THE ECOLOGY OF A TEMPERATE BIRD INTRODUCED TO A TROPICAL ENVIRONMENT: THE HOUSE SPARROW, *PASSER DOMESTICUS* (L.) IN TOWNSVILLE, NORTH QUEENSLAND.

Dissertation submitted by

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as partial fulfilment of the requirements for the degree of Bachelor of Science with Honours in the School of Biological Sciences at the James Cook University of North Queensland.

Passer domesticus (L.) male

Passer domesticus (L.) female

ABSTRACT

The ecology of the house sparrow *Passer domesticus* (L.) was studied in Townsville in order to examine behavioural, population and morphological changes in temperate bird species adapting to tropical climates. A study of geographic variation in Australian house sparrows was also conducted.

House sparrows in Townsville used communal roosts for the full period of study rather than deserting them in autumn and winter. Roosts in Townsville contained smaller numbers of birds than those in temperate areas. Birds left the roost at sunrise and flew to feeding areas for the day, returning just before sunset. The times of departure and return varied seasonally.

The proportion of juvenile ("snco") birds in the population was similar to that in temperate locations in May and decreased over the year because of mortality, dispersal and ossification of the skull. The sex ratio did not differ from parity over the study period, though males always made up 50 to 60 per cent of the population. The population under study decreased in size by two-thirds from March to October.

The diet of house sparrows in Townsville included animal food for a longer period of the year than it does in temperate areas because of the longer availability of insects. Insects were captured by active searching of leaves, by flycatching and by collection from cobwebs.

Testicular recrudescence occurred from March to May and nest-sites were established and nests built at this time. In June, regression of the testes occurred as temperatures reached their minimum levels. Reproductive activity commenced again in July and the breeding season began in September. Because of the timing of the project, insufficient breeding data could be obtained to allow breeding parameters to be calculated for Townsville populations. Temperate Australian populations breed from October to January; their average clutch-size is 4, of which 3 survive to fledgling stage.

Relative to that in house sparrows of temperate localities, seasonal variation in body weight in Australian house sparrows was reduced, as was seasonal variation in bill length.

Significant geographic variation was found in body weight, male wing length and male tail length. Intrapopulation variability was similar to that in European and North American populations. Interpopulation variability in Australia was similar to that found in North America, though it was less than that found in England. Sexual dimorphism in size increased from south to north in the samples collected. There was no geographic variation in variance of bill length.

STATEMENT OF SOURCES

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institute of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

G.K. Jones
November 1982

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CHAPTER ONE

INTRODUCTION

1.1 Adaptation and geographic variation

The wide distribution of birds from the poles to the tropics presupposes physiological and other adaptations for surviving and reproducing in extreme as well as moderate climates. The Class Aves originated in the tropics (Darlington, 1957), and dispersal into the polar regions with their great seasonal fluctuations in temperature, photoperiod, food resources and other factors must have required progressive evolutionary adaptations (Kendeigh and Blem, 1974). Because climate varies geographically, adaptation of a species to local conditions over its range results in geographic variation of the species (Mayr, 1963).

Modifications of birds and other homeotherms in response to geographical and seasonal changes in climate occur in physiology, behaviour and morphology. Considerable attention has been paid over the years to climatic trends in some of these characters and attempts have been made to relate them to environmental parameters. However, problems arise when geographic variation is studied in established species - here, only the end result of adaptation may be seen. In order to study the mechanisms of evolutionary change, case histories of adaptation and differentiation are required; these have been provided by the introduction, in the period 1850 to 1870, of numerous mammalian and avian species.

1.2 Introduced birds

Bird species have been introduced by man to a variety of new environments in different parts of the world, the reasons for their introduction being varied and often difficult to determine. Long (1981) lists the following as reasons for bird introductions: aesthetics; food,hunting and sport; pest control; aviculture and escapees; and accidental introduction. Accidental transport is a major contributor to the introduction and spread of some species, and occurs by birds accompanying ships, travelling in railway carriages, etc. The house sparrow appears to have spread into northern South Australia (Alexander, 1958) and reached New Guinea (Ashford, 1978) in this way. Table 1.1 lists a selection of birds introduced to Australia, the manner in which they were introduced and the reasons for their introduction.

A total of 71 bird species have been released in Australia since European settlement; of these 25 species are now definitely established. The numbers of bird species introduced to seven areas of the world are shown in Table 1.2.

The introduction of birds to areas where they do not occur naturally has caused problems in many areas of the world; exotic species compete with native species for food and habitat, introduce diseases and parasites, and many cause damage to agricultural crops (Long, 1981). However, the introduction of birds presents the opportunity to observe the evolutionary processes of adaptation and differentiation in action. These "experiments in nature" (Grinnell, 1919) are of great importance to evolutionists since both the time frame and the parent stocks are well documented.

Table 1.1: Bird species introduced to Australia
(adapted from Long, 1981)

Species	Date introduced	Manner introduced	Reason
1. Ostrich	1869	deliberate	feather industry
2. Mute swan	1886,1897-1912?	semi-feral escapee	ornamental
3. Mallard	1860s-1912	deliberate?	?
4. Cattle egret	*1933(W.A.)	deliberate	insect control
	1940s	natural colonisation	-
5. California quail	1930	deliberate	game
6. Common pheasant	1910,1928,1950	deliberate	?
7. Feral pigeon	after 1788	feral	domestic
8. Spotted turtledove	1870,1872,1874, 1881,1898,1912	deliberate	aesthetic?
9. Laughing turtledove	1898	deliberate	aesthetic
10. Skylark	1854-1881	deliberate	aesthetic?
11. Red-whiskered bulbul	1880	deliberate and escapees	cage-birds
12. Red-vented bulbul	1917	?	?
13. Blackbird	1860-1882	deliberate	?
14. Song thrush	1859-1880	deliberate	?
15. European goldfinch	1863-1879	deliberate	?
16. European greenfinch	1863,1872	deliberate	?
17. House sparrow	1863-1872	deliberate	aesthetic
18. Tree sparrow	1863-1881	deliberate	?
19. Nutmeg mannikin (Spice finch)	about 1930	escapee	cage-birds
20. White-winged whydah	about 1931	deliberate	?
21. Common starling	1857,1863-1881	deliberate	?
22. Indian myna	1862-1872	deliberate	insect control
23. House crow	*1926 on	ship-borne	-

"*" indicates introduction unsuccessful

Scientific names of species listed in this table may be found in the Appendix.

Table 1.2: Numbers of birds introduced to various regions (from Long, 1981)

Region	No. introduced species	Definitely established	Possibly established
New Zealand	126	32	2
Hawaiian Islands	159	43	25
Australia	71	25	2
North America	98	25	12
Europe	42	12	6
South America	15	7	1
Africa-Arabia	19	8	6

1.3 Aims of present study

Because of its status as an agricultural pest, its wide latitudinal distribution, the speed at which it has spread through various continents and the ease at which large numbers of specimens may be collected, the house sparrow has become a major subject in the study of evolutionary processes. However, little work has been done on the species with regard to its dispersal into, and adaptation to, tropical environments.

The aims of this study were therefore to trace the spread of the house sparrow into the tropical regions of Australia, and to investigate its adaptation to life in a tropical environment. This was accomplished by undertaking a population study and a study of seasonal and geographic variation in morphometric variables.

Characteristics of Australian tropical and temperate climates are described in Chapter Two. In Chapter Three, the house sparrow, its relationship with man and the history of its introduction to various parts of the world are described in order to provide a basis for the following population and morphological studies. Since the aims of this study were to elucidate behavioural, population and morphometric changes in tropical sparrows, only those features showing distinct changes and other features not showing expected changes are discussed. At all times the attempt has been made to compare data from Townsville with data from temperate areas of Australia and other continents, where these were available.

CHAPTER TWO

THE STUDY AREAS

2.1 The Australian Climate

Australia lies between latitude 10°41'S (Cape York) and 43°39'S (South Cape, Tasmania), a position which ensures a sub-tropical to cold temperate climate (Keast, 1959). Climatic conditions in Australia are predominantly continental but the insular nature of the land mass is significant in producing some modification of the continental pattern. The island continent of Australia is relatively dry with 50 per cent of the area having a median rainfall of less than 300 millimetres per year and 80 per cent less than 600 millimetres. Extreme minimum temperatures are not as low as those recorded in other continents because of the absence of extensive mountain masses and because of the expanse of ocean to the south. However, extreme maxima are comparatively high, reaching 50°C over the inland, mainly due to the great east-west extent of the continent in the vicinity of the Tropic of Capricorn (Cameron, 1982).

The rainfall pattern in Australia is strongly seasonal in character with a winter rainfall regime in the south and a summer regime in the north. The main features of the seasonal rainfall are:

(a) marked wet summer and dry winter of northern Australia;

(b) wet summer and relatively dry winter of south-eastern

Queensland and north-eastern New South Wales;

(c) uniform rainfall in south-eastern Australia - much of New South Wales, parts of eastern Victoria and in southern Tasmania;

(d) marked wet winter and dry summer of south-west Western Australia and (to a lesser extent) of much of the remainder of southern Australia.

(e) arid area comprising about half of the continent extending from the north-west coast of Western Australia across the interior and reaching the south coast at the head of the Great Australian Bight.

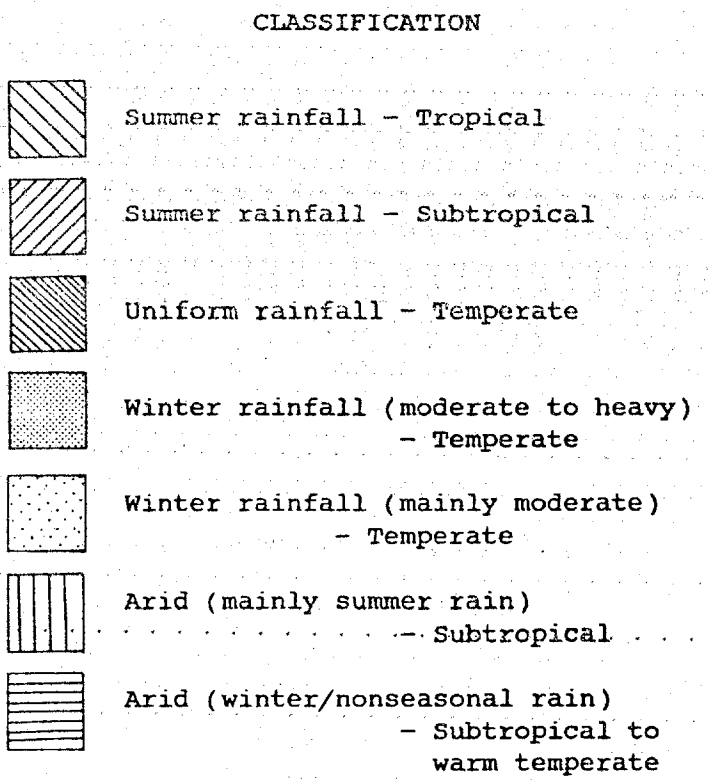
This pattern dominates over other climatic elements and as a result seven climatic zones are recognized in Australia; characteristics of these zones are shown in Figure 2.1.

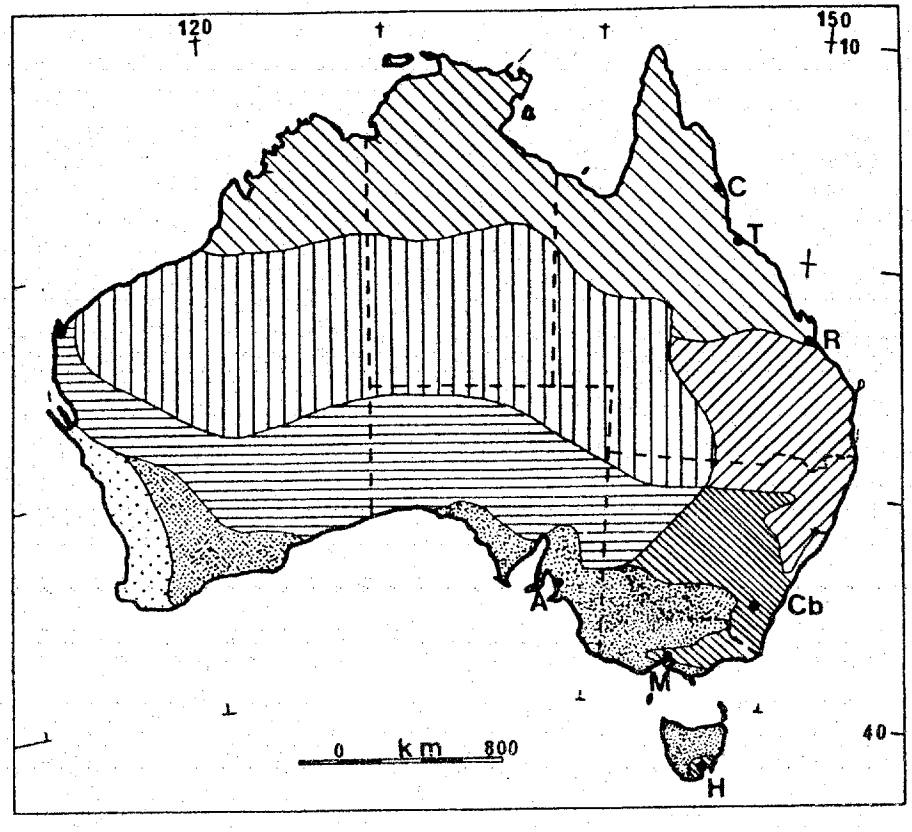
2.2 Townsville

The Townsville region is part of a dry corridor extending to the coast from the inland, though its climate is warm and sub-humid (Christian *et al*, 1953). The average annual rainfall of Townsville is 1204 millimetres, of which 90 per cent falls between November and April (Figure 2.2). As a result, there are two distinct seasons - a hot, wet summer and a warm, dry winter. Rainfall varies significantly from year to year in its duration and intensity, as indicated by the figures for the period January to September, 1982 (Data from the Bureau of Meteorology, Garbutt weather station). From January to March, 1982 (Figure 2.2) 458.6 millimetres of rain fell in Townsville, compared with an average of 873 millimetres for

Figure 2.1: The Climatic zones of Australia

(from Cameron, 1982)





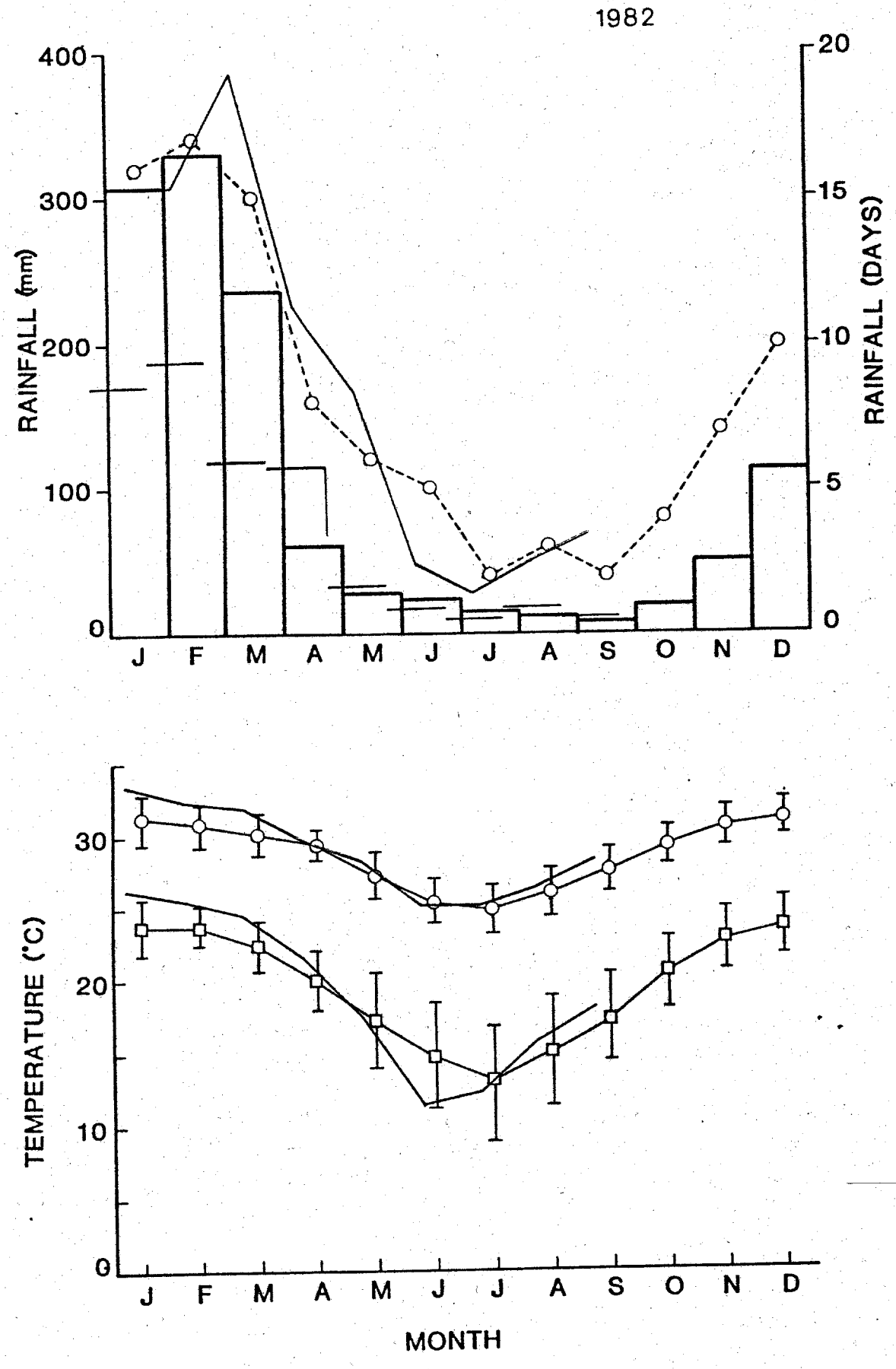
AUSTRALIAN CLIMATIC ZONES

Figure 2.2: Climatic data for Townsville

(Bureau of Meteorology, 1975)

KEY

Histogram:	Mean monthly rainfall
○——○	Mean monthly maximum temperature (indicating 14 and 86 percentile values)
□——□	Mean monthly minimum temperature (indicating 14 and 86 percentile values)
Overlay:	Monthly weather data for January to September, 1982 (data from Bureau of Meteorology, Garbutt weather station)
○- - -○	Number of rainy days


1982
RAINFALL (mm)
RAINFALL (DAYS)
400
300
200
100
0
20
15
10
5
0
J F M A M J J A S O N D
TEMPERATURE (°C)
30
20
10
0
J F M A M J J A S O N D
MONTH

the three month period. In April almost twice the average amount of rain fell, while the period from May to September was slightly drier than average.

Humidity varies little throughout the year in Townsville, ranging from 47% to 71% over this time. Mean daily maximum temperatures vary from 24.9°C in July to 31.3°C in January, while mean daily minimum temperatures fall between 13.1°C (July) and 23.8°C (January). There is considerable yearly variation in minimum winter temperatures; however, summer temperatures and mean maximum winter temperatures vary little from year to year. In 1982, summer temperatures were warmer than average, while winter temperatures were lower; the mean daily minimum temperature in June was lower than the 14 percentile level.

In Townsville, the difference between the longest and shortest days of the year is 2.4 hours.

2.3 Other Australian localities

Climatic data for six Australian localities from which data on house sparows were collected are compared in Table 2.1. Cairns, Townsville and Rockhampton are in the tropical zone (Figure 2.1), characterised by hot, wet summers and warm, dry winters. Canberra, Sydney and Hobart have uniform rainfall though the average value is less than that of the tropical localities. Adelaide is characterised by low rainfall occurring mainly in winter and irregularly in summer. All of the temperate localities have warm to hot summers and cool to cold winters.

Table 2.1: Climatic data for eight localities in Australia
(from Bureau of Meteorology, 1975)

Location	RAIN	MINW	MAXW	MINS	MAXS	HUM9	HUM3
Cairns	2001	16.7	25.4	23.7	31.5	71	59
Townsville	1204	13.1	24.9	23.8	31.3	64	56
Rockhampton	858	8.6	22.9	21.7	31.7	67	44
Sydney	1160	8.3	17.1	19.0	25.8	67	57
Canberra	633	-0.5	11.1	12.8	27.5	70	46
Melbourne	573	4.6	13.0	15.1	26.4	67	52
Adelaide	459	6.7	14.8	15.5	28.0	59	48
Hobart	567	3.7	12.0	11.7	22.2	67	55

Location	AMIN	AMAX	LATIT	LONGIT	ELEV
Cairns	20.7	28.9	16°53'	145°45'	3.0
Townsville	19.5	28.7	19°15'	146°46'	3.4
Rockhampton	16.3	28.2	23°23'	150°29	7.9
Sydney	14.0	22.0	33°52'	151°12'	92.0
Canberra	6.1	19.4	35°19'	149°12'	570.6
Melbourne	9.2	19.6	37°40'	144°50'	109.7
Adelaide	11.0	21.3	34°57'	138°32'	7.6
Hobart	7.6	17.2	42°50'	147°32'	2.4

Abbreviations used for climatic variables:

RAIN - Mean annual rainfall (mm)
MINW - Mean minimum temperature of coldest month (^{o}C)
MAXW - Mean maximum temperature of coldest month (^{o}C)
MINS - Mean minimum temperature of warmest month (^{o}C)
MAXS - Mean maximum temperature of warmest month (^{o}C)
HUM9 - Mean annual 9 a.m. humidity (%)
HUM3 - Mean annual 3 p.m. humidity (%)
AMIN - Mean annual minimum temperature (^{o}C)
AMAX - Mean annual maximum temperature (^{o}C)
LATIT - Latitude (S)
LONGIT - Longitude (E)
ELEV - Elevation (m)

CHAPTER THREE

THE HOUSE SPARROW

3.1 Description

The house sparrow *Passer domesticus* (L.) is a weaver finch of the Family Ploceidae (subfamily Passerinae - Appendix) and is the most widespread member of the family. *P. domesticus* is sexually dimorphic in plumage (frontispiece); the female is pale brown with a light eye-stripe and is the plainer bird. The male is characterised by its grey crown, nape and lower back, chestnut stripe over the eye, white cheeks and black throat and breast (Witherby *et al*, 1938, 156-160). The bill of the male is black in the breeding season and fades to a horn colour at times when gonadal activity is low.

