin but shorter than in European populations. By 1998 the wings of male birds had reduced to the same size as in Asian birds but in females wing length remained unchanged, at a little longer than in Asian birds but shorter than in European populations (Fig. 4.05a). In 1980 tails were shorter in Zimbabwe than in either Asian or European birds of both sexes and they became even shorter over time. Flight structures of extant populations of the house sparrow in Zimbabwe therefore had become significantly shorter than those of both Asian and European birds.

Generally, beak size increased over time in Zimbabwe. Zimbabwean beaks started at more or less the same length and depth as in Asian birds and became longer and deeper in both sexes than in Asian birds (Fig. 4.06). In males, beaks also became wider over time but were still thinner than in both parent populations by 1998 (Fig. 4.06b). Female beaks did not change in width, remaining thinner than in both Asian and European birds. Thus, beaks became larger overall in males and they were deeper in females than in Asian birds. However, the results of the ANOVA conducted

on the climatic variables to determine the effect of climate on the changes in Zimbabwean sparrows indicated significant differences in both precipitation ($F = 3.01$, $P < 0.05$) and relative humidity ($F = 7.12$, $P < 0.001$) for the periods pre1970, 1980 and 1998 with both rainfall and relative humidity increasing between 1970 and 1998. If dry conditions produce larger and harder seeds, then beak would be larger following dry seasons and vice versa. In this case however, beak size was modifications were not correlated with climatic trends in time. Thus, morphological changes, especially those related to beak size and shape were not just a result of the effects of climate.

In North American birds, a considerable degree of the latent differentiation present in the original inoculum was realised within 100 years of introduction. Differentiation in North American birds was less than that in western European sparrows (Johnston 1973, Johnston & Selander 1972). More male and female characters had ranges equal to or larger than those of England and Germany but fewer had similar ranges to European traits. Since the birds of North America came from England mainly, this was consistent with expectations for differentiation in the new habitats. Zimbabwean house sparrows equalled or exceeded Asian birds in the mean ranges of six characters and European birds in the ranges of four characters.

Male wing length decreased by 1.6mm and male tarsus increased by 0.5 mm. Male beak depth went up 0.47mm and female beaks increased by 0.33mm. These figures were comparable to observations in North America where wing length increased by 1 mm in 55 years and 2.5 to 3 mm in 110 years (Calhoun 1947, Johnston & Kiltz 1977). In North America, New Zealand and Australia similar morphometric variation occurred within 100 years and was closely correlated with genetic differentiation (Cole & Parkin 1981 1986, Fleischer 1983, Parkin & Cole 1984 1985, Johnston 1969b, Johnston & Selander 1964 1971 1972, Selander & Johnston 1967). In the Azores genetic differentiation in 37 years was close to that in New Zealand after 100 years of occupation (Melo Medeiros 1997).

Because large numbers of house sparrows were introduced to Zimbabwe either deliberately or by unassisted spread from South Africa, the possibility of a founder effect was minimised. Thus, evidence from morphological analysis of local populations of the birds of Zimbabwe in relation to their ancestors from Asia and Europe suggests that the introduced populations had differentiated significantly from the parent populations. Males had differentiated in six characters from the Asian birds (wing, claw, tail length, beak length, width and depth) and in four characters in relation to the European birds (wing length, beak length, width and beak depth). Morphological evidence thus, suggests that tarsi, claws, tails and beaks were of Asian origin but the origin of wings could not be readily determined. Wings seemed to be of mixed origin.

4.5 Discussion

Significant geographic and temporal variation was detected in males for six of the seven traits examined (all except claws) and in females, tail length as well as bill width and bill depth had undergone significant levels of differentiation in Zimbabwe. Longer tarsi and bigger beaks as well as shorter wings and tails were selected for in both sexes. In addition, beaks became more conical in females. Thus, females responded more to factors relating to feeding behaviour while males tended to change in general body size. Different patterns of modification of morphological characters of male and female birds suggest that different selection forces were operational between the sexes in Zimbabwe. Further, Zimbabwean populations of the house sparrow had differentiated considerably from both Asian and European parent populations in all seven characters assessed. Morphometric evidence suggests that more of the characters of the birds of Zimbabwe may have derived from Asian rather than European birds.

There were significant differences in patterns of geographic and temporal variation between the sexes. The birds of Harare and Bulawayo responded differently to selection pressure. Generally, birds in more humid conditions in Harare were bigger than in hot arid Bulawayo. Reversed size dimorphism in tarsus length of Harare birds was inconsistent with observations in house sparrows elsewhere (Baker 1980, Selander & Johnston 1967). Variation in general size of sexes may be related to intrasexual fighting. Large size in males would confer a selective advantage in male-male combat followed by female choice of winners of the intrasexual fights (Moller 1988 1989 1990, Selander 1965). Longer wings in females may be related to a need for females to fly more frequently in search of food as a result of sexual competition for resources. Beak depth was under the most intense selection pressure in Zimbabwean birds and this could be related to limited diversity of food type and size. Intraspecific competition for food resources might influence increase in beak dimensions. Smouse (1971) observed that strong sexual dimorphism persisted where there was ecological partitioning of habitats along sexual lines and trends in Galapagos finches (Grant 1986) and also in house sparrows in the Azores (Melo Medeiros 1998) were consistent with this observation. Where there was a low diversity of food size, bill size varied strongly between the sexes. Therefore, shorter, more conical beaks conferred a selective advantage on the females of Bulawayo.