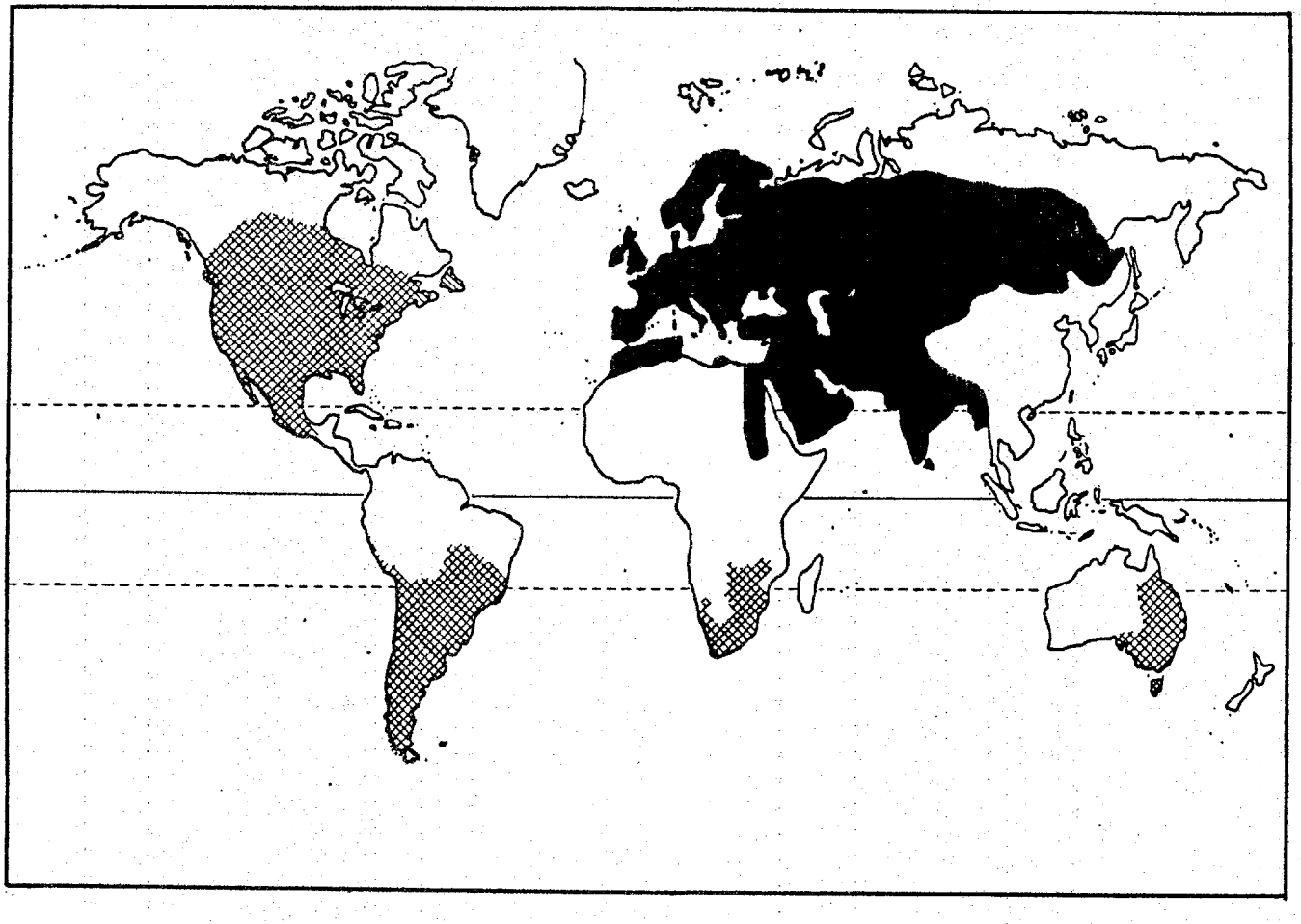
The natural distribution of the house sparrow includes the British Isles, all of mainland Europe and across central Siberia to Amurland. It extends south to Southern Morocco, Algeria, Tunisia, Egypt, Sudan, Arabia, Iran, India, Sri Lanka and southern Burma (Figure 3.1). In addition, the sparrow has been introduced in the last 130 years to many areas of the world and has extended its breeding range in Eurasia (Long, 1981). The origin and distribution of the house sparrow will be described in the next section.

The house sparrow is an obligate commensal of man, being unable to survive and reproduce away from human habitations (Summers-Smith, 1963) - man supplies the house sparrow with food, nest sites and

Figure 3.1 World distribution of the house sparrow

(after Long, 1981)

Natural distribution is shown in black; introduced distribution is hatched. Lines of latitude shown are the Equator, the Tropic of Capricorn and the Tropic of Cancer.



DISTRIBUTION OF THE HOUSE SPARROW

nest-building materials. As a result of numerous examinations of stomach contents that have been made in other parts of its range (Kalmbach, 1940; Southern, 1945; Hammer, 1948; MacMillan, 1981) much is known about the diet of the house sparrow. This species is very catholic in its choice of food and takes many different types of vegetable and insect species. Animal food is particularly important in the diet of the nestlings, though it is taken at any time of the year depending on availability.

All of the true sparrows (*Passer* species) build domed nests, the house sparrow most frequently building under the eaves of houses and in other suitable holes and crevices in buildings (Summers-Smith, 1963). Nests are also built in creepers on the walls of buildings, in the walls of the nests of larger birds and (rarely) in natural tree holes; in England, tree sites are used predominantly by the tree sparrow, *P. montanus*. Sites in stone walls and cliffs have also been reported in England, though in practically all cases the nests have been within a few hundred metres of an occupied house.

The house sparrow is monogamous, forming pairs which remain together until the death of one or the other member of the pair. The formation of pairs, the acquiring of nest sites and the building of nests may take place at the end of summer and during autumn, though all are intensified as the breeding season approaches (Summers-Smith, 1963). An integral component of the breeding cycle is the behaviour known as the communal or group display, in which a group of up to a dozen males chase a single female in rapid, close flight, eventually disappearing into a hedge or other cover where loud calling and sexual displays take place; because of the volume

of the sound produced during these displays, they are often called sparrow "parties". The display lasts for up to a minute and functions as a means of sexual stimulation (Summers-Smith, 1963). Sexual development in the male, leading to spermatogenisis, occurs in response to external stimuli, in particular in temperate climates to changing daylength; the sexual development of the female occurs later than in the male and does not advance to ovulation without the additional stimuli of the presence of a male with a suitable nest site, nesting material and courtship display.

3.2 Origin and distribution

The sparrows are thick-billed, mainly seed-eating birds and, except for recent introductions by man, are confined to Africa, Europe and Asia. The genus *Passer* contains 15 species (Appendix), several of which have long occurred in or near (1) tropical Africa, (2) the Far East, (3) eastern China, and (4) southeast Asia, four of the six "centres" of earliest agricultural man (Johnston and Klitz, 1977); commensalism is common amongst these species though *P. domesticus* is the only obligate commensal. The distribution of the genus suggests an origin in tropical Africa; this is supported by the fact that all of its members build a domed nest, a characteristic of tropical species. In addition, the communal display with its mutual stimulation leading to breeding synchronisation may have originated in the tropics where seasonal changes in daylength and other factors are not as significant in determining the onset of breeding (Summers-Smith, 1963). From an ancestral habitat of forest edges and scattered trees (savannah) the

sparrows spread and radiation occurred, some species moving into arid regions, others into water-rich bush country, and several into cultivated lands with habitations. Johnston and Klitz (1977) suggest that two waves of colonisation from Africa occurred, using the Nile River as a pathway to temperate areas. The first wave reflected a *P.montanus*-like species which spread and radiated in Asia, and the second a *P.hispaniolensis/domesticus*-like species which radiated in the Mediterranean basin.

The association of the house sparrow with man apparently began in the Near East, before the advent of agriculture. The ancestor of the house sparrow was probably migratory - since no mid-latitude continental population of any other *Passer* species is permanently resident (Johnston and Klitz, 1977). As man's settlements developed, overwintering in the Near East became an advantage since (1) grain would have been available to birds all winter; (2) the hazards of migration - moving to unfamiliar areas, setting up winter quarters and moving back in spring - would have been avoided, and (3) optimal nest sites and nest-building material around man's habitations would have been available to overwintering birds before returning migrants. Non-migratory individuals would have lived under lower risk of death, and would have had a reproductive advantage over migrants; therefore, non-migratory commensals became predominant among birds around man's settlements. Such non-migratory individuals would have tended to mate with others of like behaviour, thus establishing partial genetic discontinuity between old-line migrants (*P. hispaniolensis*-like birds) and the developing house-type sparrows. After the considerable climatic improvements in the period 10000 - 50000 B.P. man moved into

eastern and central Europe, and, for the first time the presumptive house sparrows met climatic conditions different to those in which they evolved. Moving into Europe would have thus intensified the relationship with man, at least as it concerned finding shelter in winter, and further isolation between the old-line sparrows and the house sparrow would have occurred. Since man's spread into Europe occurred over just a few centuries, the house sparrow must have undergone rapid evolutionary adjustment to the new climatic conditions encountered there. Similarly, the house sparrow followed agricultural man into western India.

Since 1800 the house sparrow has become almost certainly the most widespread species of land bird in the world; this has occurred for two major reasons: (1) the development of agriculture and communications in northern Asia, and (2) the colonisation of much of the world by man fron western Europe and the subsequent introduction of the house sparrow, along with other species, into these parts. The present world distribution of the house sparrow is shown in Figure 3.1. Introductions of house sparrows were made partly for sentimental reasons - the desire of the colonists to have familiar things around them to remind them of their homelands - and partly in the hope, usually mistaken, that the sparrows would help to combat plagues of harmful insects (Summers-Smith, 1963). The first of these introductions, and the most successful, was to North America (summarised by Barrows, 1889), where it now occurs from Churchill, in northern Manitoba on the Hudson Bay, to southern Mexico and Guatemala. The spread over this range has taken place in only 130 years from 1850. Introductions have also been made to South America, New Zealand, South Africa, Australia and to various

oceanic islands.

3.3 Introduction and spread of the house sparrow in Australia

The first successful introduction of house sparrows to Australia occurred in January,1863, when nineteen individuals arrived in Victoria (Long, 1981). Large numbers were released in both Melbourne and Sydney in that year and, in Melbourne, further releases were made at intervals up to 1872 (Summers-Smith, 1963). Ryan (1906) reported that in 1863, 120 sparrows were liberated in the Melbourne Botanical Gardens; 125 more were released in 1864; "another lot" in 1866 and 100 more were imported and liberated in 1872. In 1867, many birds about Melbourne were caught and were distributed "generally over the state of Victoria" (Ryan, 1906, p.111). Sparrows were also introduced to Adelaide in 1863 (Condon, 1962) and to Launceston, Tasmania (Summers-Smith, 1963) - apparently in mistake for tree sparrows.

From these points of introduction the house sparrow spread rapidly and by 1906 was distributed "well over Victoria ... in southern New South Wales and in South Australia, as well as in Tasmania and the intervening islands" (Ryan, 1906, p.111). Penetration into Western Australia occurred near Eucla in about 1917 and sparrows reached Mundrabilla Station, 100 kilometres west in 1918. In the summer of 1918-1919 they died out at Mundrabilla and there has been no further invasion along this route (Serventy and Whittell, 1976); in 1976, the nearest colony in South Australia was at Coorabie, near Fowler's Bay and at Tarcoola on the Transcontinantal railway.

Sparrows were released at Brisbane in 1869, but they failed to survive (Chisholm, 1919); the sparrows now present in Queensland are, therefore, descendents of birds introduced at Sydney in the year 1863. The south-eastern interior of Queensland was reached via the New England Tableland of northern New South Wales, the sparrow being present in Toowoomba by 1903 (E.C. Chisholm, 1926) and spreading to Brisbane and the Darling Downs by 1919 (Storr,1973). By 1926, the house sparrow was well established in Rockhampton, just north of the Tropic of Capricorn (A.H. Chisholm, 1926).

Therefore, in just 60 years from the time of introduction, the sparrow had spread from Sydney (34°S) to Rockhampton (23°22'S). In contrast, it required another 40 years to reach Townsville (19°16'S) and other northern Queensland centres. The present distribution of the house sparrow in Australia is shown in Figure 3.2.

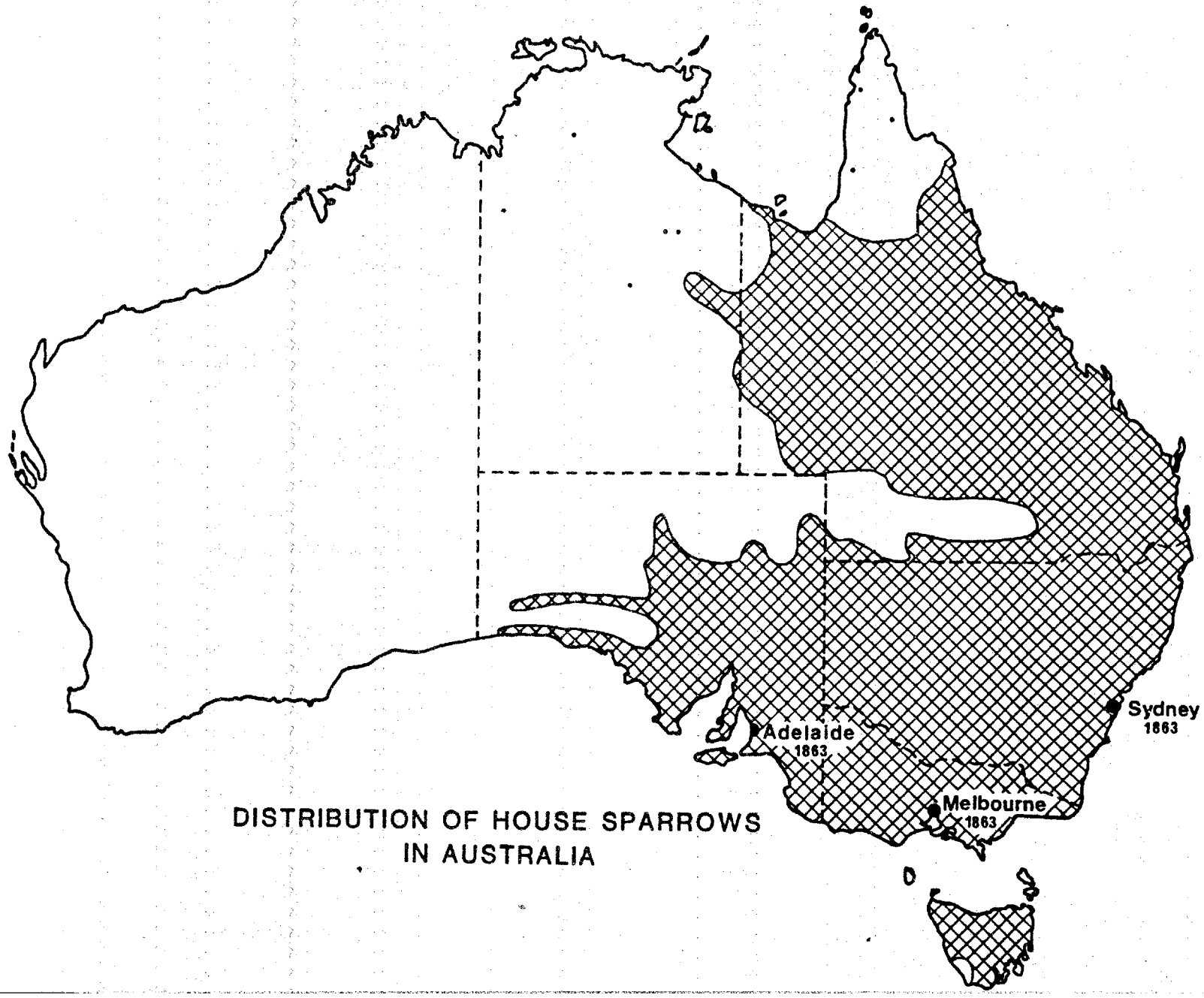
According to Storr (1973) the sparrow arrived in Cloncurry in the early 1950s and Taldora by 1962. Mount Isa was colonised in 1964 (Horton, 1976). From Cloncurry the sparrow apparently spread back to the coast, arriving at Stuart Prison near Townsville in December, 1959 (W.B. Lound, pers. comm.), Townsville City by 1963 (Lavery and Johnson, 1968), and Millaroo and Ayr in 1963 (R.A.O.U., 1964). In 1964, it was seen in Innisfail and Ravenshoe (Gill, 1970), Cairns City, North Cairns, Atherton, Mareeba and Mount Carbine (Wheeler, 1967), and Chillagoe (Tresize, 1964); it arrived in Georgetown in 1967 (Storr, 1973). The sparrow has since spread northward along Cape York Peninsula and in 1978 arrived on several islands in the Torres Strait (S. Garnett, pers. comm.). It was reported in New Guinea in 1976 (Ashford, 1978) but has apparently died out there with no subsequent recolonisation. Since September

Figure 3.2 Distribution of the house sparrow in Australia

(data from the Royal Australasian Ornithologists Union, Atlas of Australian Birds)

Places of introduction of the house sparrow to mainland Australia are indicated.

Isolated points in northern Australia refer to localities outside the main distribution where house sparrows are found.



DISTRIBUTION OF HOUSE SPARROWS
IN AUSTRALIA

1981 it has arrived at Kowanyama and Rutland Plains on the western side of Cape York Peninsula (K. Jones, pers. comm.). The sparrow is now found in many towns throughout North Queensland, and it is present on farms and at homesteads of various cattle properties in the region.

Sage (1957) determined that Victorian house sparrows were *Passer d. domesticus* and northern birds are presumed to be descended from this race. However, Storr (1973) states that "in contrast to its slow advance northward from the Darling Downs and Rockhampton, its spread through North Queensland in 1962-65 was so rapid as to make one wonder whether a tropical race (e.g. *indicus*) was involved" (p.135).

This apparently slow rate of spread into North Queensland followed by rapid expansion may be explained in two other ways:

(1) sparrows, originating in temperate areas may have needed to adapt in some significant way to life in a tropical environment, or

(2) the sparrow did not necessarily slow down its rate of advance but spread inland through the grain-growing areas of Longreach and Emerald and thence to Cloncurry - this route is indicated in Figure 3.3.

3.4 Methods of spread

Much of the initial spread of the house sparrow through Victoria and South Australia appears to have been with the assistance of the acclimatisation societies of these states. For example, in 1867, the Victorian Acclimatisation Society announced that sparrows had been distributed to various localities throughout

Figure 3.3 Spread of the house sparrow in Queensland

Key to localities

B:	Brisbane	M:	Mackay
C:	Cairns	MI:	Mount Isa
Cl:	Cloncurry	R:	Rockhampton
K:	Kowanyama	T:	Townsville
L:	Longreach		

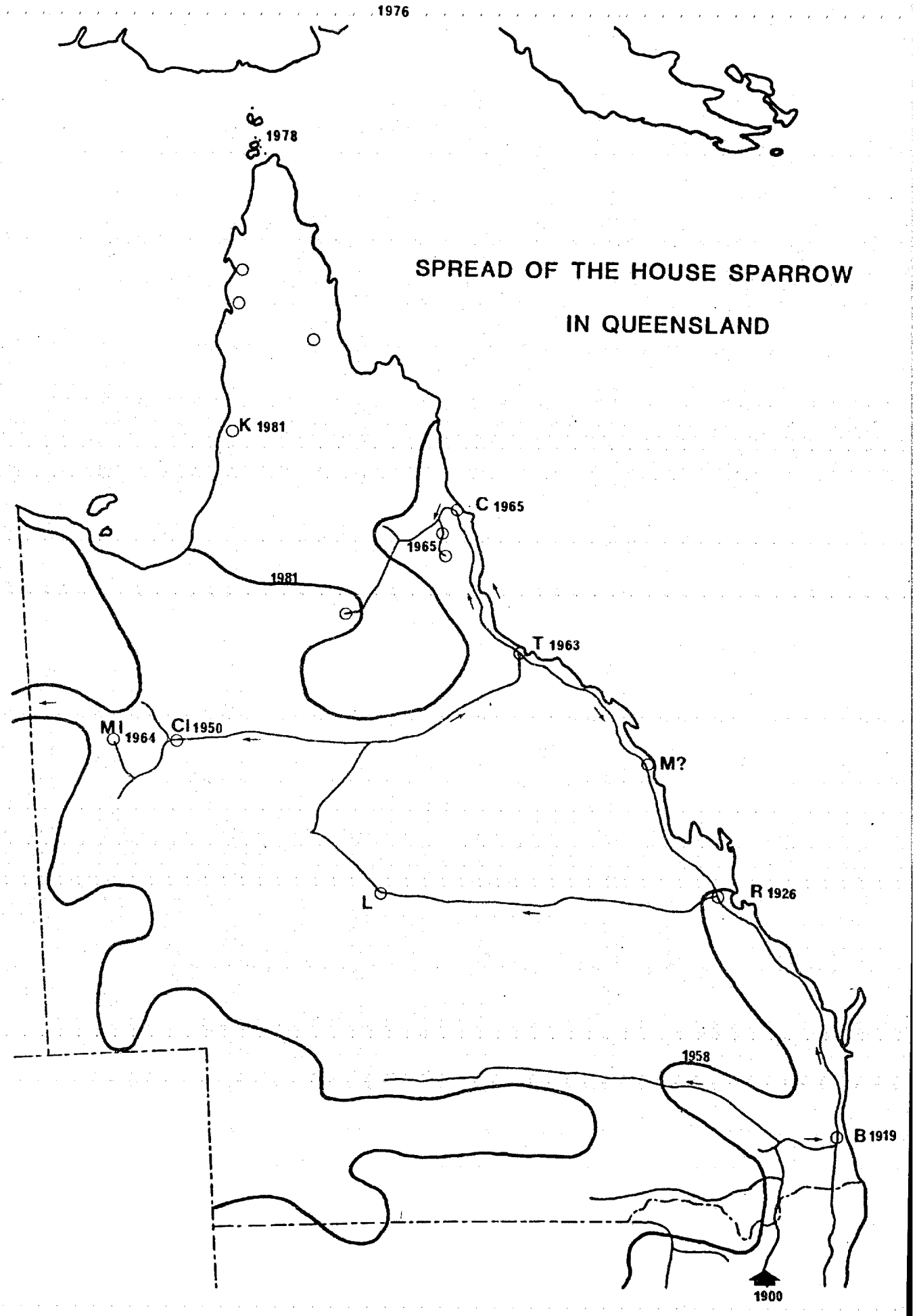
Dates at each locality indicate the year of arrival of the house sparrow.

KEY

1981 Limits of distribution in 1981 (R.A.O.U., Atlas of Australian Birds)

1958 Limits of distribution in 1958 (Summers-Smith, 1963 - accuracy doubtful)

——— Railways


1976
1978
SPREAD OF THE HOUSE SPARROW
IN QUEENSLAND
K 1981
C 1965
1965
1981
T 1963
MI 1964
CI 1950
M?
L
R 1926
1958
B 1919
1900

Victoria (Tarr, 1950). Rolls (1969) traces the role of acclimatisation societies in the spread of the house sparrow in the early years. Members of the public were also involved in the early distribution of house sparrows. However, by 1868 there were complaints about the release of sparrows, as the birds had taken to eating fruit in Collins Street, Melbourne (Long, 1981); within 20 years of the first introductions the sparrow was spreading without direct human aid.