Although sexual selection for increasing size in males is the main source of sexual size variation in house sparrows, relative niche width may influence body size variation at a locality (Hamilton & Johnston 1978, Selander 1966). In New Zealand sexes responded differently to environmental variation and males changed in more characters than females (Baker 1980). There was considerable geographic variation in relative niche widths due to the high diversity of habitats available and this could explain some of the sexual differences in interlocality differentiation. Similarly, a high diversity of habitats exists in Zimbabwe, resulting in considerable geographic variation in niche width.

Geographical variation in climatic conditions in Zimbabwe (especially precipitation and minimum temperature) may affect the range in seed size and abundance. Large amounts of seeds of variable sizes become available a few weeks after the onset of the rains when the annual grasses mature. However, at the end of the short rain season, smaller seeds quickly disappear and only the larger seeds are more readily available for most of the year. Thus, beak depth would be adapted for the generally low seed size variability prevalent in this type of climate (Boag 1983, Grant 1986).

While size variation is largely affected by climatic constraints, it can also be influenced by interspecific competition (Smouse 1971). In Zimbabwe, *P. domesticus* found other granivorous passerines and in particular two congeners, *P. griseus* and *P. diffusus*. The resultant interspecific competition for feeding and breeding resources would influence morphological variation in *domesticus*. However, competition for breeding sites is possibly stronger than competition for food since *domesticus* has become omnivorous rather than strictly granivorous like the other species that it interacts with, especially in urban and suburban areas. This is evident from the relationship between *domesticus* and *diffusus*, both of which nest mainly around human dwellings. While *domesticus* successfully established in the south and east of Zimbabwe where its range overlaps that of *griseus*, it failed to do so in the north and west where *diffusus* is more predominant.

In species that are commensals of man temperature regulation may be achieved by alteration in insulative properties and behaviour and therefore, a wide range of tolerance to environmental factors is developed (James 1970). It is not clear how the relationship of the house sparrow with humans and its largely omnivorous habits might affect morphological and physiological variation.

Observed morphological differences between Zimbabwean populations and their Asian ancestors could either be evolutionary (due to a restricted or diverse genetic base of founder population from Asia or Europe, that is, a small inoculum) or be due to ecogeographic variation in the new habitats. Normally, it takes several thousands of years for evolutionary changes to take place in birds but the high level of differentiation of house sparrows in North America (Johnston & Selander 1964 1972 1973a), New Zealand (Baker 1980) and the Azores (Melo Medeiros 1997) provides strong evidence for rapid rates of evolution. Similarly, significant differentiation occurred in Zimbabwe within 100 years of introduction. However, in view of the short period of the changes elsewhere the 100 year estimate for Zimbabwe is conservative. The changes could, in fact occur over a shorter period.

An analysis of differentiation of Zimbabwean populations of the house sparrow was successfully conducted and it was established the introduced populations of Zimbabwe had differentiated significantly from their ancestors of Europe and Asia. The greatest differentiation was in beak size and shape for both males and females. Selection favoured larger beaks in males and more conical beaks in females. Large size conferred a selective advantage in males. Further work should determine whether the phenotypic adjustments observed in Zimbabwe have become genetically controlled and if so, how much of the morphological variation is genetically based and how much is ecophenotypic. Also, it should be possible to use more quantitative genetic methods to establish the persistence or otherwise of the *domesticus* and *indicus* genes and to determine to what extent the evolutionary potential of the house sparrows has been realised.

Table 4.01. Differentiation in Zimbabwean house sparrows in relation to Asian and European parent populations.

Character	sex	Combined samples (n = 246 M, n = 373 F)		Analysis of variance ¹ Zimbabwe and Asia (n = 216 M, n = 103 F)		Zimbabwe and Europe (n = 229 M, n = 116 F)	
		d.f.	F ratio	d.f.	F ratio	d.f.	F ratio
Wing length	M	242	21.88***	212	20.0***	227	22.83***
	F	125	8.02***	102	1.25	114	4.70**
Tarsus length	M	241	9.82***	212	9.28***	226	15.32***
	F	125	7.23***	102	0.08	114	6.69**
Claw	M	239	8.73***	212	2.48	224	12.65***
	F	125	5.50***	102	0.17	114	3.96*
Tail	M	236	38.66***	207	5.51**	221	59.25***
	F	116	13.29***	93	5.76**	105	17.18***
Bill	M	240	21.27***	211	5.76**	225	28.06***
	F	124	17.77***	101	0.41	113	18.77***
Bill width	M	241	37.96***	212	22.45***	226	57.32***
	F	124	19.62***	101	4.62**	113	26.97***
Bill depth	M	239	24.45***	211	17.42***	224	36.38***
	F	124	9.89***	101	4.80**	113	10.42***

¹ANCOVA of morphological characters of Combined samples (Zimbabwean pre1980, post1980 samples + Asian + European samples); Zimbabwean and Asian samples; Zimbabwean and European samples.

Sample sizes for male (M) and female (F) birds denoted by n.

Significant inter-population variation at *P<0.05; **P<0.01; ***P<0.001.