The use of horses as the prime means of transport until the early 1900s facilitated the spread of the sparrow since it could obtain grain from horse feeding troughs or from droppings (Jenkins, 1959). The replacement of the horse by the motor vehicle undoubtedly served to slow the progress of the sparrow in some areas.

However, the major contributory factor to the spread of the sparrow must have been the railway. In many areas sparrows feed in and around carriages holding grain and some inevitably become trapped. Alexander (1958) reported that sparrows arrived at Oodnadatta in an empty carriage which had contained grain. Many first reports of sparrows in towns have been at railway stations and at railway employees house (for example, Bravery, 1970) and the early distribution maps of the sparrow (the 1958 line in Figure 3.3) illustrate that spread is most rapid along railway lines. Stidolph (1922) reported sparrows nesting in the ventilator of a guard's van on a train making daily runs between stations. Initial penetration into Western Australia occurred along the Trans Australian Railway (Jenkins, 1959); however, the Western Australian Department of Agriculture were quick to recognize the danger of sparrow

introductions and took vigorous steps to prevent sparrows entering the state, both by the coastal route and along the railway.

The house sparrow is also known to expand its range by ship-borne introduction. Since the early invasion of Western Australia in 1917 most, if not all, sparrows arriving in the state have probably entered by sea from the eastern states (Long, 1972). Ashford (1978) reported that house sparrows arriving in New Guinea had probably done so aboard a ship from Cairns.

CHAPTER FOUR

POPULATION STUDIES

4.1 Introduction

Population studies are concerned with the "numerical aspects of the populations - numbers, sex ratio, rate of increase and so on - together with the properties of the animals and the properties of the environment that determine these values" (Caughley, 1977, p.1). The ultimate objectives of populations studies are quantitative data on the number of young produced per year (productivity), the rate of population increase, how these parameters vary geographically and temporally and explanations of these phenomena. The study of population regulation also includes aspects of social behaviour, dispersion and feeding since these factors contribute to the maintenance of population size.

Estimates of density for the house sparrow exist for many places in Europe (Dyer *et al*, 1977) and much is now being assembled in North America about its distribution and relative density through the breeding birds census (Robbins, 1973). However, little is known about densities of sparrows elsewhere in the world; nor is there data on the population dynamics of house sparrows in tropical areas. The aims of this section of the project were therefore to obtain estimates of population density, sex ratio, mortality and dispersal of house sparrow populations in Townsville. Additionally, information was collected on activity patterns, the use of communal

roosts and the presence of insects in the diet of Townsville populations, since these are aspects of the ecology of the house sparrow which were expected to vary geographically.

4.2 Methods

4.2.1 General Methods -

Observations of house sparrow behaviour and activity patterns were made opportunistically from March until July. In early August and mid-September, four all-day watches were made in order to provide data on daily activity patterns at the end of winter and in spring. On these days the activity of birds was noted at five-minute intervals from sunrise until after dark, and the proportion of time spent feeding, maintaining nests and engaging in other activities was calculated for each hour.

A communal roost was studied from April to October in order to obtain data on arrival and departure times, number of birds using the roost and the way in which birds departed from and returned to the roost. As sparrows returned to the roost in the late afternoon, records were made for each returning group of the number of birds in the group and the direction from which the group returned - morning counts were made in a similar way as birds left the roost. The roost observed was in a group of eight screw-palms (*Pandanus spiralis*) planted in a median strip on Charters Towers Road (Figure 4.1). Other communal roosts used by house sparrows in 1982 were in mango trees, tall palm trees and other trees with dense foliage. The locations of four roosts used in 1982 are shown in Figure 4.2.

House sparrows were captured monthly from March to September at

Figure 4.1 The communal roost on Charters Towers Road

Height of trees: 7-8m.

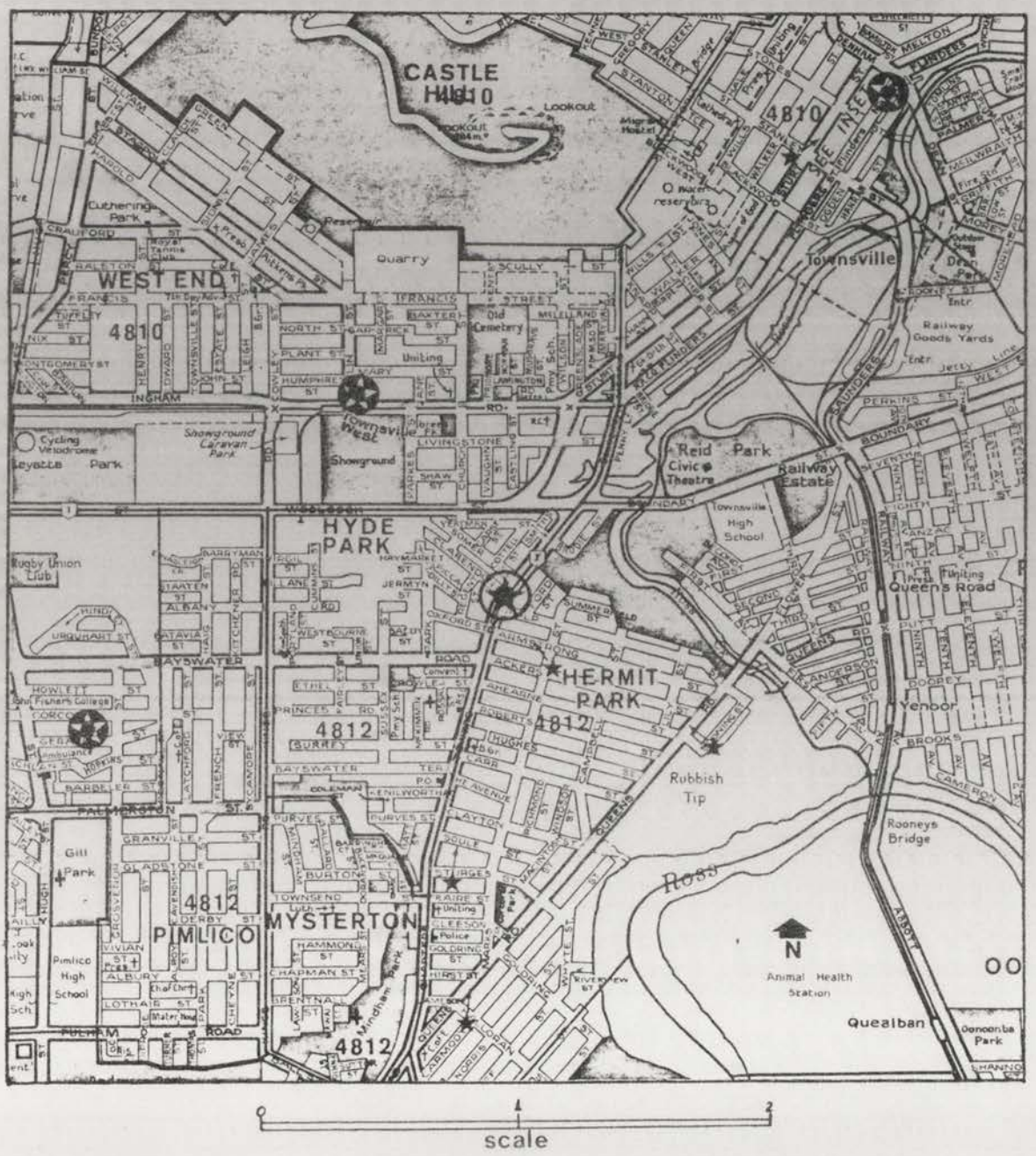
Height to foliage: 2.5m.

Figure 4.2 Locations of four communal roosts used in 1982

Study roost

Other roosts

Localities from which birds were observed returning to roosts


CASTLE HILL
Lookout
Quarry
WEST END
4810
HYDE PARK
HERMIT PARK
4812
PIMLICO
MYSTERTON
Townsville
Reid Park
Civic Theatre
Railway Estate
Townsville High School
Queen's Road
Rubbish Tip
Rooneys Bridge
Ross
Animal Health Station
Queanban
Pimlico High School
Gill Park
Rugby Union Club
Showground
Cycling Velodrome
Railway Goods Yards
N
scale

the roost on Charters Towers Road. Of those caught a sample was collected and frozen immediately for later dissection. The remaining birds were banded using aluminium leg bands supplied by the Australian Bird-Banding Scheme (A-class permit no. 1046) and measurements were taken as described in Section 5.2. Banded sparrows were then released.

In the laboratory, birds collected from the roost were defrosted and measurements taken. Individuals were classified as first-year or adult birds on the basis of the amount of ossification of the skull (Section 4.2.2). The testes of five males were collected each month and stored in alcohol. Since testes had been subjected to freezing followed by storage in alcohol, it was considered that any measurements made on them would not be meaningful; therefore, testes size was represented as a mean testis score. At the end of the study period a testis score was calculated for each individual by arranging the samples in order of increasing size and allocating the smallest testes a score of one and the larger testes a score of two; testes intermediate in size were given a score between one and two. Individuals in which testes were not discernible were allocated a score of zero. Mean testis scores were calculated for each month of the study period. No gonadal material was found in females from March to September.

4.2.2 Age determination -

In the house sparrow, unossified areas persist in the cranium for six to twelve months (Nero, 1951); thus, "snco" (= skull not completely ossified) birds are first-year individuals. Most specimens showing complete ossification ("sco") are more than a year old in

March; however, in later months, the skulls of first-year individuals become fully ossified and distinguishing first-year and adult birds becomes more difficult. If breeding began in October in 1981, then the number of first-year birds with fully ossified skulls should gradually increase after April, as will, therefore, the number of first-year birds incorrectly classified as adults.

4.3 Results

4.3.1 Communal roosts -

Data obtained for the Charters Towers Road (C.T.R.) roost are summarised in Figures 4.3 to 4.8 and Tables 4.1 and 4.2.

(a) Number of birds and period of use

The C.T.R. roost and other roosts observed during the year were in use over the full period of study. In April and May about 2500 birds were using the C.T.R. roost; this number decreased to 1500 by July and remained at that level until the end of the study period. The proportion of first-year (snco) birds at the roost site declined from March to September as shown in Table 4.2. The ratio of snco to sco birds in late autumn (May) was similar to that found in autumn samples collected by Niles (1973) in North America (34 snco: 11 sco, $G=0.0597$, $0.90>p>0.75$). Monthly changes in the numbers of first-year and adult birds, calculated on the basis of proportions of snco and sco birds in the samples taken are shown in Figure 4.3. The number of adult birds in the roost increased by 75% from March to April but more gradually from then, reaching a peak in July. The number of snco females using the roost dropped between March and May. Similarly, the number of first-year males using the

Table 4.1: Summary of birds caught and number at roost

(a) House sparrows collected in Townsville

Date	Time	No. Birds	No. Males	No. Females	No. Coll.	No. Band.	No. Recap.	No. Moult.
March 29-31	0420 0405	110	52	48	28	81	1	100
April 23	0505	52	28	24	16	36	0	1
June 4	0510 0600	36	21	15	21	13	2	0
June 24	0545	24	14	10	23	0	1	0
August 1	0530	26	13	13	25	0	1	0
Sept. 5	0530	28	22	6	21	7	0	0
October 1	0515	20	12	8	19	0	1	0
TOTAL	-	296	158	109	153	137	7	101

Abbreviations: Coll. - No. collected; Band. - No. banded; Recap. - No. recaptured; Moult. - No. showing signs of moult.

(b) Number of birds using roost

Date	No. of birds	Average group size a.m.	Average group size p.m.
April 2	2521	10.2	3.05
May 11	2678	13.2	4.10
July 30	1519	53.6	3.50
August 31	1403	-	2.70
October 1	1485	7.6	2.50

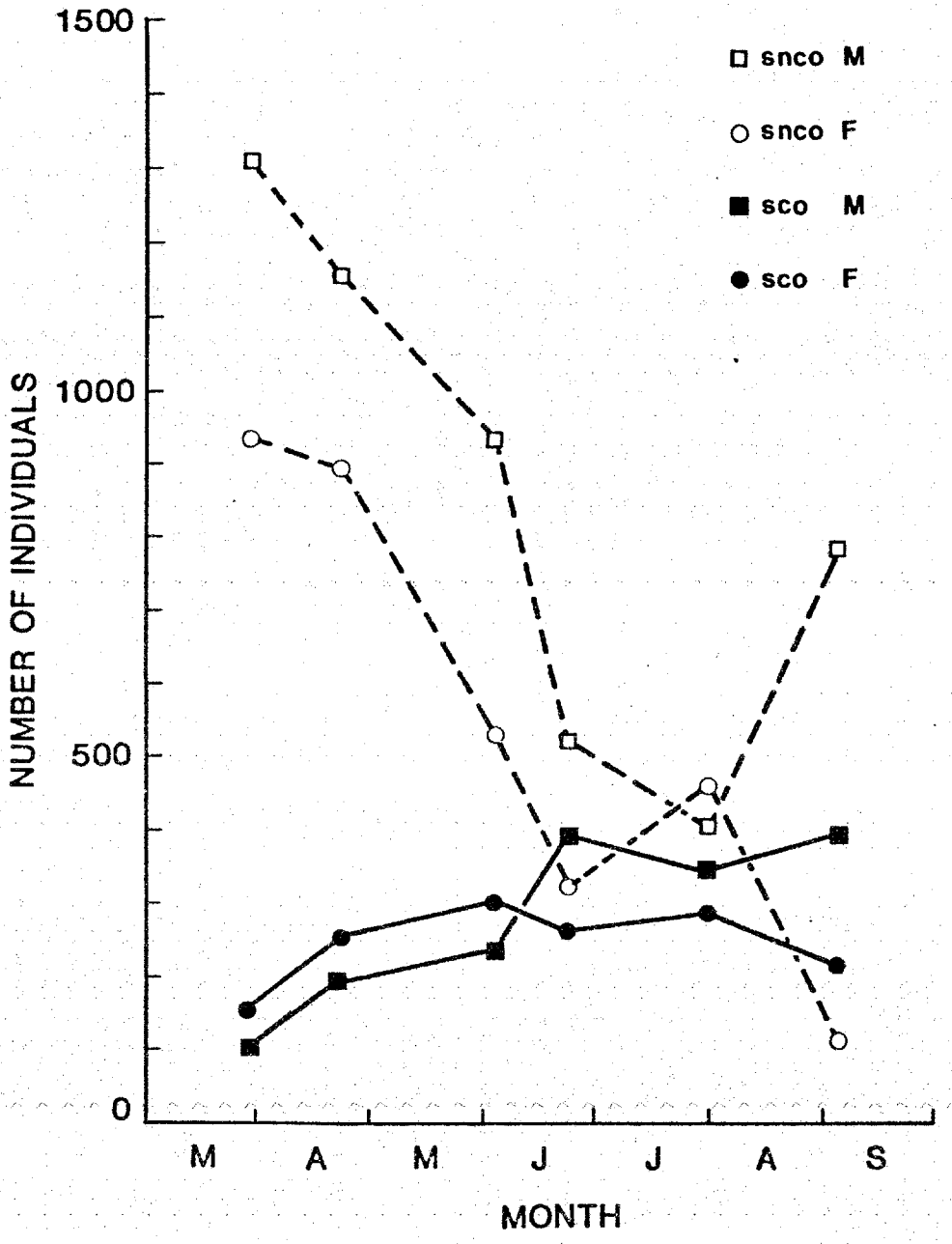

1500
1000
500
0
NUMBER OF INDIVIDUALS
snco M
snco F
sco M
sco F
M
A
M
J
J
A
S
MONTH

Table 4.2: Sex ratio and proportion of first-year birds at the roost

(a) Sex ratio

	Townsville				Blackwood			
Date	Male	Female	% Male	χ^2	Male	Female	% Male	χ^2
M	62	48	56.4	1.536 ns	198	203	49.4	0.040 ns
A	28	24	53.8	0.173 ns	88	65	57.5	3.163 ns
M	21	15	58.3	0.694 ns	43	49	46.7	0.272 ns
J	14	10	58.3	0.375 ns	76	47	61.8	6.374 **
J	13	13	50.0	0.038 ns	72	92	43.9	2.201 ns
A	22	6	78.6	8.040 **	133	103	56.4	3.564 ns
S	12	8	60.0	0.450 ns	123	85	59.1	6.582 **
TOT.	172	124	58.1	7.460 **	733	644	53.2	5.624 **
TOT. (-August)	150	118	56.0	3.586 ns				

(b) No. of first-year (snco) birds

Date	snco	sco	% snco	χ^2
M	25	3	89.3	15.75 **
A	13	3	81.3	5.06 *
M	15	6	71.4	3.05 ns
J	13	10	56.5	0.17 ns
J	15	11	57.7	0.35 ns
A	12	9	57.1	0.19 ns

Note: significance levels:- ns = not significant, * = $p<0.05$, ** = $p<0.01$.

roost decreased from March to July but increased again in the August sample (September 5th); the discrepancy in this sample resulted in lower numbers of snco females in the sample than in other months and is probably attributable to sampling error. Combining the sexes yields an exponential decrease in the number of snco birds at the roost at a rate of 23.24% per 30-day period ($N_t=2337 \times 0.7676^t$, t= no. of 30 day periods from March 30th; r=0.942, 3 d.f., $p<0.005$); this value can not be distinguished from the value of 4.6% mortality given by Summers-Smith (1963) for English birds (95% confidence limits for Townsville birds: 1.6% to 40.1%).

(b) Sex ratio

With the exception of the August sample the sex ratio of birds at the roost did not deviate significantly from parity during the period of study (Table 4.2), though there was a slight tendency for males to outnumber the females, making up between 50% and 60% of the samples. Data collected by Dr. C.R. Jenkin (unpublished) over a period of eight years in Adelaide show that this slight excess of males also occurs in the temperate regions of Australia (Table 4.2).

(c) Waking behaviour

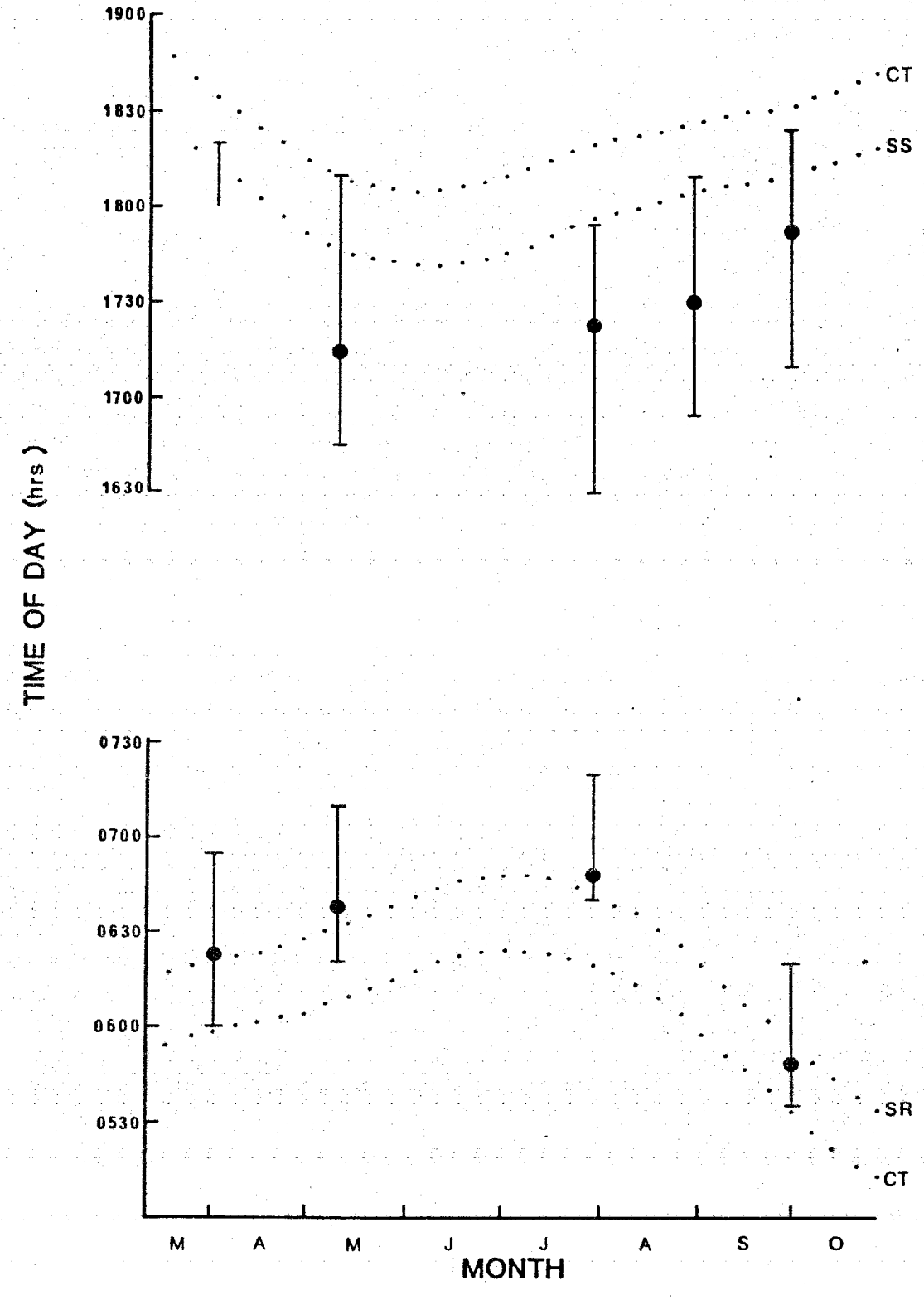
Breakup of the roost in the morning was preceded by a long period of communal singing, beginning between 125 and 80 minutes before sunrise and continuing as the birds left the roost. The times of first departure, median leaving time and the period of breakup are compared in Figure 4.4 with sunrise and morning civil twilight times (data for Townsville from Nautical Almanac, 1982).

Times of first departure occurred close to the times of morning civil twilight in autumn and spring; however, in winter the time of first departure became later so that the first birds left the roost

Figure 4.4 Arrival and departure times of house sparrows using the C.T.R. roost

KEY

	Median arrival or departure time and period of movement.
CT	Time of civil twilight
SS	Time of sunset
SR	Time of sunrise


1900
1830
1800
1730
1700
1630
CT
SS
TIME OF DAY (hrs)
0730
0700
0630
0600
0530
SR
CT
M
A
M
J
J
A
S
O
MONTH

just before sunrise. Half of the birds had left the roost by several minutes after sunrise in autumn and winter. In spring, the median departure time was seven minutes before sunrise. Periods of departure decreased from April to October, and associated with this decrease in departure time was an increase in the size of the groups leaving the roost (Table 4.1). In autumn and spring birds left either singly or in large groups (Figure 4.6) probably representing birds with nests (single birds or pairs) and first-year birds and others without established nest sites (larger groups). Groups remained together while they were still in sight, indicating that they were not just incidental gatherings of single birds. In May almost half of the birds left in groups of between 12 and 22 individuals and less than 10% left singly or in pairs. Departures in winter were much less ordered, with large groups leaving the roost at short intervals and spreading out in several directions before dividing into smaller feeding flocks for the day. On leaving the roost the birds initially flew upwards at an angle of about 45° but levelled off when they were higher than the buildings on either side of Charters Towers Road. In contrast, birds returning to the roost at night flew in low over the surrounding buildings and entered the roost by passing high over the palms and dropping down onto them, or by flying low over the road and up into them (Figure 4.5).