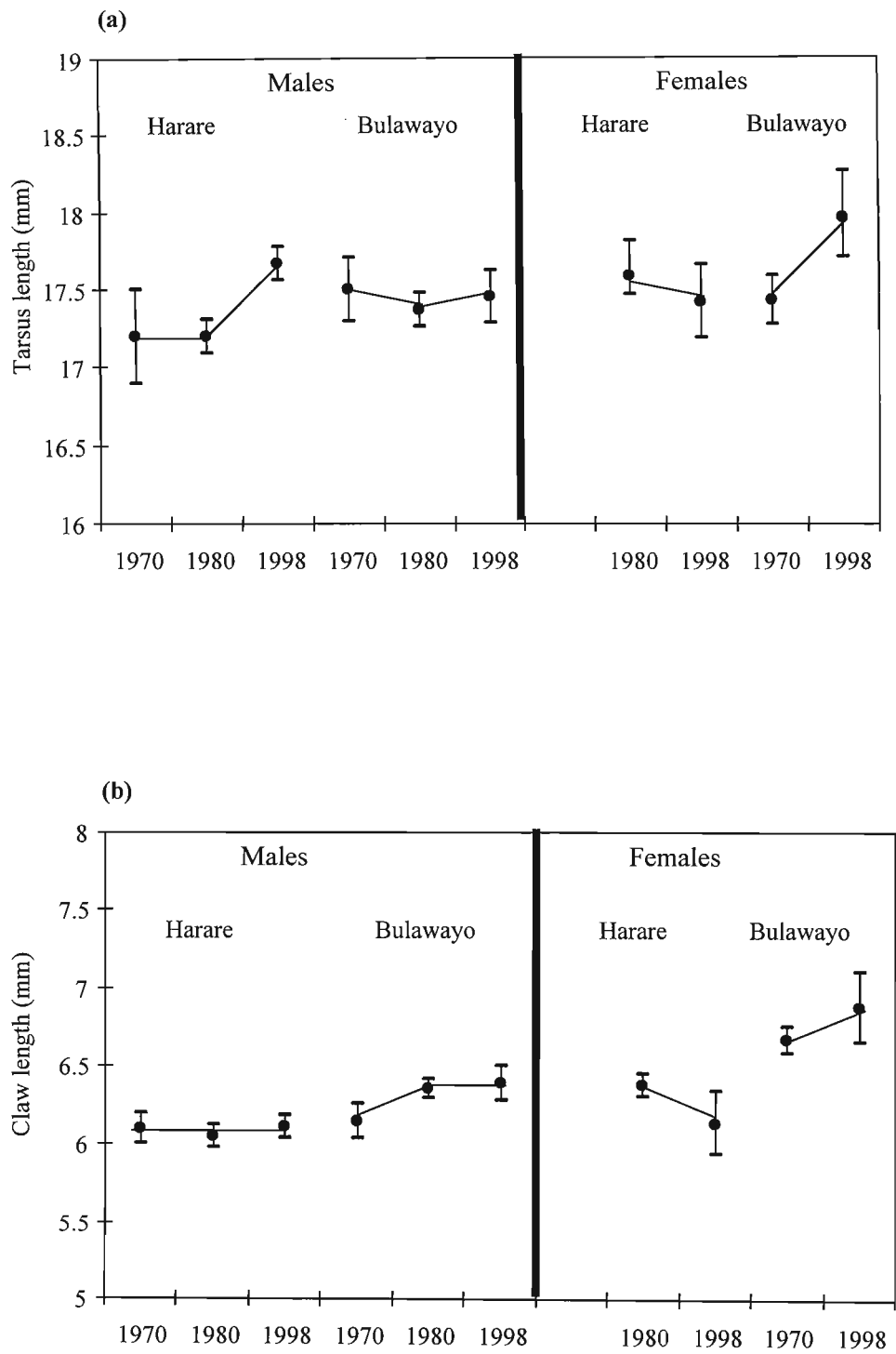


Figure 4.01. Mean values \pm standard error of (a) tarsus length and (b) claw length of house sparrows in Bulawayo and Harare.

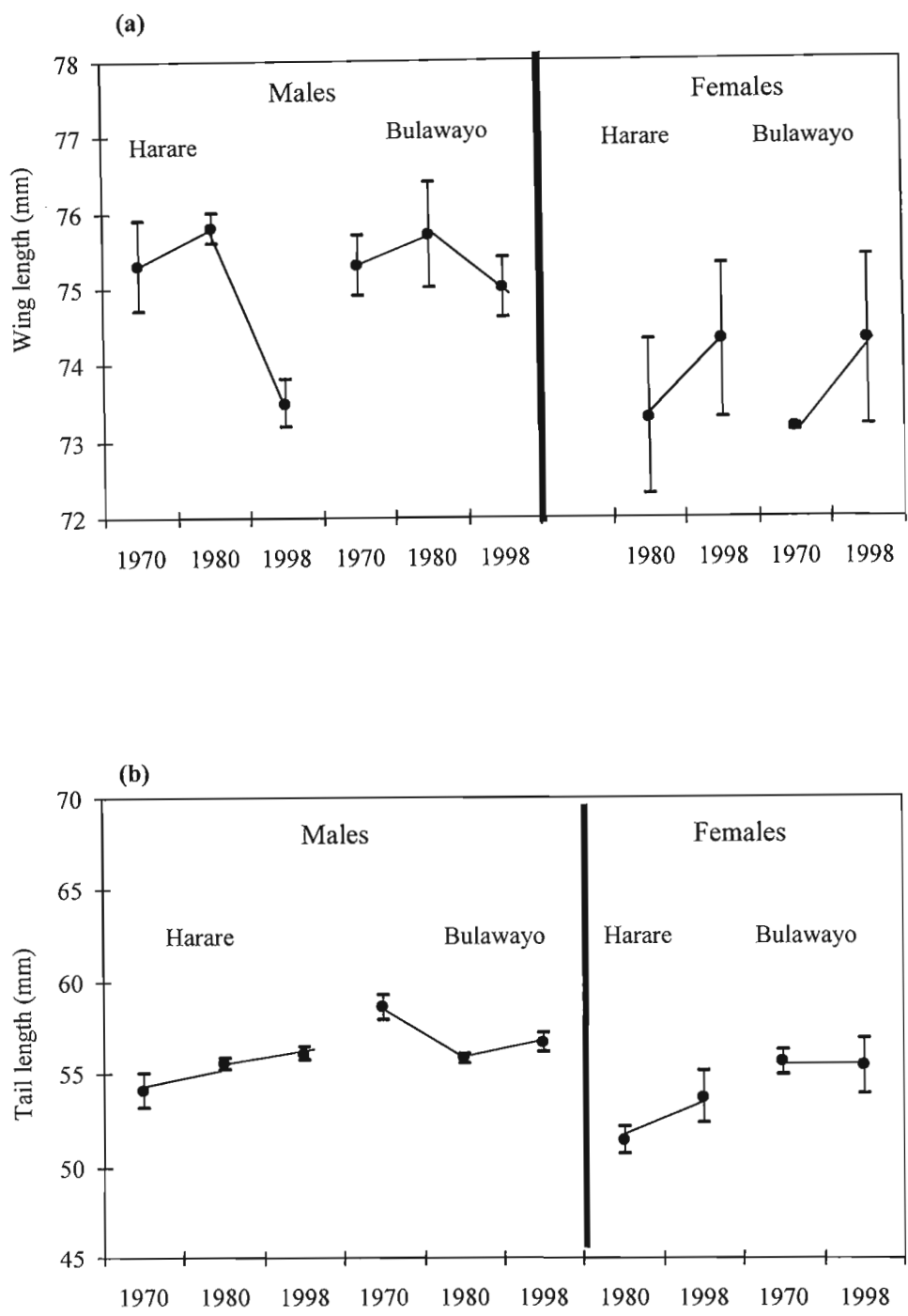


Figure 4.02. Mean values \pm standard error of (a) wing length and (b) tail length of house sparrows in Bulawayo and Harare.