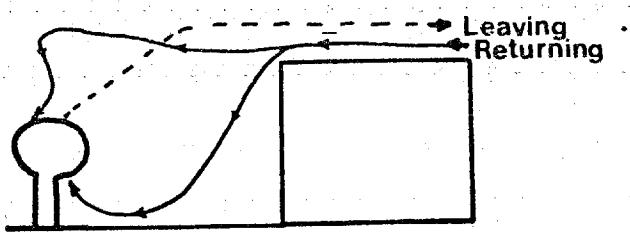


Figure 4.5: Flight paths on leaving and reurning to the roost.

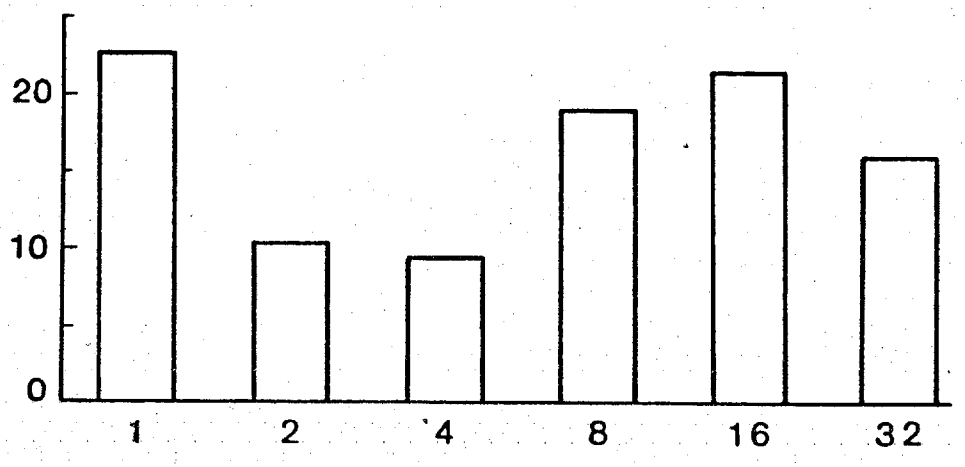
Figure 4.6 Seasonal variation in size of flocks leaving roost

i. April 2

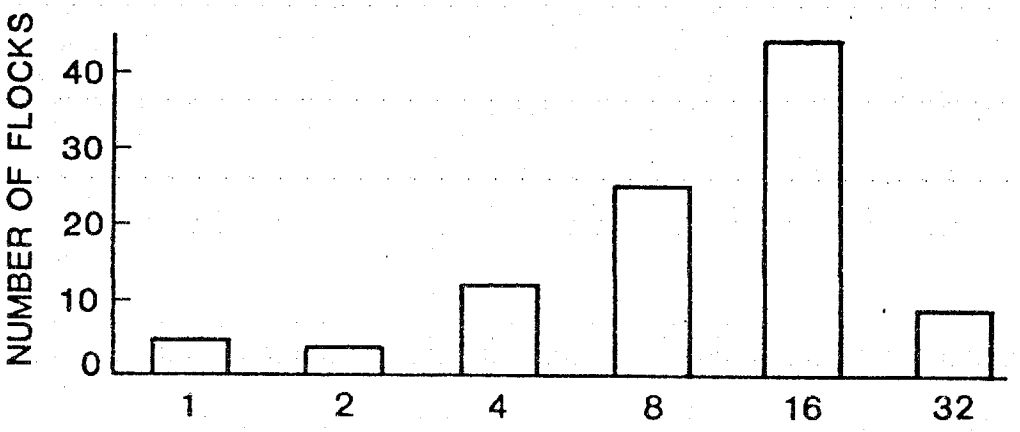
ii. May 11

iii. October 1

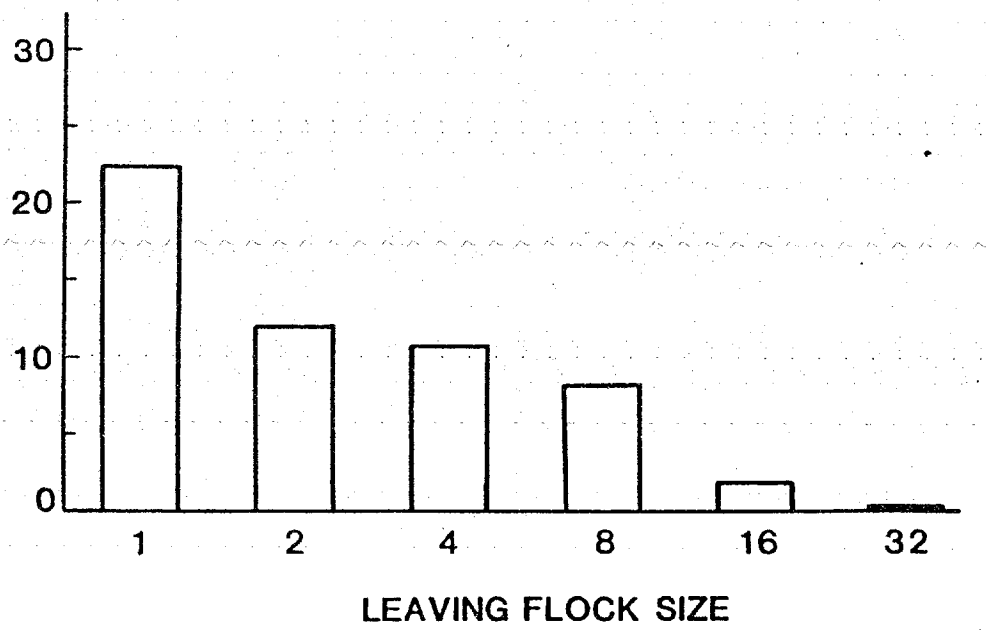
i.


20
10
0
1
2
4
8
16
32

ii.


NUMBER OF FLOCKS
40
30
20
10
0
1
2
4
8
16
32

iii.


30
20
10
0
1
2
4
8
16
32
LEAVING FLOCK SIZE

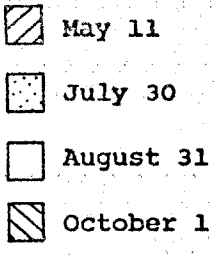
From March to June all house sparrows left the vicinity of the roost during the day, and returned only to roost at night. During this period, the screw-palms were used as nest sites by the introduced spice finch (*Lonchura punctulata*). From July a number of sparrows remained at the roost throughout the day, re-establishing nest sites for use in the approaching breeding season and feeding in the nearby car-parks and car-sales yards. None of these birds was observed with young.

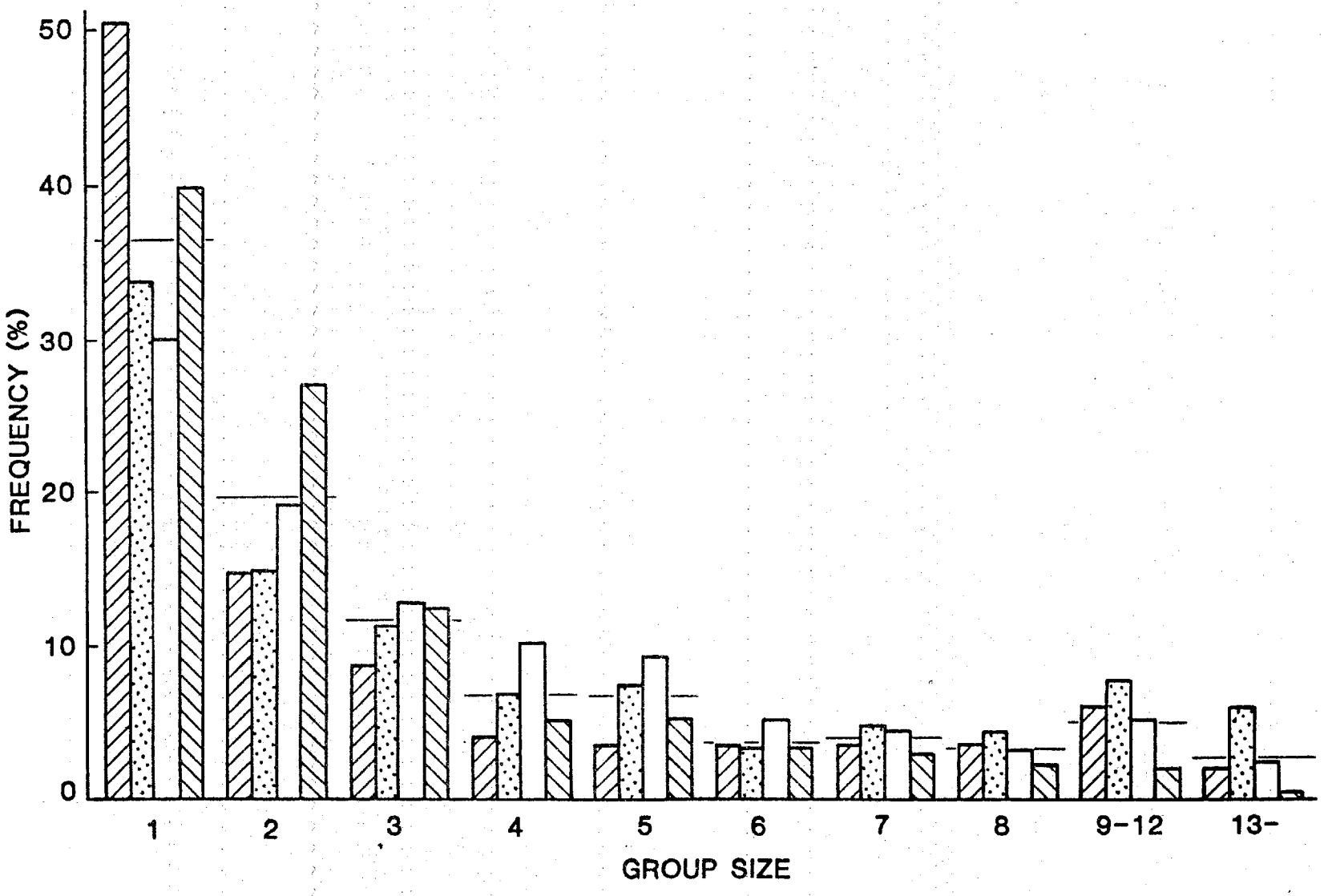
(d) Roosting behaviour

Sparrows began arriving at the roost 60 to 87 minutes before sunset (Figure 4.4) and all were in the roost by the time of civil twilight. The median arrival time ranged from 32 to 40 minutes before sunset and the period of arrival from 75 to 85 minutes. The average size of flocks returning to roost remained approximately constant over the period of study (Table 4.1); however, the distribution of flock sizes about this mean varied from month to month (χ^2=142.3, 27 d.f., $p<<0.01$). Figure 4.7 illustrates the major seasonal differences: (1) in April, more birds arrived singly than in other months and fewer in groups containing two to five birds; (2) in May, birds arrived in groups of eight or more and the number arriving in pairs was reduced - about one third of the birds arrived singly; (3) the number of single birds was reduced in winter flocks as was the number of large flocks - there were proportionately more flocks of intermediate size; (4) in spring, the proportion of flocks containing more than three individuals was reduced as more birds returned alone or in pairs.

The size of returning flocks was determined by the activity being undertaken immediately before the birds returned to roost.

Figure 4.7 Seasonal variation in size of flocks returning to roost




50
40
30
20
10
0
FREQUENCY (%)
1
2
3
4
5
6
7
8
9-12
13-
GROUP SIZE

Flocks observed feeding late in the afternoon flew to the roosts as one group. An exception to this was the gathering of flocks of sparrows into pre-roosting congregations. In these gatherings birds searched through foliage for insects. After feeding in these congregations sparrows flew off, either singly or in flocks of up to five birds, and returned to the roost. The high proportion of single birds and small groups returning to the roost in the few months of study was probably a result of this activity and of the tendency of the adult birds to remain in their home ranges to feed even when nest maintenance was at a minimum. Seasonal variation in the proportion of single birds and small groups was dependent on attendance at nests - in mid-autumn and spring, birds tended nests during the day and remained separate from feeding flocks for much of the time. In spring, males with mates often remained at the nest until sunset but moved to the roost before civil twilight.

(e) Directions of flight

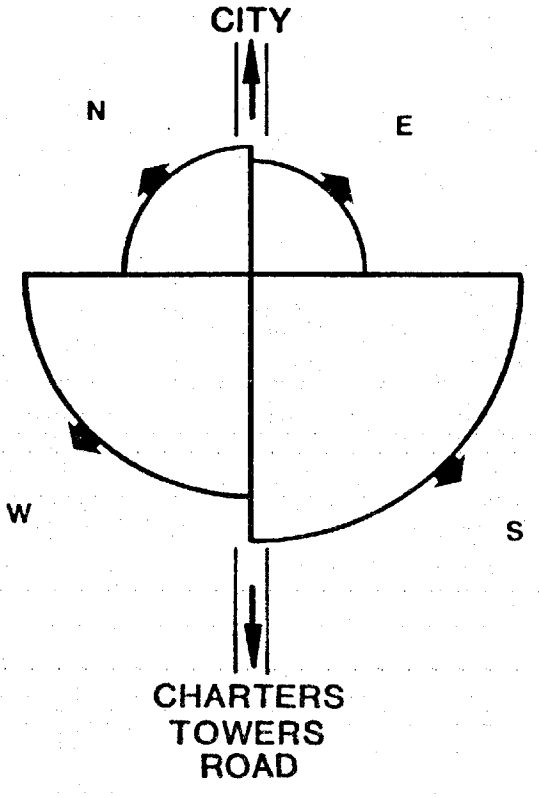
The proportion of birds flying in each of four directions away from and towards the roost are shown in Figure 4.8 - averaged over the whole study period. At all times of year about 80% of the birds flew in a southerly or westerly direction away from the roost. Similarly, return to the roost was mostly from the south and west.

4.3.2 Activity patterns -

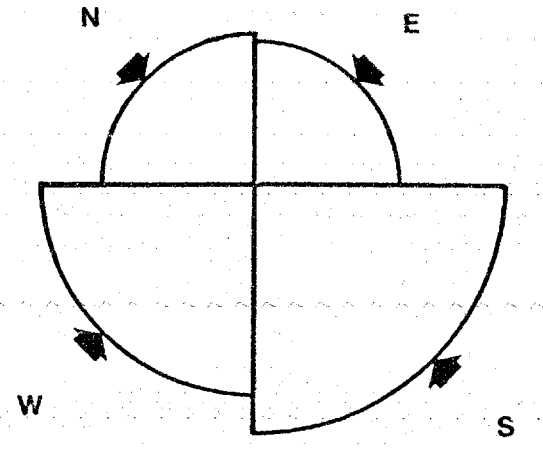
The daily activities of house sparrows were divided into three groups: (1) feeding; (2) attendance at nests, including incubating eggs and feeding nestlings; (3) other activities not associated with feeding and nesting, including preening and resting. The daily cycles of these activities are shown in Figure 4.9. In early

Figure 4.8 Directions of flight of birds on leaving and returning to the roost

Based on observations in April and May for leaving directions since numbers of individuals could not be reliably estimated in July and August. All months are included for returning groups. The area of the circle in each direction is proportional to the number of individuals leaving in that direction.

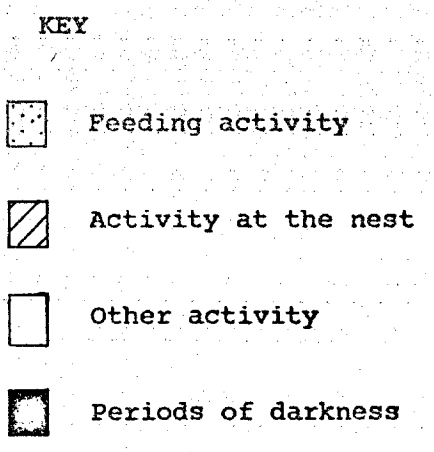


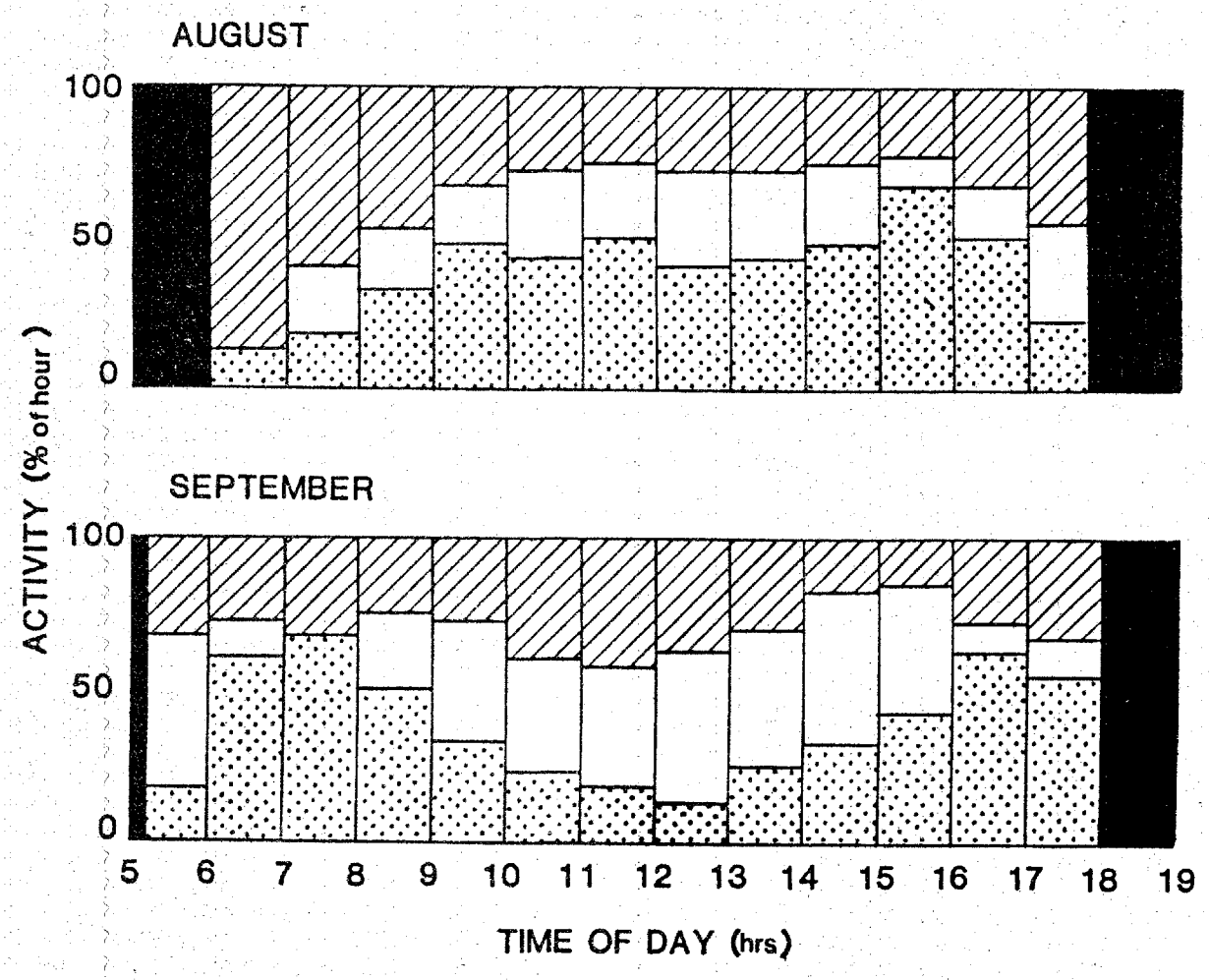
LEAVING
N-5199



RETURNING
N-7085

Figure 4.9 Daily activity patterns in August and September




AUGUST
100
50
0
SEPTEMBER
100
50
0
ACTIVITY (% of hour)
5 6 7 8 9 10 11 12 13 14 15 16 17 18 19
TIME OF DAY (hrs)

August, most early morning activity was at the nest and the proportion of time spent feeding was small. Feeding activity increased in mid-morning and remained approximately constant throughout the afternoon. There was a slight feeding peak in mid-afternoon followed by a decline just before sunset as activity at the nest increased again. Early morning and late afternoon peaks became evident in late September; however, the proportion of time spent at the nests remained approximately constant throughout the day at this time. During the middle of the day, house sparrows were found either at the nest (if they were feeding nestlings or incubating eggs) or in various trees around the nesting area.

4.3.3 Feeding -

In autumn sparrows were observed in feeding flocks ranging in size up to 25 individuals; flocks in winter and spring contained up to 15 individuals. All of the larger flocks were observed feeding on the ground, in the late afternoon or mid-morning; at other times flocks were smaller and individuals or small groups foraged on the ground or engaged in other forms of feeding activity. In autumn, sparrows in Mundingburra gathered in the morning (observed from 0715 to 1100) in a poinciana tree (*Delonix regia*) over which they searched for green caterpillars. Searching involved climbing and hovering over the upper surface of the leaf and hanging upside down under the leaf to search the lower leaf surface. When a caterpillar was seen it was plucked off the leaf and the sparrow flew with it to a nearby hedge or shrub. After positioning the prey lengthwise in its bill by shaking its head, the sparrow was able to swallow it whole. Active searching of trees for insects was observed until

June 3rd, and took place in the late afternoon (1600 to sunset) while birds were in pre-roosting congregations, as well as in the mornings. From June to mid-August sparrows fed mainly on the ground and leaf-searching behaviour was observed several times only, though with no apparent success. In mid-August leaf-searching began to yield insects once again.