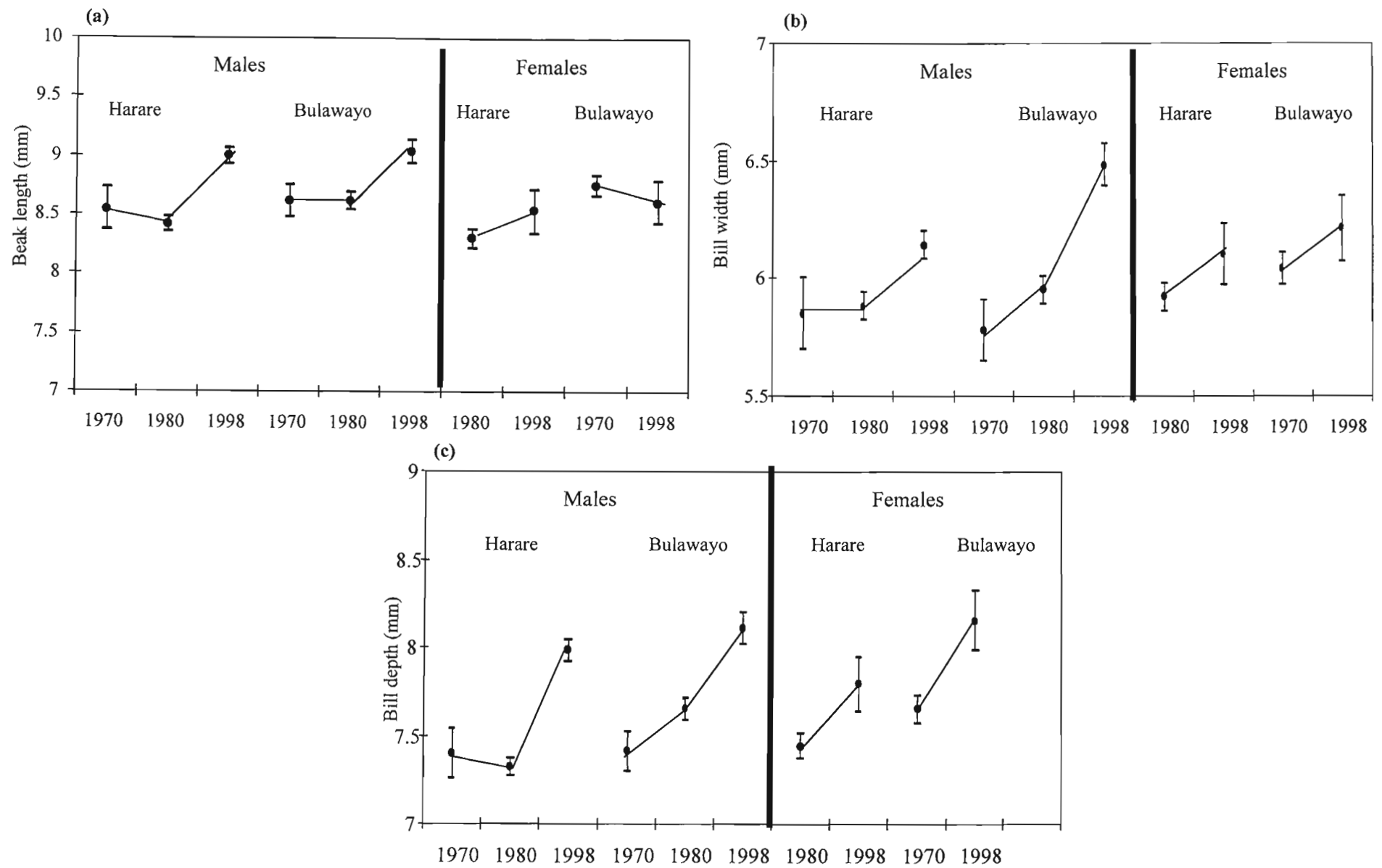


Figure 4.03. Mean values \pm standard error of (a) beak length, (b) beak width and (c) beak depth of house sparrows in Bulawayo and Harare.

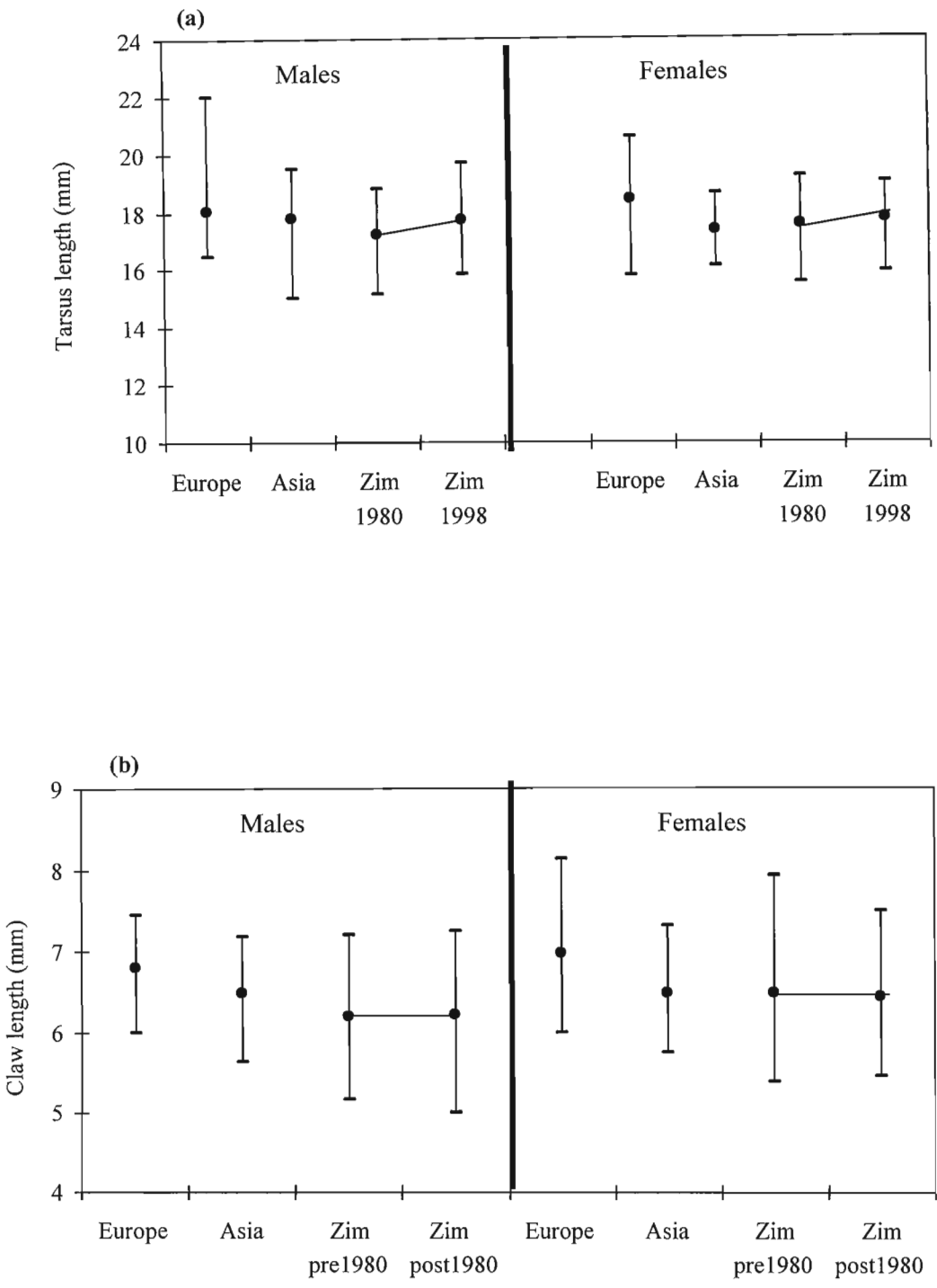


Figure 4.04. Mean values and ranges of (a) tarsus length and (b) claw length of Zimbabwean (Zim pre1980 and Zim post 1980) house sparrows, showing differentiation in relation to Asian and European parent populations.