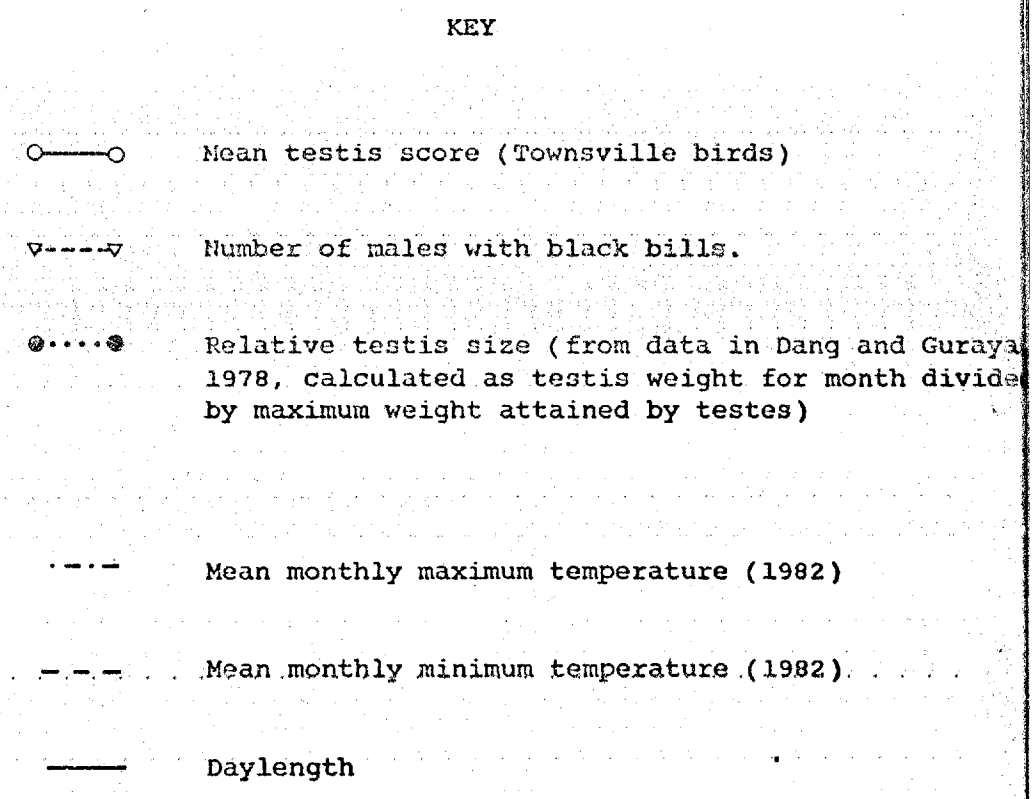
In addition to methodical leaf-searching as a technique for capturing insects, house sparrows have been observed "hawking" or "flycatching" (November, 1981). Flycatching involves the sparrow darting out from a perch and catching slow-flying insects (Nix, 1979) and is quite common in English house sparrows (Summers-Smith, 1963) when insects are available. House sparrows began searching under eaves and patios in September, for insects trapped in cobwebs. By hovering under the web or by perching on ledges the sparrow was able to take the prey - flies and other small insects. This activity was confined to the period between sunrise and 0900 in September, though sparrows feeding nestlings in October engaged in web-searching throughout the day.

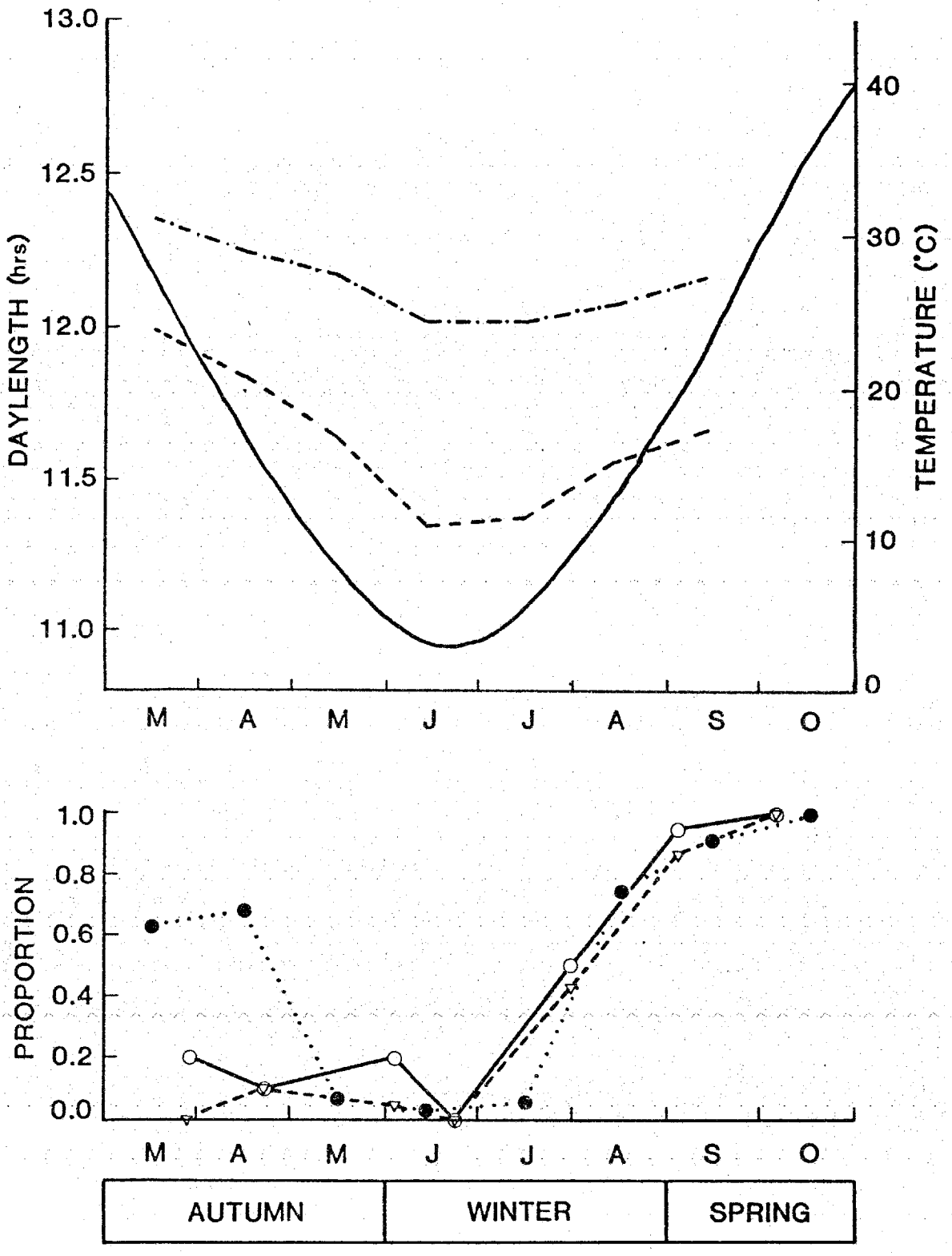
4.3.4 Reproduction -

(a) Reproductive status

The reproductive status of male house sparrows over the study period is plotted in Figure 4.10. In March, April and May there was slight gonadal activity; however, none of the birds examined in June had discernible testes. From July, the mean testis score increased, reaching 1.0 at the end of September. Mean monthly minimum and maximum temperatures and daylength for the study period are plotted in Figure 4.10 for comparative purposes and indicate

Figure 4.10 Seasonal variation in reproductive status in relation to environmental variables




13.0
12.5
12.0
11.5
11.0
DAYLENGTH (hrs)
40
30
20
10
0
TEMPERATURE (°C)
M
A
M
J
J
A
S
O
1.0
0.8
0.6
0.4
0.2
0.0
PROPORTION
M
A
M
J
J
A
S
O
AUTUMN
WINTER
SPRING

that the period of testes regression occurred at the time of shortest days and lowest temperatures; the increase in mean testis score follows that of daylength and mean monthly temperatures. The pattern of testis recrudescence and regression is similar to that followed by house sparrows in the Punjab region of India (Dang and Guraya, 1978) - Figure 4.10.

The proportion of males in the population with black bills is also indicated in Figure 4.10 for each month. The number of black-billed males follows the same pattern as the mean monthly testis score. The colour change of the bill from winter to spring is illustrated in Figures 5.7 and 5.8.

(b) Attendance at nests

From March to June house sparrows attended their nests daily, cleaning and repairing them for use in the spring. At the same time individuals searched through guttering and under eaves for suitable nest holes. Initially this was done fairly quietly and little aggression was shown between the birds - birds with nests tolerating the presence of other individuals. In early May, the calling of the birds increased in intensity as unmated males began displaying to attract partners and paired birds began defending their nests against other pairs and individuals. By the end of May there were three nests established in the guttering of one of the houses under observation in Kelso, and one or two nests in each of the other houses in the area. In mid-June activity at the nests was reduced and birds were not observed either nest-site prospecting or defending nests again until late July. In August a further three nests were established in the area of the four houses; however, these were deserted before the end of the month. The other nests

were maintained until the end of the study period.

(c) Communal displays

The number of communal displays observed per full day of study from June to October are shown in Figure 4.11.

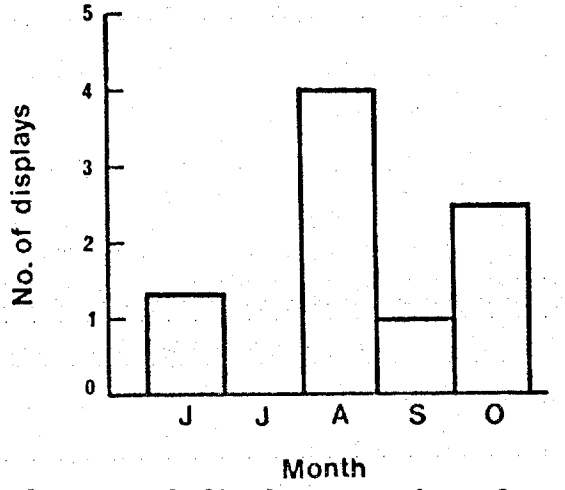


Figure 4.11: Number of communal displays per day of study - June to October

In June displays occurred at a low frequency and involved up to four males. The highest frequency of communal displays occurred in August and involved up to six males. In September the number of displays was reduced, but increased again in October. In all cases only one female was involved. Attempted coition was observed in only one case - at 1215 on October 10th - when a display involving six males ended after about 30 seconds with the female and two males on the ground. One of the males mounted the female but did not continue - the three birds then flew off. All displays observed occurred in the morning with the exception of the above case.

(d) Soliciting and mating

Soliciting was observed on four occasions from August to October. On three occasions (August 29th, September 20th and September 21st) solicitation was commenced by the female and

culminated when the male mounted her four or five times in rapid succession. On the final occasion (October 24th), a male strutted in front of the female in the "standing to attention" posture described by Summers-Smith (1963); however, the female showed little interest and the display ceased after 30 seconds.

(e) Breeding

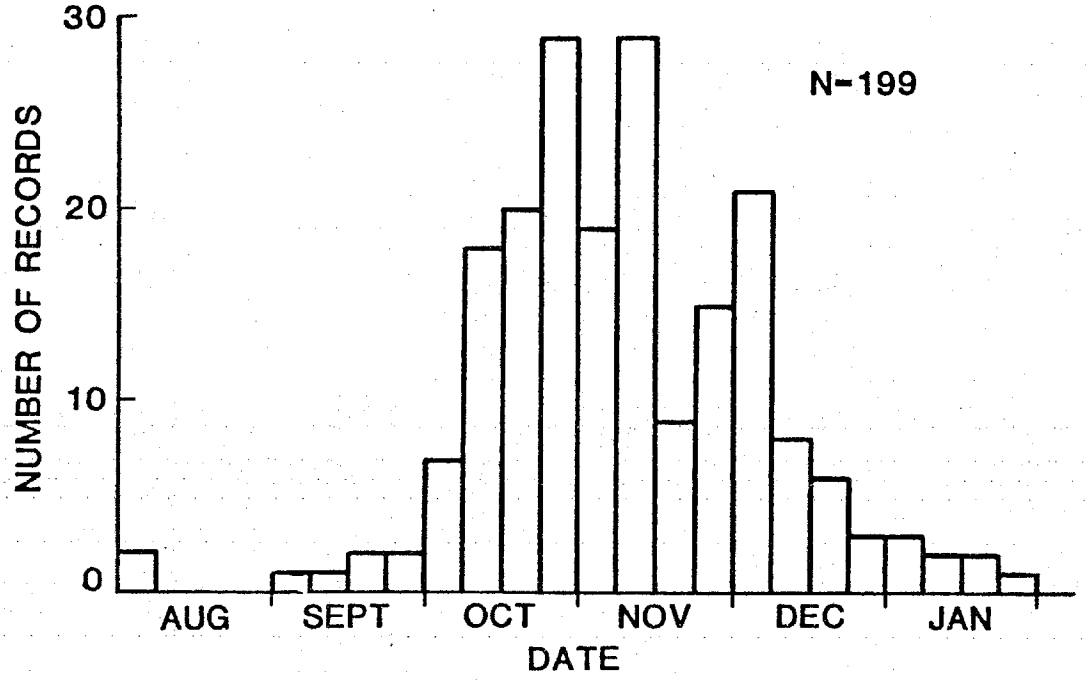
The first clutch observed in 1982 was laid in the second week of September. Another two clutches were commenced in the third week, and one in the last week of September. No new attempts at egg-laying were observed in the first week of October; however, in the second and third weeks several clutches were laid. Two of the clutches laid in early September produced one fledgling each in October.

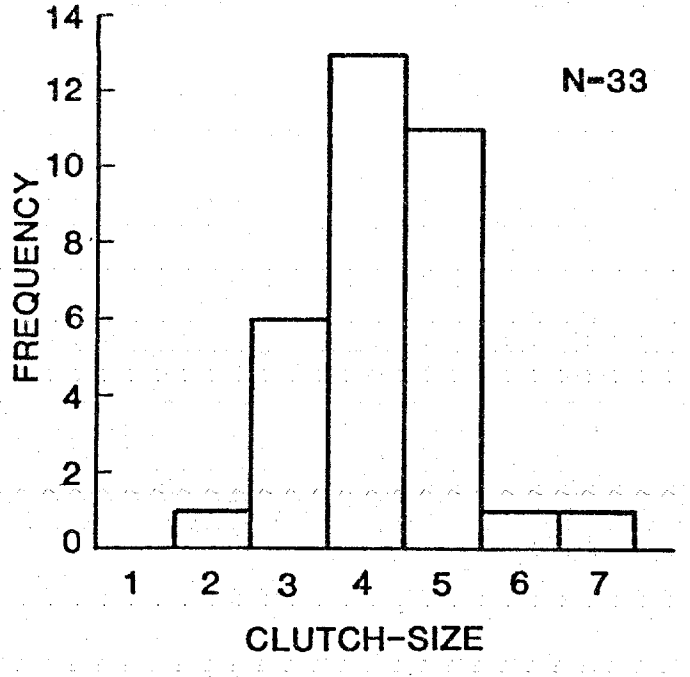
Analysis of Nest Record Cards from the R.A.O.U. Nest Record Scheme resulted in dates of commencement of 199 clutches, clutch-size data for 33 of these and the number of young successfully fledged for 19 nests for which initial clutch-size was known. No records were available for nesting in northern Australia. The breeding season of house sparrows in southern Australia (judged by the dates of commencement of clutches) is shown in Figure 4.12 which indicates that the majority of first clutches were laid in mid-October, followed by peaks representing laying of second and third clutches in early to mid-November and early December. The average clutch-size of house sparrows in southern Australia was 4.2 (s.d.=1.0) as indicated in Figure 4.12. Of those laid an average of 3.25 (s.d.=0.9) hatched and 3.17 (s.d.=0.9) successfully fledged.

Figure 4.12 House sparrow breeding records for southern Australia

Upper: The number of clutches started per 8-day period of each month

Lower: Clutch-size frequency distribution


30
20
10
0
NUMBER OF RECORDS
N-199
AUG
SEPT
OCT
NOV
DEC
JAN
DATE


14
12
10
8
6
4
2
0
FREQUENCY
N-33
1
2
3
4
5
6
7
CLUTCH-SIZE

4.3.5 Predators -

Two forms of predation on house sparrows were observed in Townsville during the study period: attacks by raptores and accidental deaths by motor vehicles. During observations at the roost site several instances of attacks by raptores were recorded. These included: (1) a successful attempt when a collared sparrowhawk *Accipiter cirrhocephalus* flew into the roost and emerged with a sparrow in its talons (1730: July 30th); (2) an unsuccessful attempt by a sparrowhawk which made two dives into the roost but came out with nothing (0650 and 0705: July 31st); (3) an unsuccessful attempt by a brown falcon *Falco berigora* (1805 and 1915: October 1st). On all days when the roost was being studied black kites *Milvus migrans* flew over the roost at irregular intervals, but had no obvious effect on the behaviour of the sparrows. On the occasions when the sparrowhawks and brown falcon were at the roost the behaviour of the sparrows in the roost changed, the change depending on the time of day. In the mornings the presence of a bird of prey resulted in a reduction in activity at the roost and a reduction in the volume of communal singing as the sparrows retreated into the palms. The presence of raptores in the afternoon resulted in an increased volume of sound as birds began to call in an agitated manner - some birds left the roost at this stage and flew to nearby bushes until the predator left the area.

4.4 Discussion

4.4.1 Communal roosts and population dynamics -

As house sparrow young leave their nests and become independent of their parents they collect in flocks at suitable feeding places; these flocks increase in size as the season advances (Summers-Smith, 1963). At night the birds roost communally in thick hedges or trees. When the adults have finished with their breeding duties they join the feeding flocks and some join the communal roosts at night. In Europe, communal roosts are commonly formed in fields at the edge of the breeding area (Summers-Smith, 1963). In Oklahoma, North America, North (1973) found that roosts were not formed near feeding areas, but were located well within the residential districts of the city with the birds making daily flights of up to three kilometres to the feeding areas. In Townsville, birds were observed returning to the roost from up to two kilometres away (see Figure 4.2). Moreau (1931) reported that house sparrows in Egypt flew as far as four miles from a communal roost during the day.

The number of sparrows using the roosts varies from place to place. In Egypt, one roost contained around a hundred thousand birds (Moreau, 1931), clearly associated with a locally plentiful supply of food; this was provided by the roofless store house which were heaped with boatloads of grain brought down the Nile River. Summers-Smith (1963) reported a roost in London containing approximately nineteen thousand birds and indicated that large roosts were common in England and Europe. In contrast, North (1973) found that the largest roosts in his North American study site contained about a thousand birds. The communal roost studied in Townsville contained about 2500 birds, suggesting that smaller

roosts are characteristic of the house sparrow in its introduced range. However, Guthrie (1971) wrote that up to twenty to fifty thousand birds crossed the Tweed River each afternoon in summer, presumably on their way to a communal roost; this observation indicates that large roosting congregations do occur in Australia, at least in temperate areas. Communal roosts are vacated in late autumn in temperate regions (Summers-Smith, 1963; North,1973; Guthrie, 1971), as the leaves are lost from deciduous trees. In these areas birds move from the summer roosts to more numerous, smaller and more sheltered roosts for the winter. Communal roosts in Townsville were maintained throughout the period of study, although house sparrows were observed roosting under the eaves of houses at all times. Changes in the number of birds using the roost were a result of nesting activity and the loss of birds from the population. Loss of snco birds may be attributed to mortality, dispersal, or the development of cranial ossification. In his study of house sparrow movements in Stillwater, Oklahoma, North (1973) found that 7.5% of birds in populations feeding in the grain fields at the edge of the city were adults, compared with 48.8% in the central areas; he suggested that immature birds continually shifted from roost to roost until they reached the periphery of the city. The same pattern may hold in Townsville, though more intensive banding would need to be done over the summer to elucidate this point. Summers-Smith (1963) found that the young birds in his study area returned to the breeding areas from which the flock was drawn, though not necessarily to the area in which they were born; this meant that the majority of the young birds moved only a mile or so from their birthplace and that little, if any, wider dispersal took

place. However, in America, expansion of the range of the house sparrow occurred at a rate of 20 - 30 kilometres per year (Barrows, 1889), and indications are that it expanded at a similar rate in Australia (Sydney to Rockhampton - 1780 km - in 60 years); this implies that sufficient long distance dispersal occurs that potential habitat is continually monitored. In addition, the adults are essentially sedentary, maintaining the same nest site over a number of years (Summers-Smith, 1963); such a population structure is conducive to the continued dispersal and subsequent establishment of the house sparrow in new areas.

Figure 4.13 shows the change of numbers of house sparrows in a 100 acre area of MacLeansboro, Illinois, North America (Will, 1973),using mortality rates calculated by Beimborn (1967) and Summers-Smith (1963) for North American and English house sparrows respectively. Also included in this figure are the estimated numbers of first-year and adult birds in the study population in Townsville for each month of the study period. Each curve is based on a total population of 100 birds at the end of September (March in the northern hemisphere). The curve for Townsville adults was calculated from the maximum number of sco birds in the roost over the year, assuming that adult mortality was similar in both of the study areas. The fact that the actual values obtained for the period July to October parallel the downward trend in the North American population suggests that this assumption is quite reasonable; the reduced number of adults at the beginning of the study period reflects the period of nest attendance in autumn. Numbers of snco birds were estimated from the exponential curve obtained in Section 4.3.1 (a).

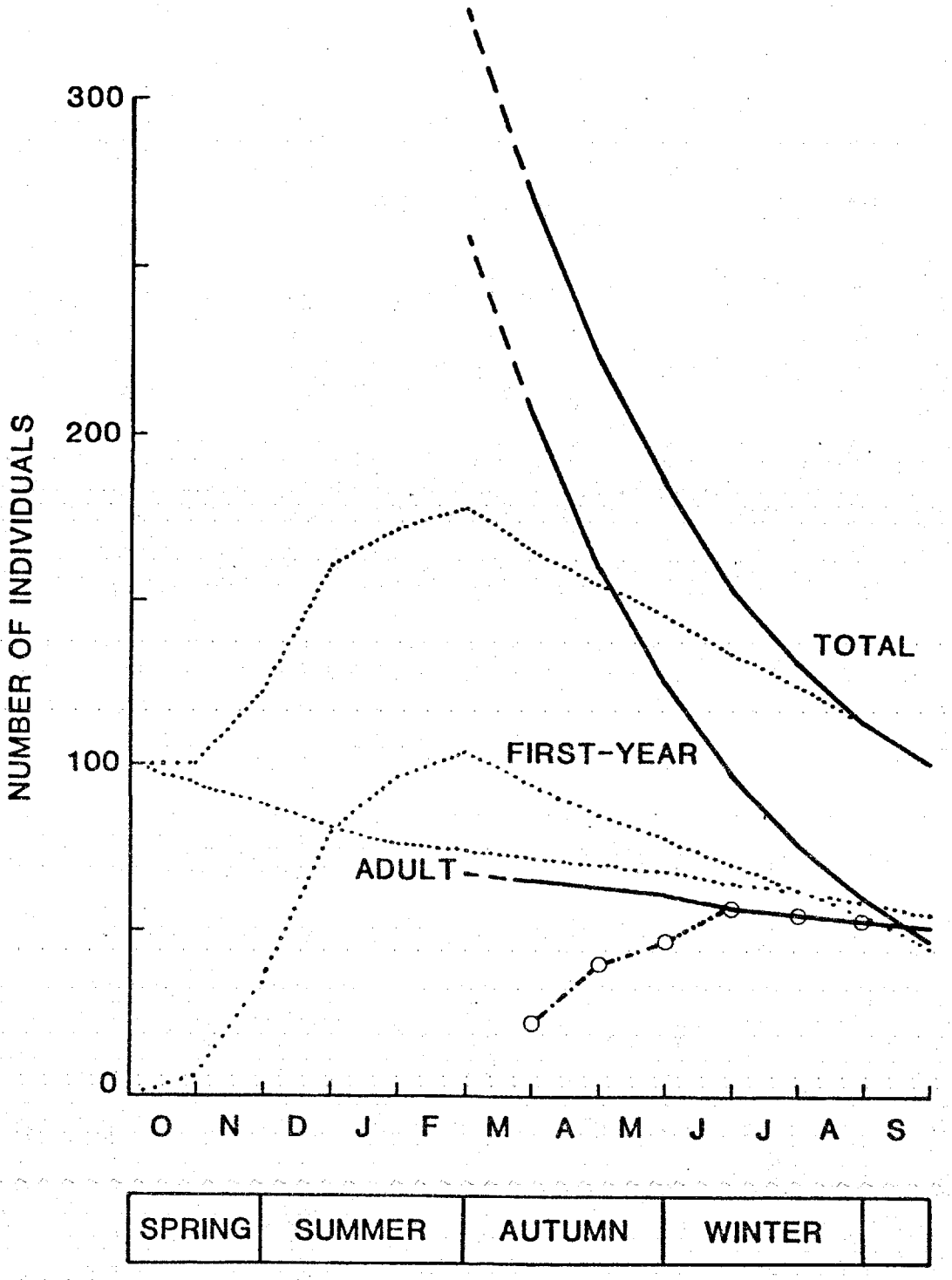
Figure 4.13 Comparison of population changes over year in Townsville with a temperate locality

KEY

..... McLeansboro, Illinois (Will, 1973)

——— Townsville

O-·-·-·-O Number of adults using roost in Townsville


300
200
100
0
NUMBER OF INDIVIDUALS
TOTAL
FIRST-YEAR
ADULT
O N D J F M A M J J A S
SPRING
SUMMER
AUTUMN
WINTER

These data suggest that the maximum population size in Townsville may have occurred in February and for the study area reached a peak of about 3750 birds (750 adults: 3000 first-year birds). A surprising feature of the population represented here is that the population size of house sparrows in Townsville appears to decrease by two-thirds over the winter period, while in Europe (Summers-Smith, 1963) and North America (Will, 1973), the population decreases by less than 50% over the same period. This rapid drop-off in numbers may be due to higher mortality in Townsville or to a higher dispersal rate. Both of the northern hemisphere studies were undertaken in areas where the sparrow populations had been established for long periods; these populations were probably more stable with less dispersal. In contrast, there are still areas of Townsville which have no house sparrow populations and dispersal into these areas is still occurring - for example, house sparrows have arrived on the James Cook University campus in recent years.

According to Summers-Smith (1963), most birds alive at the end of winter are likely to breed in the approaching spring. The limited data available for Townsville (Lavery *et al*, 1968; pers. obs.) suggest that the breeding season of house sparrows begins in September and continues until early January; therefore, three or four clutches should be completed in this time, since each clutch requires about one month from laying to fledging (Summers-Smith, 1963). In order to produce 300 young per 100 adults (50 pairs), each pair would need to raise one or two young to fledgling stage; this value is in accord with the few observations made of the number of fledglings produced by Townsville birds. Will (1973) found that Illinois birds produced an average of 1.05 fledglings per breeding

attempt, though with only three clutches per season. It appears, therefore, that Townsville populations may be capable of increasing dramatically over the breeding season due to the extra month available for breeding, and that wide disersal of first-year birds may occur as suggested by North (1973).

4.4.2 Reproduction -

The pattern of reproduction of an animal is a part of its genetic make-up and is to a certain extent autonomous (Amoroso and Marshall, 1960); however, it can be modulated by environmental factors to a degree which varies according to the species. Of particular interest in studies of introduced birds is the ease with which most species adjust their reproductive habits to a trans-equatorial shift. Thomson (1922) records that reversal of breeding season as a result of interhemisphere introduction is widespread in birds introduced to New Zealand. This is caused by the reversal of the seasonal patterns of climatic factors which trigger or inhibit breeding (Kikkawa and Yamashina, 1966). The breeding cycle may be upset in the introduced birds during the first few years of introduction, and adjustment to local conditions may occur gradually. Rolls (1969), for instance, records that the house sparrow began to breed in April when it was first introduced into Australia. The time required before the breeding is adapted to the period most favourable for raising young probably depends in part on whether the proximate factors, such as daylength, etc. vary in the same way as those in the country of origin (Sage, 1957).

Reproduction is a cyclic phenomenon, and the majority of avian species are seasonal breeders; therefore, the reproductive organs

of most birds undergo a great annual variation in size and functional activity (Lofts and Murton, 1973). Figure 4.10 demonstrates the conspicuous seasonal fluctuations in the reproductive status of the house sparrow in Townsville. These results agree with observations of previous workers on the house sparrow (Threadgold, 1960; Dang and Guraya, 1978) and on other bird species (Lofts and Murton, 1973). Autumnal recrudescence of the gonads appears to be less pronounced in Townsville than in the Punjab of India (30°56'N; Dang and Guraya, 1978), suggesting that nest attendance at this time was reduced in Townsville. In England, adult house sparrows attend nests and first-year birds prospect for nest sites in autumn as communal roosts begin to disband (Summers-Smith, 1963). This activity may occur earlier in Townsville, as indicated by the increase in numbers of adult birds using the roost in April and May - presumably since nest sites are now fully established and the birds do not remain in them during the night. Daily activity at the nests continued until June when testis regression occurred over the cold winter period. Mean testis scores increased at the end of winter in parallel with daylength and temperature and at the same time activity at the nest and the frequency of communal displays were increased. This pattern is similar to that in house sparrows in India where daylength and temperature have been found to control breeding activity (Guraya and Chalana, in Dang and Guraya, 1978). Daylength and temperature are also known to influence the reproductive activity of other bird species, but their mode of action in relation to other environmental factors is still not precisely known (Lofts and Murton, 1973).

The breeding season of the house sparrow varies with latitude

in Australia, as has been found in other species in other parts of the world (see Baker, 1938). In temperate Australia the main egg-laying season of the house sparrow is from October to early January (about 100 days); however, in Townsville it appears to be extended to include September (about 130 days). Similar results have been found in Europe and North America. In the wet subtropical climate of regions around Baroda, India (22°18'N), the breeding season of the house sparrows lasts from the middle of February (equivalent to mid-August in the southern hemisphere) to the middle of October (mid-February) - about 245 days - with only a short summer break; sporadic broods may be recorded even in December (Naik and Mistry, 1973). Since the climate of Townsville is highly seasonal (Chapter Two), a similar extension of the breeding season does not occur here, though it may be found in more tropical localities such as Cairns, Cooktown and Thursday Island - no records are as yet available to verify this.

4.4.3 Activity patterns -

The daily activity patterns of house sparrows begin when birds awaken and leave the roost or nest site, and end when they return in the evening. The data collected in Townsville indicate that house sparrows departed from the roost later in relation to civil twilight in winter than in autumn and spring, and return to the roost earlier in winter than at other times. Summers-Smith (1963) related this to attendance at the nest, birds with nests leaving early in the morning and returning late in the evening. In winter, attachment to the nest is at a minimum and birds remain in the roost longer in the morning and return earlier in the evening. Similarly, Counsilman

(1974) found that the Indian myna left its roosts earlier and returned later in summer than in winter. Aschoff and von Holst (1960) showed that the crow *Corvus monedula* departed from its roosts earlier and returned later in relation to civil twilight during the winter than during the summer, and suggested that this adjustment tended to reduce the pronounced seasonal influence of light on activity time at higher latitudes, by changing the sensitivity to entrainment by light.

The bimodal distribution of feeding activity which develops as days become hotter is characteristic of birds in the tropics and in other warm climates (King and Farner, 1964), and is one of several behavioural mechanisms for avoiding heat stress. Reduction of locomotor activity is of importance in confining the increased heat production which necessarily accompanies food procurement to parts of the day when the difference between the temperature of the body surface and the ambient temperature is greatest, and thus heat loss is maximal. The behavioural thermoregulatory mechanisms constitute the most important battery of mechanisms for temporary adaptation and adjustment of body temperature in hot environments (King and Farner, 1964). Other mechanisms include:

(1) selection of favourable microclimate. Selection of a position in the shade facilitates conductive and convective heat loss.

(2) postural control of convective and conductive heat loss. Partial extension and drooping of wings increases the surface for heat loss and exposes the more lightly feathered underwing and axillary surfaces.

(3) bathing.

(4) standing or sitting in water.

During September, house sparrows which were not feeding or attending nests, were perched in trees and avoided heat stress by remaining in the shade. Birds attending nests were perched on the edge of the guttering with wings drooped, and were panting. Bathing was not observed in August or September, though both water- and dust-bathing were observed in July.

Activity at the nests was greatest in the early mornings in August since most sites were still being established and it was in this time that communal displays were observed. The number of communal displays decreased in September when several pairs were incubating eggs and feeding nestlings, but increased again in October, presumably as a stimulation for females to prepare for the laying of second clutches (Summers-Smith, 1963).

CHAPTER FIVE

MORPHOLOGICAL STUDIES

5.1 Introduction

The emphasis of the taxonomist has almost always been on morphological characters since he works mostly on preserved material. Morphological characters of birds include those of size and proportions, epidermal structures, patterns of colouration, anatomy and cytology (Mayr, 1963). Size is probably the character most universally subject to geographic variation as it varies in virtually every species of animal which has an extensive geographic range.

Considerable attention has been paid over the years to climatic trends in morphological characteristics of birds and other animals. Some of these trends have been formalised as Bergmann's, Allen's and Gloger's rules (summarised by Mayr, 1963: 318-327) and physiological reasons for them sought (for example, Kendeigh (1969) on tolerance of cold and Bergmann's rule).

The first attempts to demonstrate evolutionary size changes in introduced birds were made by Barrows (1889), Grinnell (1919) and others (see Johnston and Selander, 1964), working on house sparrows in North America. Lack (1940) found no significant divergence of bill and wing dimensions of North American and Hawaiian house sparrows from the Old World stock. These results were used as

evidence for the slow rates of evolution of avian races, thought to take up to 4000 years (Mayr, 1963:579). Using larger sample sizes and more refined analytical methods, Calhoun (1947) showed that wing length of house sparrows of eastern and central North America increased slightly more than one millimetre between the time of introduction and 1930, and that average length of wing, femur and humerus were correlated with duration and severity of freezing temperatures. Johnston and Selander (1964) supported Calhoun's findings with their conclusions that "conspicuous adaptive differentiation in colour and size" (p.548) had occurred in the house sparrow in North America and the Hawaiian Islands and that patterns of geographic variation in North America paralleled those shown by native polytypic species, in agreement with Gloger's and Bergmann's ecogeographic rules. The speed at which these changes had occurred indicated that racial differentiation of house sparrow populations may have required no more than fifty years.

Studies of geographic variation in introduced birds have involved birds from one northern temperate locality to another (the house sparrow in North America - Johnston and Selander, 1964 *et seq.*), from a northern temperate location to a southern temperate island (the house sparrow in New Zealand - Baker, 1980), from a northern tropical location to a southern temperate island (the Indian myna in New Zealand - Baker and Moeed, 1979) and from west to east across a continent (the house finch, *Carpodacus mexicanus*, in North America - Aldrich and Weske, 1978).

Apart from a few notes and comments, mainly concerning subspecific rank (for example, Frith and MacLean, 1975; Keve, 1976, Sage, 1957), little has been published on the morphometrics of birds

introduced to Australia. The aims of this section of the project were, therefore, to make an introductory study of geographic variation in Australian house sparrows, and to investigate how this geographic variation changes with season.

5.2 Methods

5.2.1 Seasonal variation -

House sparrows were mist-netted monthly from March to September as described in Section 4.2, and the following measurements were taken: (1) body weight: to the nearest 0.5 grams - measured on a "Pesola" spring balance; (2) wing length: chord of unflattened wing; (3) tail length: distance from point of insertion of central pair of rectrices to tip of second rectrix (retrices numbered from central pair, 1-1 to outer pair, 6-6); (4) bill length: measured from tip of bill to base of skull; (5) tarsus length: from joint of tibiotarsus and tarsometatarsus to the last undivided scute before the toes separate.

In the laboratory, frozen specimens were defrosted and weighed, and measurements were taken as described above.

Banding schedules for the house sparrow were obtained from the Australian Bird-Banding Scheme to enable comparison of seasonal variation in Townsville birds with that of temperate Australian populations.

5.2.2 Geographic variation -

In June, a brief field trip was made from Cairns to Canberra in order to collect specimens for analysis of geographic variation. Specimens were collected from Cairns, Townsville and Rockhampton and arrangements were made for specimens to be sent from Brisbane, Sydney and Adelaide to provide a reasonable transect along the east coast of Australia. Specimens obtained in this way were measured as described above.

The significance of variation due to sex and locality was determined for each character by a two-way analysis of variance. Following this analysis, one-way analyses of variance of the effect of locality were computed for each sex followed by a Student-Newman-Keuls procedure which ordered the locality means into homogeneous subsets. The extent of intrapopulation variability in each character was examined and comparisons made between the sexes and between localities using Wilcoxen's Signed-Ranks Test (Sokal and Rohlf, 1981) and the Bartlett-Box F-Test (Nie *et al*, 1975). Correlations and regressions were calculated for pairs of characters and were tested for homogeneity between localities and sexes - using the z^* transformation of Hotelling, for small sample sizes (Sokal and Rohlf, 1981). Sexual dimorphism was investigated using character means for each sex and by discriminant function analyses using each sex as a group and the four linear measures as discriminating variables. The statistic used as a measure of sexual dimorphism was the Mahalanobis distance measure, D^2 (Nie *et. al.*, 1975).

Correlation coefficients between the locality means and 12 climatic variables (Table 2.1) were calculated.

5.3 Results

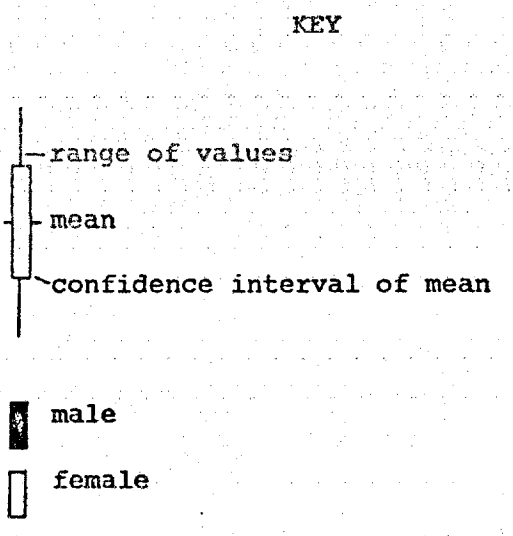
A total of 296 house sparrows were caught at the roost site in eight mornings over the study period; a summary of birds caught is contained in Table 4.1. Of the birds caught, 137 were banded, measured and released, and 153 were collected and frozen. In addition, sparrows were collected from Cairns, Townsville and Rockhampton in June, and specimens were sent from Adelaide at the same time. Sparrows promised from Brisbane and Sydney were not forthcoming. Analysis of species schedules from the Australian Bird-Banding Scheme resulted in data from five localities in southern Australia; no other banding has yet been attempted north of Sydney, with the exception of one attempt in Mount Isa (1965) during which no measurements were taken.

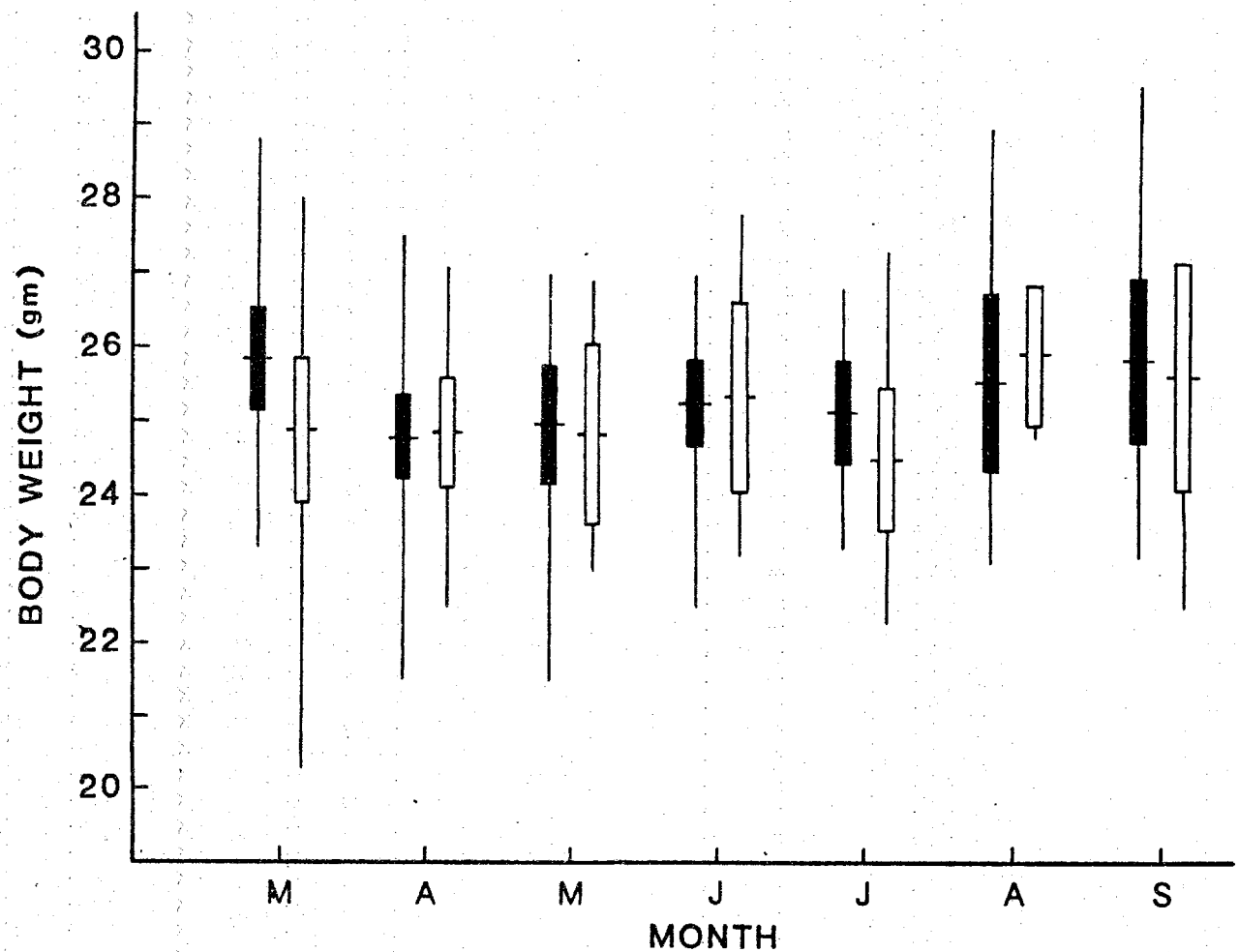
5.3.1 Seasonal variation -

(a) Body weight

The body weight of house sparrows in Townsville is plotted in Figure 5.1 for each month of the study period. For males average body weight over the study period was 25.31 grams (n=112) - for females it was 25.00 grams (n=74). This difference is not significant ($F=1.693$, 1x172 d.f., $p=0.13$). Variation over the study period was not significant in either sex (males: $F=1.491$, 6x105 d.f., $p=0.19$;females: $F=0.769$, 6x67 d.f., $p=0.60$). In contrast, variation in house sparrows from Adelaide (Jenkin, unpublished data) was significant over the period from March to September (males: $F=8.543$, 6x117 d.f., $p<0.05$; females: $F= 5.774$, 6x63 d.f., $p<0.05$). The mean body weight of Adelaide sparrows over this period

Figure 5.1 Seasonal variation in body weight




30
28
26
24
22
20
BODY WEIGHT (gm)
M
A
M
J
J
A
S
MONTH

was 26.28 grams for males (N=124) and 26.04 grams for females (N=70); this sexual difference was not significant (F=0.993, 1x192 d.f., p=0.32).

(b) Wing length

House sparrows in Townsville showed significant sexual dimorphism in wing length over the study period; the mean wing length for males was 75.59 mm, and for females it was 73.43 mm (F=59.077, 1x172 d.f., p<0.01). Wing length variation over the study period (Figure 5.2) was not significant (F=1.120, 6x172 d.f., p=0.353).

(c) Tail length

The tail length of house sparrows from Townsville is plotted in Figure 5.3 for each month of the study period. Variation over this period was not significant (F=1.492, 6x171 d.f., p=0.183). Males had a mean tail length of 57.08 mm which was significantly greater than the mean tail length of females (females: mean= 55.05 mm: F=26.01, 1x171 d.f., p<0.01).

(d) Bill length

Variation in bill length over the study period is shown in Figure 5.4. The bill length of females remained constant fron March to September (F=0.171, 6x72 d.f., p=0.984). However, male bill length varied significantly in that time (F=4.831, 6x101 d.f., p<0.05). The average bill length of males increased slightly from March to May, decreased significantly in June and increased again in July; it reached a maximum in August. Average bill length over the study period was 16.04 mm for males and 16.01 mm for females; this difference is not significant (F=0.094, 1x179 d.f., p=0.759).