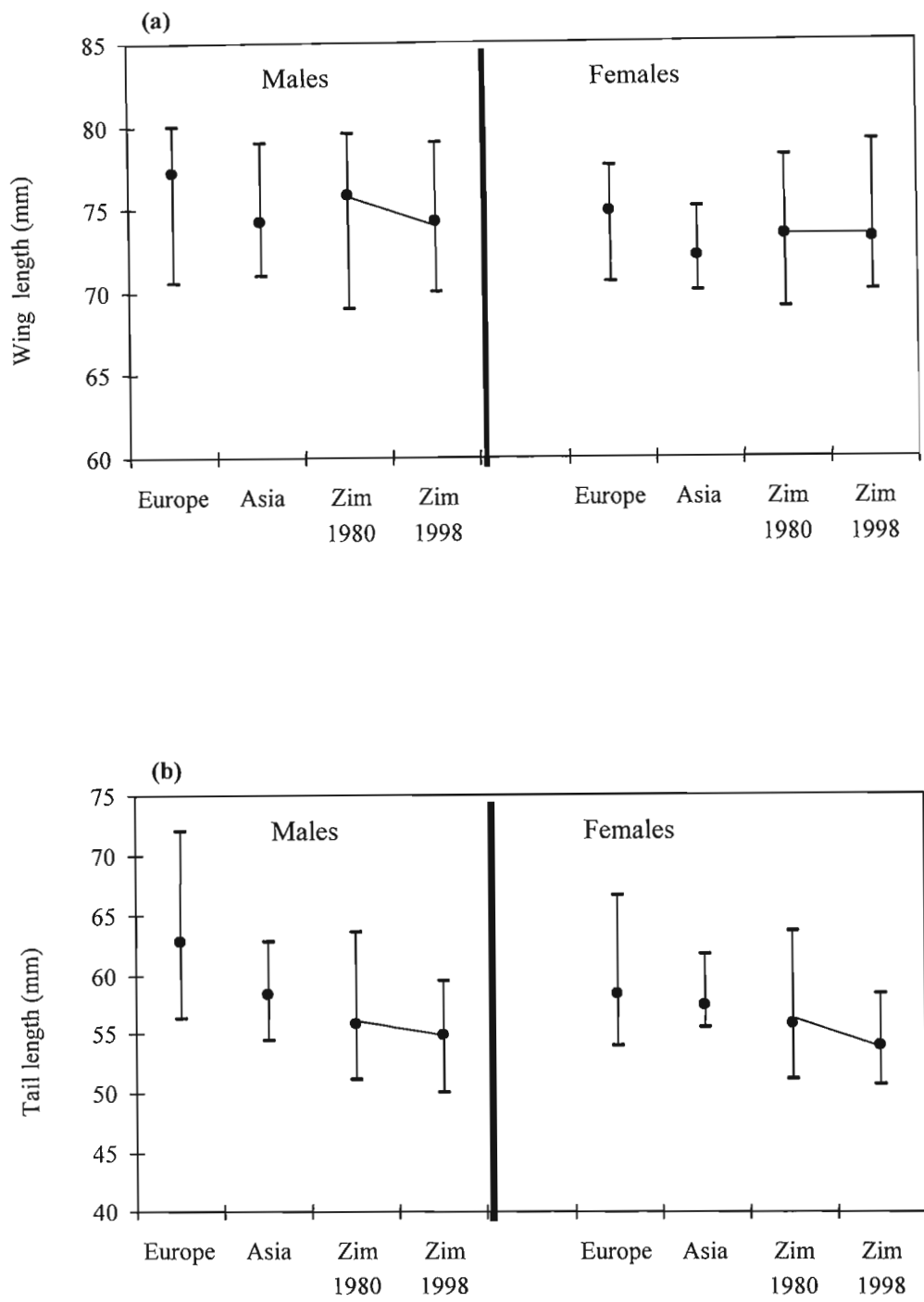


Figure 4.05. Mean values and ranges of (a) wing length and (b) tail length of Zimbabwean (Zim pre1980 and Zim post1980) house sparrows, showing differentiation in relation to Asian and European parent populations.

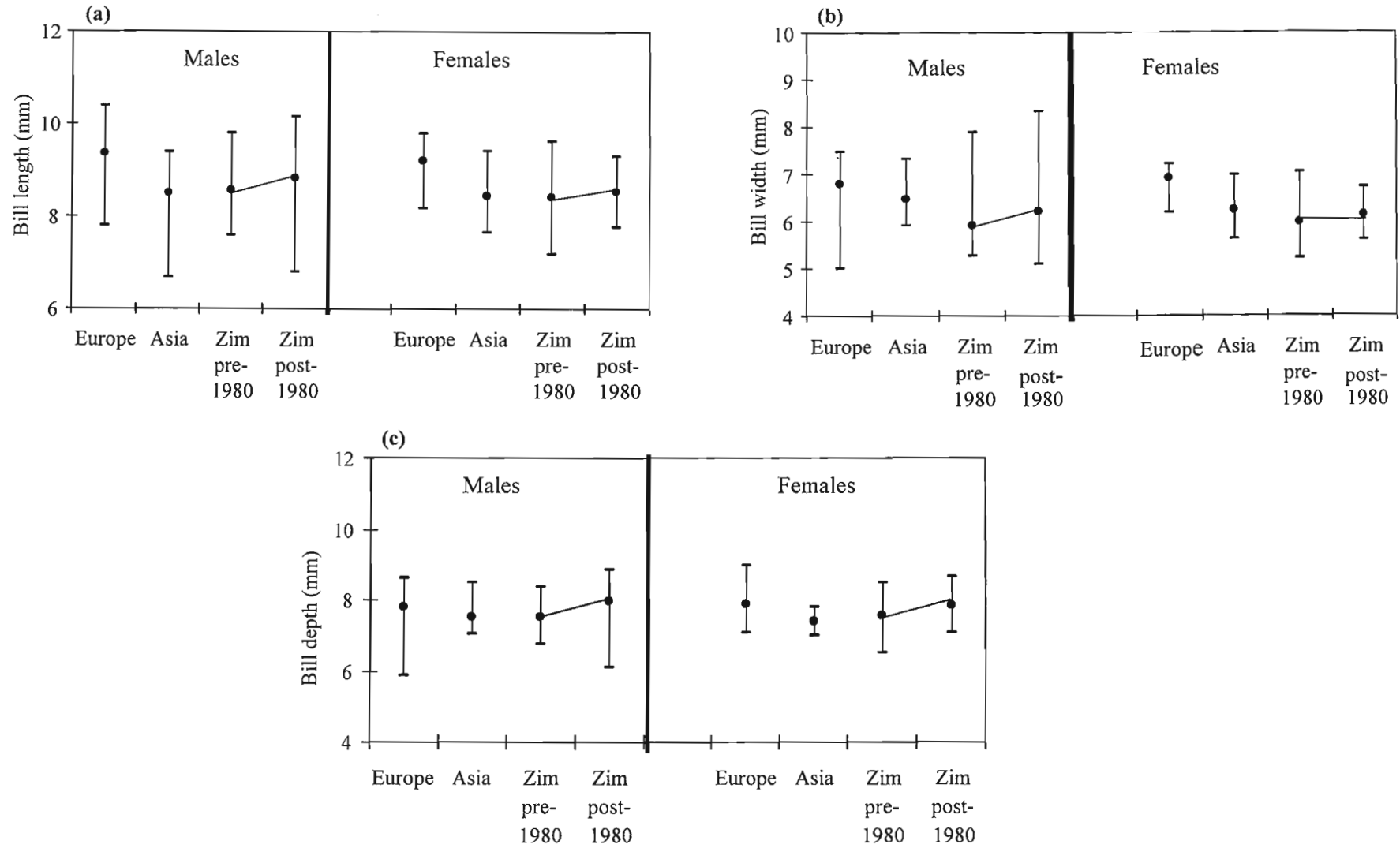


Figure 4.06. Means and ranges of (a) beak length, (b) beak width and (c) beak depth of Zimbabwean (Zim pre1980 and Zim post1980) house sparrows, showing differentiation in relation to Asian and European parent populations.

CONCLUDING REMARKS

The objectives of this study were accomplished as follows:

The invasion of the House Sparrow in southern Africa has been described as an exponential spread with a slow initial rate attributable to the Allee effect, followed by rapid acceleration of the rate of dispersal to more than 80km/year. Dispersal was by a combination of long-range dispersal events and diffusive movement over short distances and tended to be more rapid along the railway line and to large towns.

Significant interlocality morphological differentiation was detected in southern African house sparrow samples collected by 1980. Single character size varied clinally in a north-south direction and male birds were more variable than females. Geographic variation was greatest in flight characters and feeding appendages. General body size was also clinally ordered with a latitudinal trend. Birds tended to be larger in the south of the range in conformity with Bergmann's rule. The biggest birds occurred in coastal South Africa from Durban to East London. However, tarsus length varied discordantly with Allen's rule, with long tarsi occurring in the mesic sites in South Africa. Selection favoured longer flight characters and shorter tarsi in male birds and longer tarsi and shorter beaks in females. There was close correlation between morphological characters and environmental factors, especially minimum temperature and humidity. Beaks were broader in more arid conditions in Zimbabwe. Southern African birds, particularly in Zimbabwe, are undergoing adaptive radiation.

The effects of micro-evolutionary forces on the birds of Zimbabwe were demonstrated and significant shifts towards larger body size and beak size had occurred within 100 years of arrival in southern Africa. Zimbabwean populations of the house sparrow had differentiated significantly from the ancestral populations of Europe and Asia in response to local environmental conditions. The greatest differentiation was in beak size and shape for both males and females. Beaks of Zimbabwean female birds became broader than in Asian females while Zimbabwean males had larger beaks and shorter wings than the parent birds of Asia. It appears that new optimum values were set for Zimbabwean birds.

It can be concluded therefore, that the house sparrow has successfully invaded and settled in a tropical environment as rapidly as it has done in the more temperate habitats elsewhere in its new range. While its success in temperate climates may be explained by the similarities in conditions in the original range and in the new areas, the same cannot be said for southern Africa. It is more likely that the *indicus* genes from similar environments in Asia would be responsible for the success in southern Africa.