(e) Tarsus length

Figure 5.2 Seasonal variation in wing length

(explanation as in Figure 5.1)

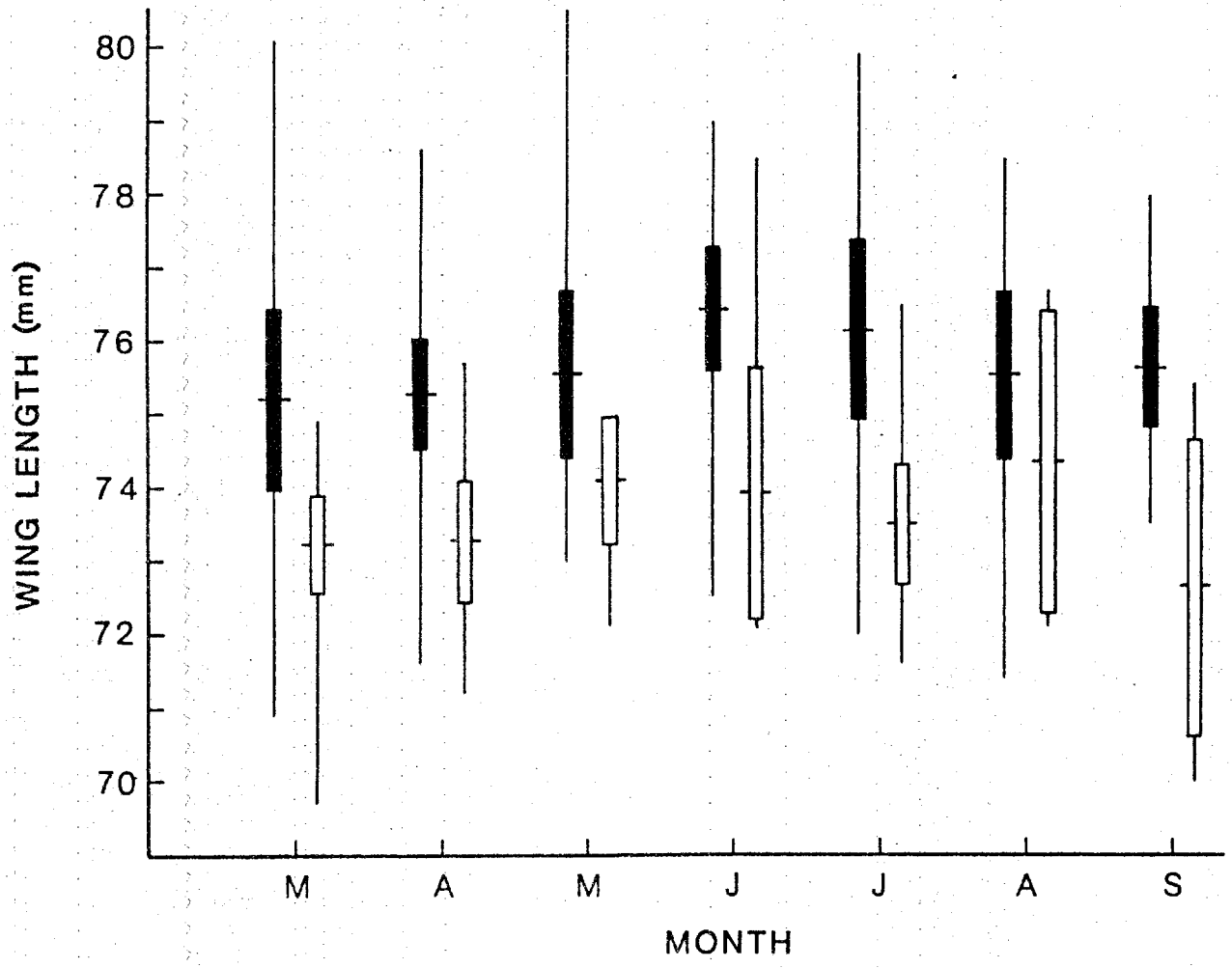

80
78
76
74
72
70
WING LENGTH (mm)
M
A
M
J
J
A
S
MONTH

Figure 5.3 Seasonal variation in tail length

(explanation as in Figure 5.1)

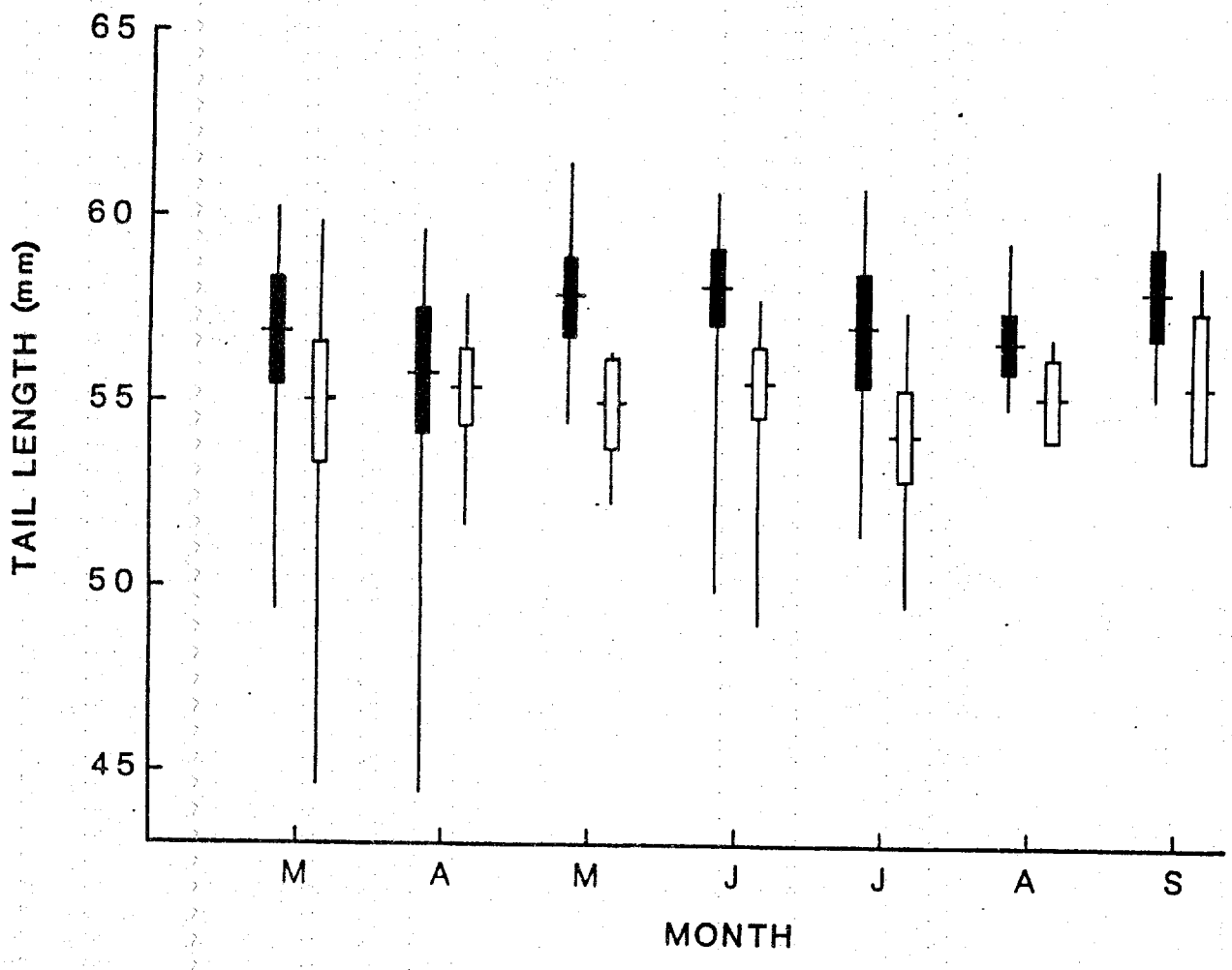

65
60
55
50
45
TAIL LENGTH (mm)
M
A
M
J
J
A
S
MONTH

Figure 5.4 Seasonal variation in bill length

(explanation as in Figure 5.1)

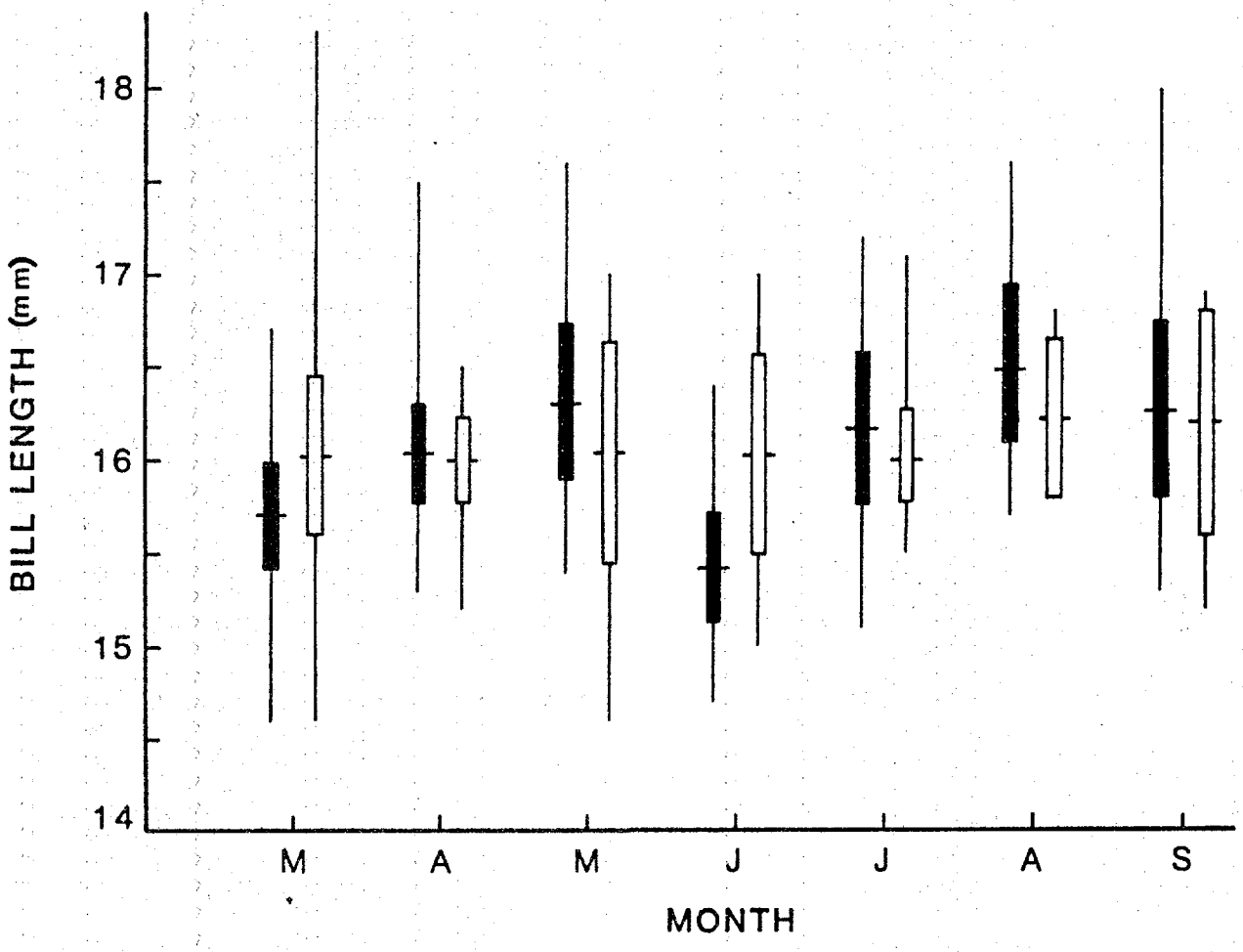
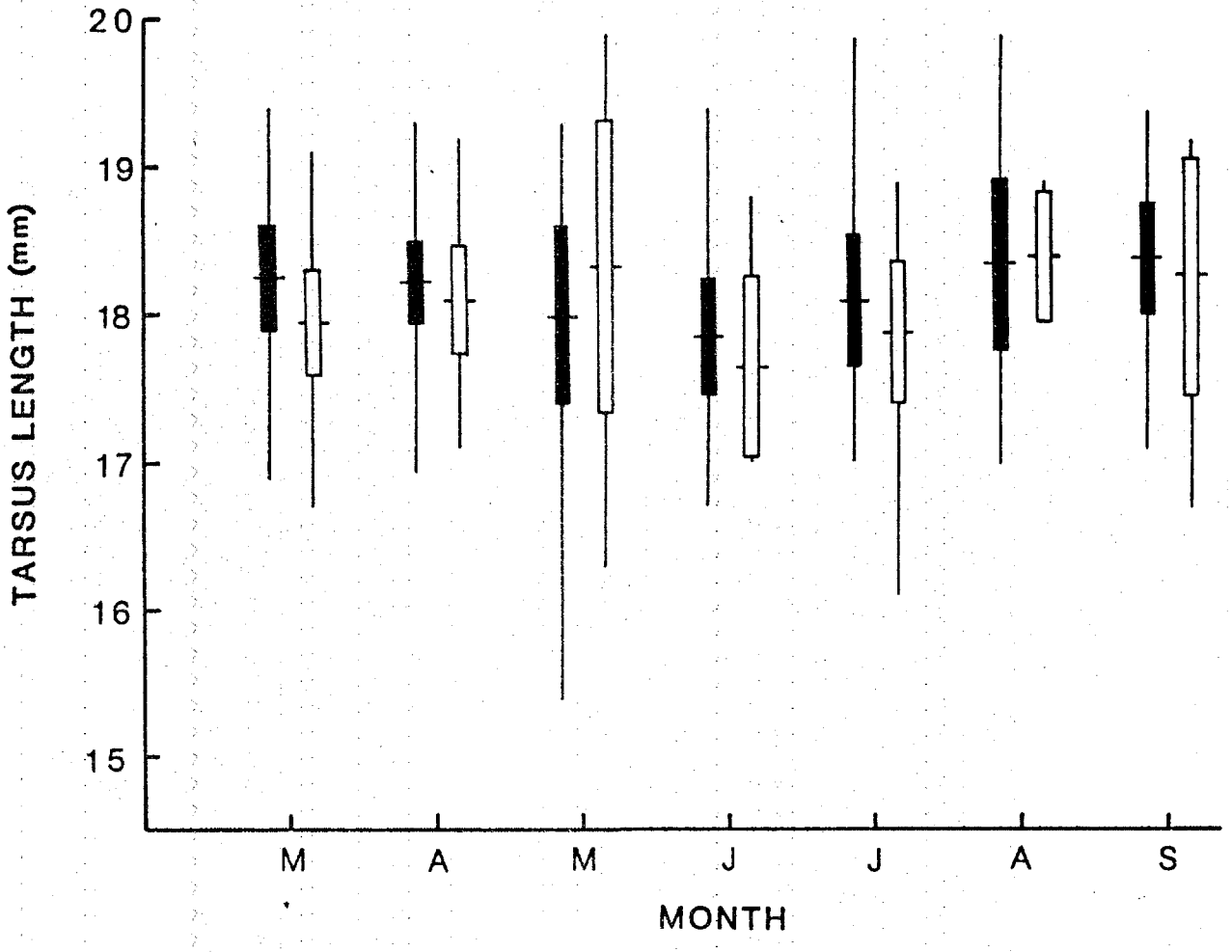

BILL LENGTH (mm)
18
17
16
15
14
M
A
M
J
J
A
S
MONTH

Figure 5.5 Seasonal variation in tarsus length

(explanation as in Figure 5.1)


20
19
18
17
16
15
TARSUS LENGTH (mm)
M
A
M
J
J
A
S
MONTH

Over the study period there was neither significant sexual dimorphism ($F=1.073$, 1x158 d.f., $p=0.302$), nor was there significant monthly variation ($F=1.447$, 6x158 d.f., $p=0.200$) in tarsus length (Figure 5.5). For males, mean tarsus length was 18.16 mm; for females it was 18.03 mm.

(f) Plumage

In March, 100 birds of 110 captured were nearing the completion of moult and were growing new wing, tail and body feathers; the remaining birds had completed their moult. By April, only one bird in 52 showed signs of moult.

The major seasonal changes in plumage resulted from abrasion of the feathers, causing slight reduction in the length of measured characters (Figures 5.2 and 5.3). Abrasion of the feathers resulted in patterning becoming more obvious with time. The newly developed contour feathers of the male house sparrow had tips of a lighter colour than the rest of the feather, thus reducing the extent of markings on the body (Figures 5.6 and 5.7). New crown feathers had light brown tips which obscured the grey and chestnut markings characteristic of the male in spring (cf. Figure 5.6 and frontispiece). In addition, black feathers produced on the breast had white tips and the extent of the black bib appeared much reduced (Figure 5.7). Abrasion of the feather tips over winter resulted in the lighter parts becoming worn and the background markings becoming fully expressed (frontispiece and Figure 5.8). In the female, newly grown contour feathers did not have the light tips characteristic of fresh male feathers and did not exhibit the obvious plumage variation over the year that males did.

Figure 5.6 Winter plumage of the male house sparrow- crown

Figure 5.7 Winter plumage of the male house sparrow - breast

Figure 5.8 Spring plumage of the male house sparrow - breast

5.3.2 Geographic variation -

Data for studies of geographic variation in Australian house sparrows came from two sources: birds collected in Cairns, Townsville, Rockhampton and Adelaide in June, and banding records of the Australian Bird-Banding Scheme. Data extracted from banding records were restricted to measurements taken in May, June and July, in order to minimise the effect of seasonal variation on the character means obtained. Banding data were not used for statistical analysis and are shown for comparative purposes only.

(a) Variation in character means

Analyses of variance (Table 5.1) indicated significant interlocality variation in body weight of both sexes and wing length and tail length of males. The mean body weights of sparrows from the sample localities are plotted in Figure 5.9. Homogeneous subsets produced by the Student-Newman-Keuls procedure show that variation is ordered similarly in both sexes, birds from Townsville being the lightest and those from Adelaide the heaviest. Wing length is ordered in the reverse direction to weight, having higher means in Townsville and Cairns than in Rockhampton and Adelaide (Figure 5.10). The tail length of male sparrows varies similarly (Figure 5.11), the northern birds having the longer tails. Bill length (Figure 5.12) and tarsus length (Figure 5.13) follow similar trends, though the differences are not significant.

(b) Intrapopulation variability

Mean coefficients of variation for linear dimensions and body weight are shown in Table 5.2. Weight is the most variable character, followed in order by tarsus length, bill length, tail length and wing length. Females had slightly higher mean

Table 5.1: Analysis of variance of size characters in house sparrows from Cairns, Townsville, Rockhampton and Adelaide.

Source of Variation	Degrees of Freedom	F-ratio[a] Weight	Wing	Tail	Bill	Tarsus
SEX	1, 69	0.327	48.312**	32.607**	0.707	1.594
LOCALITY	3, 69	13.530**	3.151*	2.610	0.742	2.452
SEX-LOCALITY	3, 69	0.777	0.021	2.821*	1.058	0.732

[a]The effect is statistically significant at the 5% level ($p \leq 0.05$), indicated by *; or at the 1% level ($p < \leq 0.01$), indicated by **.

Table 5.2: Intrapopulation and interpopulation variability in size in house sparrows from Cairns, Townsville, Rockhampton and Adelaide.

(a) intrapopulation variability

	Males		Females		
Character	mean sample size	Mean C.V.[a]	mean sample size	Mean C.V.	F[b]
Weight	10	11.86	8	10.34	1.06 ns
Wing	10	2.14	8	3.80	1.59 ns
Tail	10	3.47	8	3.88	1.08 ns
Bill	10	1.46	8	1.27	1.19 ns
Tarsus	10	2.79	8	2.01	1.35 ns

[two-tailed sign test, p=0.375, therefore mean coefficient of variation is the same for both sexes]

[a]Mean coefficient of variation (%)
[b]F value calculated as per Selander and Johnston (1967, p.229)

(b) Interlocality variability

Variable	Mean intralocality Variance	Per cent Interlocality Variation[a]
Male		
Body weight	3.139	36.36
Wing length	1.626	11.38
Tail length	2.012	29.59
Bill length	0.230	0.00
Tarsus length	0.509	3.93
Female		
Body weight	2.713	42.62
Wing length	2.799	0.45
Tail length	2.177	0.00
Bill length	0.201	5.37
Tarsus length	0.362	9.46

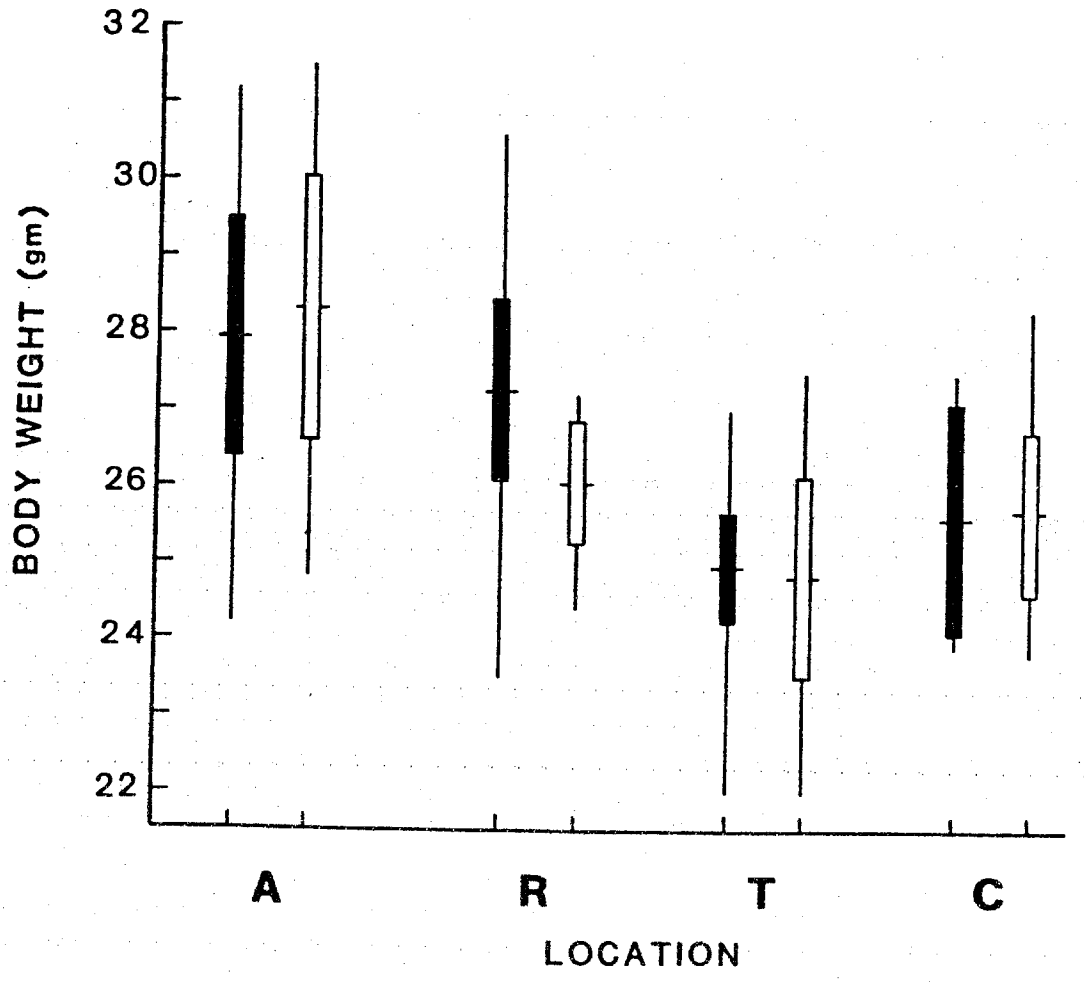
[a]Per cent interlocality variation represents the proportion of the variability in the samples that is attributable to locality (Johnston, 1976).