No obvious evidence of hybridisation was found but there is reason to believe that there has been mixing of genes not only between the races *domesticus* and *indicus* but also between the other *Passers*. In Zimbabwe both *P. griseus* (in the south) and *P. diffusus* (in the north) occur within the range of *P. domesticus* and there is constant interaction between the species. Casual observations and reports from garden bird watchers have revealed that in the south *domesticus* and *griseus* are found in the same gardens occupying different niches. The indigenous species has not been displaced. In the north in Harare it was observed that when *domesticus* came in the numbers of *griseus* went down. However, *domesticus* numbers have remained low in Harare and a more *diffusus* like sparrow is now more prevalent (Irwin pers. comm). Up in Hwange and Victoria Falls in the northwest *diffusus* is the "house sparrow" occupying the exact niche that would have been taken by *domesticus*. Here the introduced species does not seem to have penetrated and its numbers remain very low in the highly populated parts of the town. It is here that further work is required to determine interspecific relationships and possibly hybridisation. Another part of the southern African range of interest concerning hybridisation would be the Eastern Cape region and southern Lesotho where intergradation of populations of *indicus*

advancing from Durban in the east and *domesticus* spreading from East London in the south is likely to have taken place. Also the economic importance of the house sparrow in southern Africa has not been investigated. There have been isolated complaints, particularly in Zimbabwe about the birds taking food from poultry and pig feeding trays and also from the food processing industries like bakeries and granaries but no analysis of the cost of the losses has been done. Since the bird has become completely urbanised in this part of its range it does not seem to be a threat in the grain fields, that niche having been occupied instead by *Quelea quelea*.

The methods used in this study can be used to conduct similar analyses of invasive species such as the Indian myna and the European starling. These would add to our knowledge of the dynamics of invasions in southern Africa and help to predict the movements and subsequent adaptational changes that may take place. This information can then be used in deciding whether or not there is a need to intervene and apply control measures to populations of alien species.

Future work on the house sparrow should determine whether the phenotypic adjustments to the environment have become genetically controlled. It should also be possible to use biochemical methods to establish the persistence or otherwise of *domesticus* and *indicus* genes and determine to what extent the evolutionary potential of the house sparrow has been realised in southern Africa. Examination of samples of extant populations of South Africa, especially at Durban and East London, the major centres of inoculation, could help determine further the extent of microevolution in each race since introduction to southern Africa more than a century ago.

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Appendix 1. Classification of locations of house sparrows and proximity to the railway line. Settlements with a population of 50 000 or more (by 1950 for South Africa and by 1960 for Zimbabwe) were classified as large towns. Population data for South Africa was based on the 1951 census while that for Zimbabwe was based on the 1962 census figures. Position on the rail by 1950 for both South Africa and Zimbabwe.

Name	Latitude; Longitude	Population	Size	On/Off rail
South African locations:				
Johannesburg	28°00'; 26°15'	884 007	Large	On
Cape Town	33°55'; 18°22'	577 648	Large	On
Durban	29°50'; 29°59'	479 974	Large	On
East London	33°00'; 27°58'	91 264	Large	On
Bloemfontein	29°12'; 26°07'	109 369	Large	On
Pietermaritzburg	30°16'; 29°37'	74 493	Large	On
Kimberley	28°43'; 24°46'	62 439	Large	On
East Rand	26°33'; 28°67'		Large	On
West Rand	26°33'; 28°23'		Large	On
Potchefstroom	26°46'; 27°01'	32 058	Small	On
Kroonstad	27°46'; 27°12'	26 612	Small	On
Queenstown	31°52'; 27°00'	25 880	Small	On
Klerksdorp	26°58'; 26°39'	24 277	Small	On
Oudtshoorn	33°35'; 22°14'	18 729	Small	On
Bethlehem	28°15'; 28°15'	18 574	Small	On
Edendale	30°18'; 29°45'	16 922	Small	Off
Ladysmith	29°45'; 23°28'	16 413	Small	On
Cradock	32°08'; 25°36'	14 866	Small	On
Upington	21°15'; 28°25'	13 303	Small	On
King Williams Town	32°51'; 27°22'	12 480	Small	On
Beaufort West	32°18'; 22°37'	11 809	Small	On
Lichtenburg	26°08'; 26°08'	10 189	Small	On
Zimbabwean locations:				
Harare	31°03'; 17°50'	379 909	Large	On
Bulawayo	28°36'; 20°09'	222 061	Large	On
Mutare	32°40'; 18°42'	157 399	Large	On
Gutu	30°55'; 19°55'	115 949	Large	Off
Gweru	29°45'; 19°28'	105 178	Large	On
Masvingo	30°50'; 19°59'	96 449	Large	On
Mberengwa	30°00'; 20°10'	91 280	Large	Off
Kwekwe	29°50'; 18°58'	83 130	Large	On
Marondera	31°35'; 18°15'	71 661	Large	On
Nyamandhlovu	28°30'; 19°50'	67 180	Large	On
Gwanda	29°10'; 20°58'	63 413	Large	On
Kadoma	29°58'; 18°25'	59 920	Large	On
Gokwe	29°40'; 18°40'	53 288	Large	Off
Hwange	26°29'; 18°22'	51 635	Large	On
Zvishavane	30°05'; 20°15'	49 721	Small	On
Shurugwi	30°00'; 20°08'	49 659	Small	On
Nkayi	28°56'; 18°58'	40 392	Small	Off
Chimanimani	32°50'; 19°45'	40 047	Small	Off
Lupane	27°48'; 18°57'	32 187	Small	Off
Beitbridge	30°00'; 22°10'	26 447	Small	On