Figure 5.9 Geographic variation in body weight

Upper: Graphical display (symbols as in Figure 5.1)

Locations:	A	Adelaide
	R	Rockhampton
	T	Townsville
	C	Cairns

Lower: Mean character values ranked in ascending order. Homogeneous subsets (S-N-K Procedure) are indicated by the vertical lines



MALE:

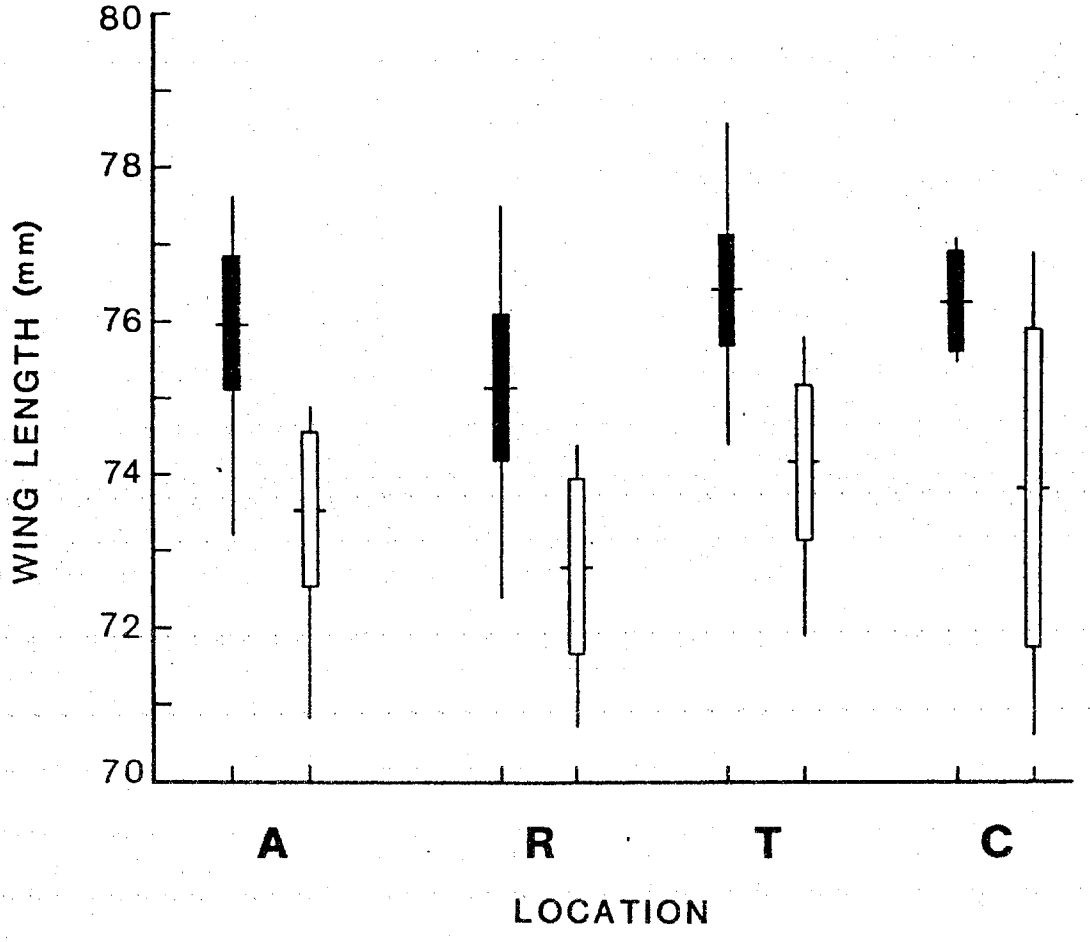
24.96 T
25.60 C
27.27 R
27.93 A

FEMALE:

T 24.83
C 25.69
R 26.06
A 28.32

Figure 5.10 Geographic variation in wing length

(explanation as in Figure 5.9)



MALE:

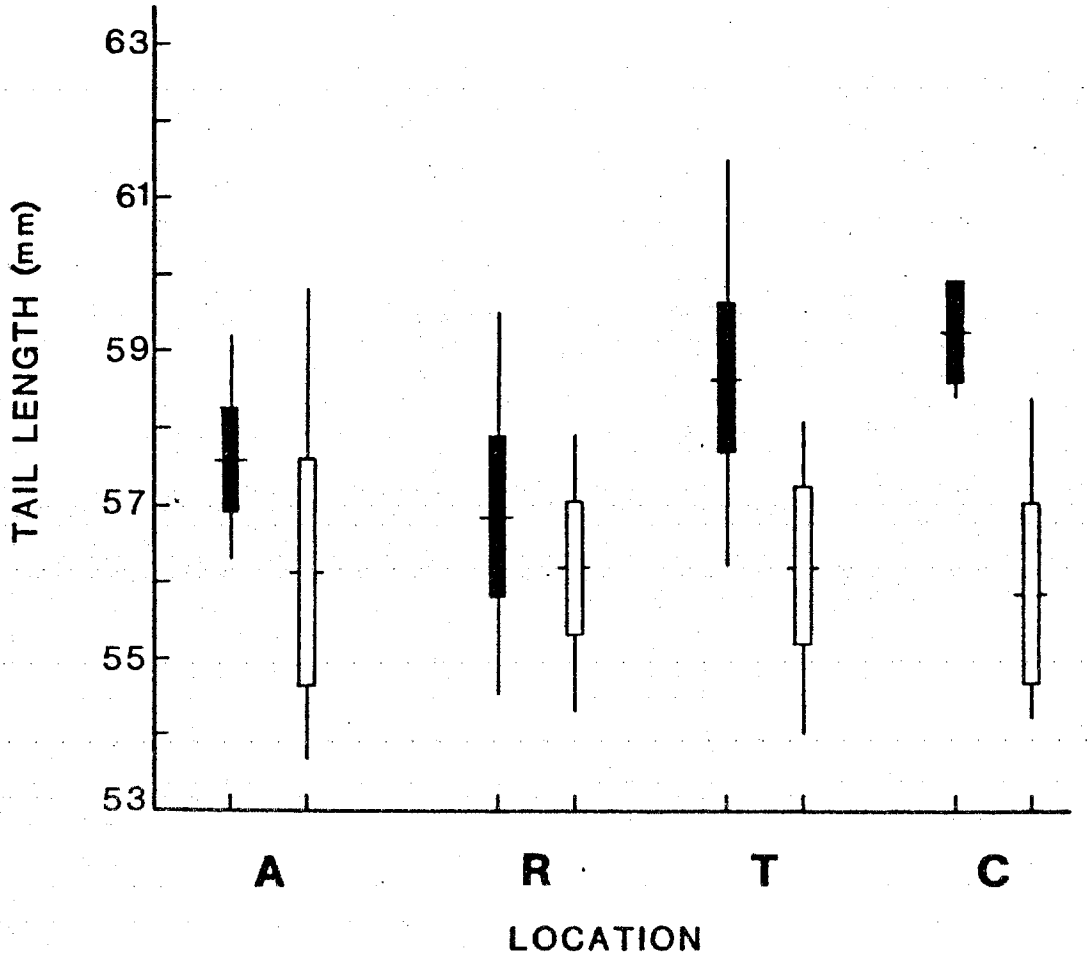
75.14	R
75.97	A
76.28	C
76.42	T

FEMALE:

R	72.80
A	73.54
C	73.84
T	74.19

Figure 5.11 Geographic variation in tail length

(explanation as in Figure 5.9)



MALE:

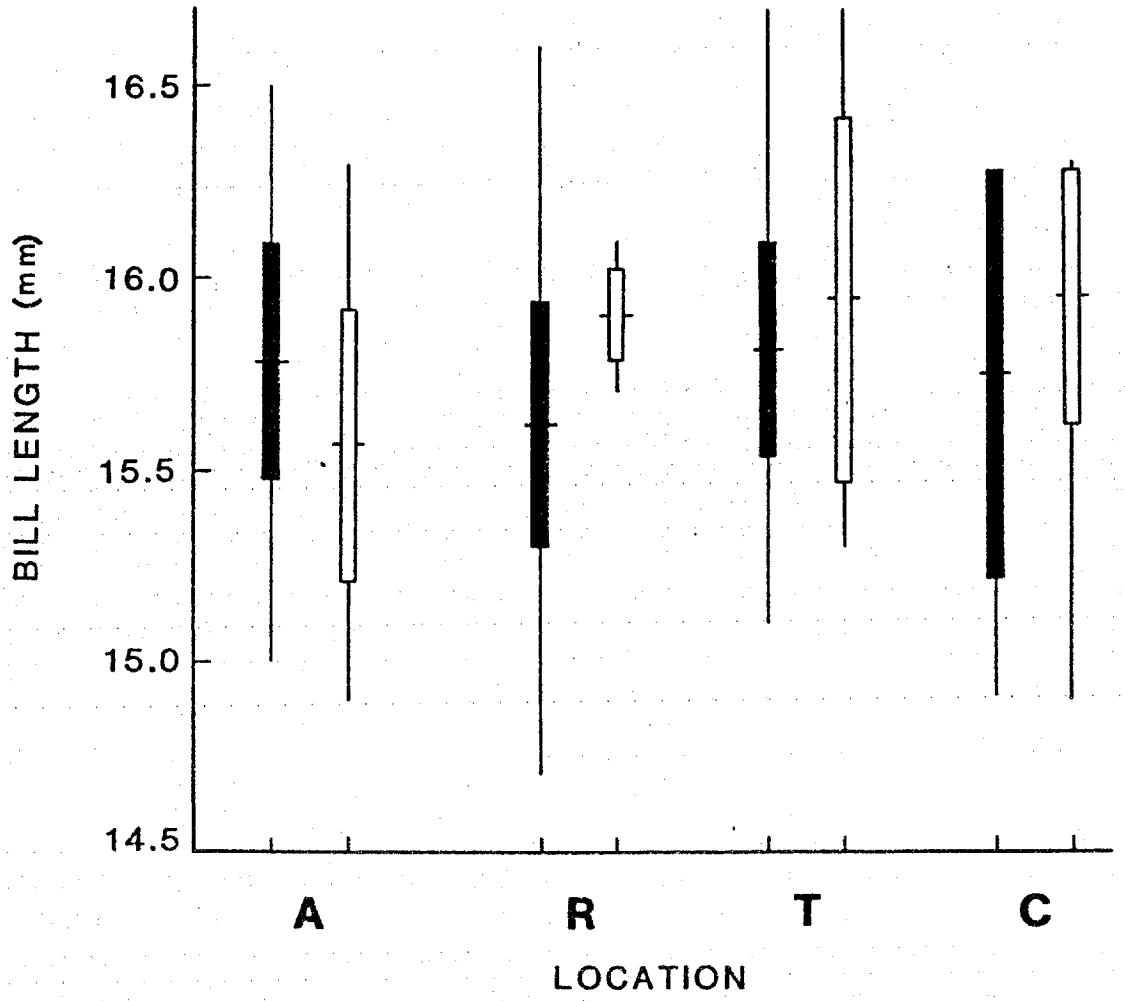
56.86	R	
57.60	A	
58.66	T	
59.28	C	

FEMALE:

C	55.86
A	56.12
R	56.19
T	56.22

Figure 5.12 Geographic variation in bill length

(explanation as in Figure 5.9)



MALE:

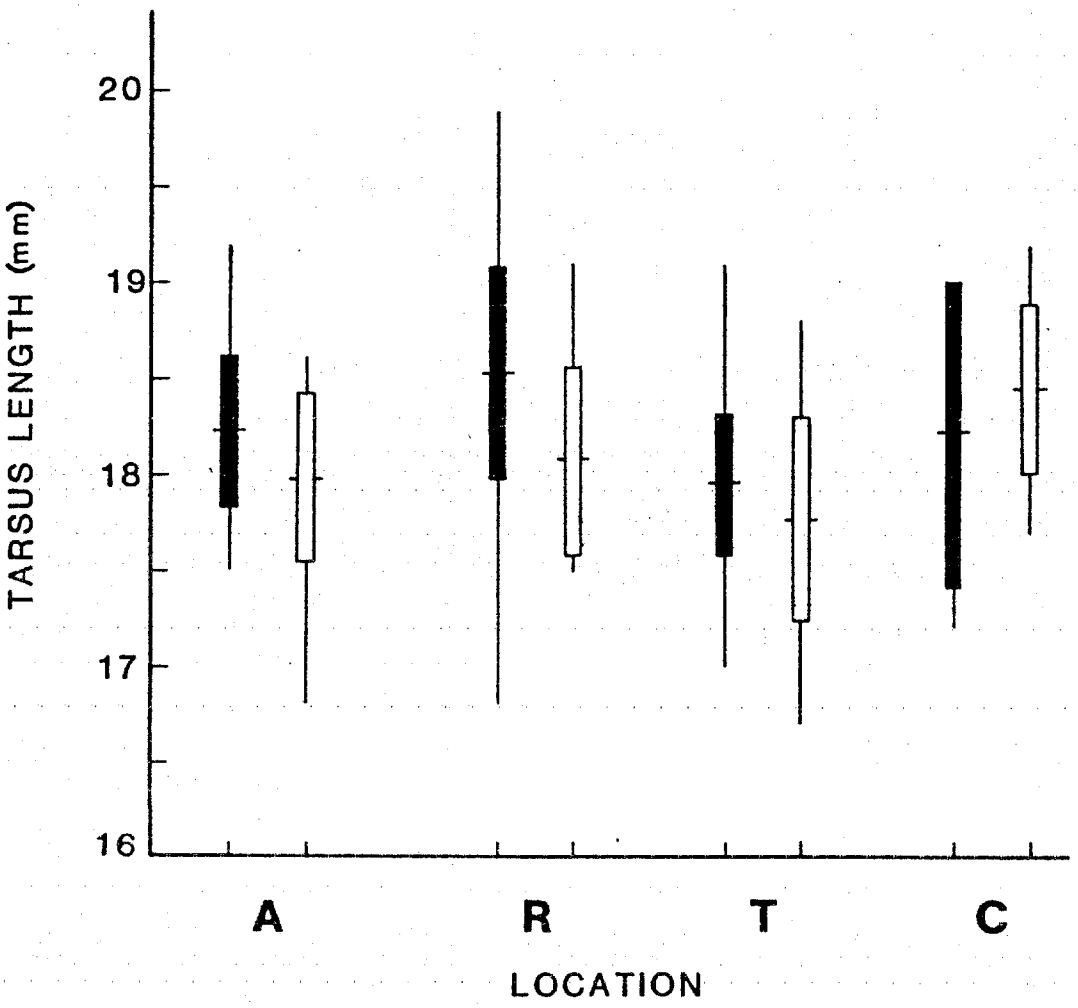
15.62	R
15.75	C
15.78	A
15.81	T

FEMALE:

A	15.57
R	15.90
T	15.94
C	15.95

Figure 5.13 Geographic variation in tarsus length

(explanation as in Figure 5.9)



MALE:

17.95	T
18.22	C
18.23	A
18.53	R

FEMALE:

T	17.77
A	17.98
R	18.08
C	18.45

coefficients of variation than males for wing length; however, for all other characters males had the higher value. Overall, these differences were not highly significant for single characters (Table 5.2). The percentage interlocality variation for each character, representing the proportion of variability in that character due to locality, are also included in Table 5.2. With the exception of male tail length, and body weight in both sexes, less than 12% of the variation in the total sample is due to locality effects.

Comparison of the amount of intrapopulation variability between populations (Table 5.3) indicates that the variance of female bill length was the only character variance that differed between geographic locations. Females from Rockhampton had the lowest bill length variance (C.V.=0.89%), while females from Townsville had the highest (C.V.=3.9%).

(c) Correlations and regressions

Correlation coefficients between paired combinations of body dimensions and weight were computed for all samples of males and females (Table 5.4). Coefficients of correlation between tarsus and wing length were heterogeneous at the 5% level for males (Table 5.5), but those for other pairs of characters were homogeneous ($\chi^2_{(4)}<7.815$, $p>0.05$). Average intrapopulation correlation coefficients for the four samples are also shown in Table 5.5. All significant correlations were positive and, with the exception of bill length, were significant at the 1% level. The strongest correlations were found between tarsus length and body weight in both sexes.

Intersexual correlation coefficients and regressions of linear dimensions and body weight calculated for the four localities are

Table 5.3: Homogeneity of variance in size in house sparrows from Cairns, Townsville, Rockhampton and Adelaide

	Males		Females	
	Variance ratio[a]	Bartlett-Box F	Variance ratio	Bartlett-Box F
Weight	3.552	1.565	5.485	1.801
Wing	5.839	1.292	3.604	1.592
Tail	7.001	2.299	3.424	0.919
Bill	1.272	0.054	19.389	3.895**
Tarsus	2.173	0.618	1.705	0.188

(** : $p<0.01$)

[a]Variance ratio = max variance/min. variance

Table 5.5: Test for homogeneity of correlation coefficients between locations. Arrangement of correlation matrix is the same as for Figure 5.4.

(a) Mean correlation coefficients for locality data
Significant correlations are shown in bold-type.

Character	Weight	Wing	Tail	Bill	Tarsus
		(n=43)			
Weight	-	0.192	-0.127	0.330	0.776
Wing	0.691	-	0.436	-0.004	0.064
Tail (n=34)	0.417	0.572	-	-0.074	-0.203
Bill	0.183	0.057	0.164	-	0.133
Tarsus	0.709	0.644	0.272	0.068	-

(b) Chi-square values
Values with $p<0.05$ are shown in bold-type.

Character	Weight	Wing	Tail	Bill	Tarsus
Weight	-	3.570	3.216	1.280	0.510
Wing	2.391	-	0.830	0.939	10.435
Tail	6.228	5.057	-	2.786	1.869
Bill	2.778	1.533	0.499	-	6.036
Tarsus	0.348	0.672	1.301	1.463	-

Table 5.4: Correlations of size characters in house sparrows from all localities. Coefficients for males are in upper triangles; those for females are in lower triangles. Sample sizes are indicated.

(a) Cairns

Character	Weight	Wing	Tail	Bill	Tarsus
		(n=6)			
Weight	-	-0.128	-0.440	0.560	0.756
Wing	0.644	-	0.166	-0.066	0.920
Tail (n=8)	0.841	0.896	-	0.642	0.125
Bill	0.544	0.045	0.302	-	-0.344
Tarsus	0.756	0.553	0.534	0.199	-

(b) Townsville

Character	Weight	Wing	Tail	Bill	Tarsus
		(n=14)			
Weight	-	-0.128	-0.440	0.560	0.756
Wing	0.703	-	0.448	0.208	-0.384
Tail (n=9)	0.452	0.153	-	-0.170	-0.466
Bill	0.371	0.064	0.055	-	0.609
Tarsus	0.649	0.513	-0.038	0.271	-

(c) Rockhampton

Character	Weight	Wing	Tail	Bill	Tarsus
		(n=12)			
Weight	-	0.153	-0.016	0.213	0.603
Wing	0.275	-	0.586	-0.213	-0.067
Tail (n=8)	-0.304	0.561	-	-0.252	0.008
Bill	0.222	0.441	0.369	-	-0.265
Tarsus	0.563	0.641	0.448	0.203	-

(d) Adelaide

Character	Weight	Wing	Tail	Bill	Tarsus
		(n=11)			
Weight	-	0.351	-0.165	0.246	0.663
Wing	0.823	-	0.399	-0.027	0.164
Tail (n=9)	0.464	0.450	-	-0.147	-0.264
Bill	-0.315	-0.260	0.049	-	0.093
Tarsus	0.693	0.757	0.269	-0.325	-

Figure 5.14 Correlations and regressions of mean measurements of male and female house sparrows

KEY

——— regression of female measure on male measure

—·— regression of male measure on female measure

Regressions:

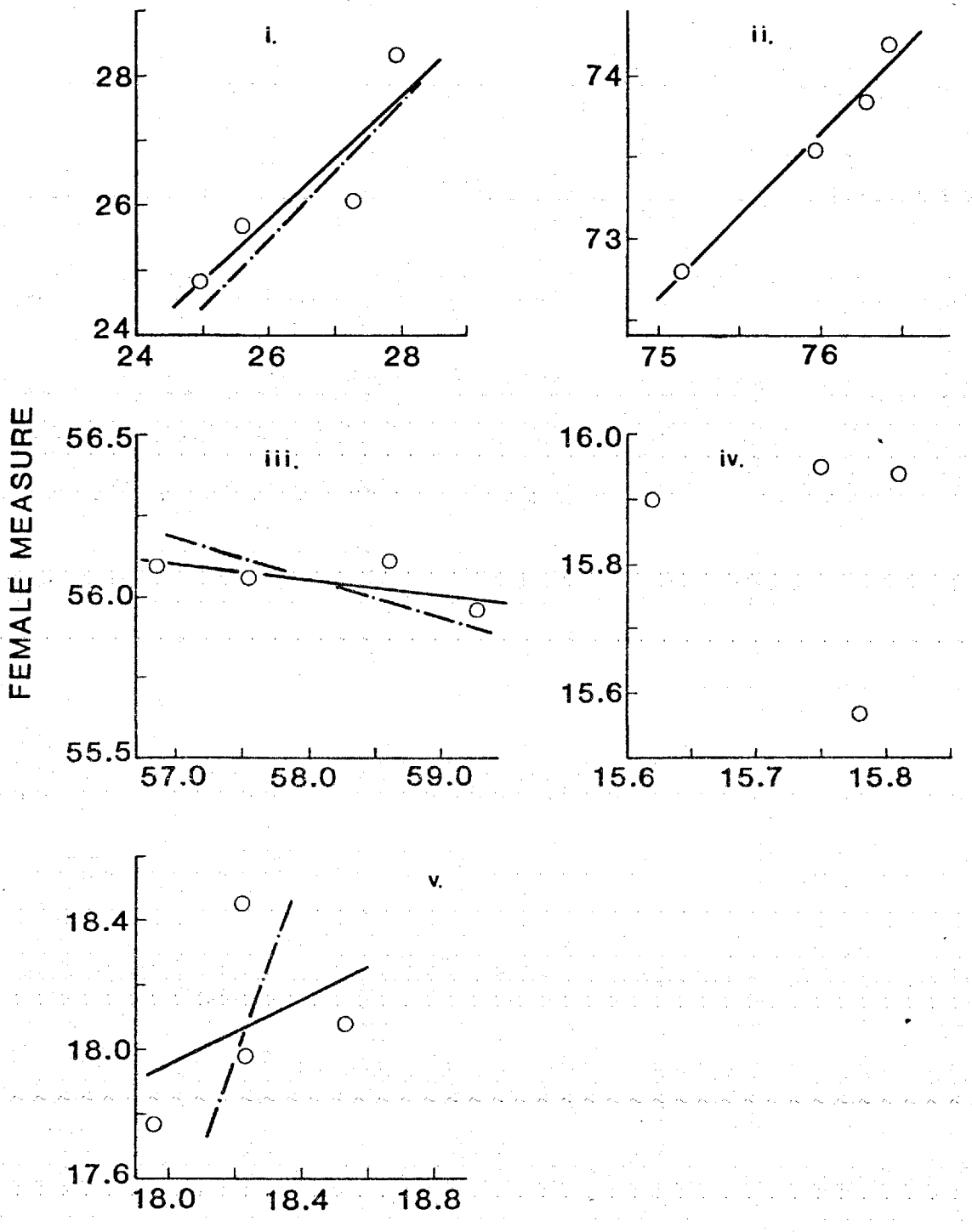
i. Body weight
r=0.885 (ns)
F = 0.95 M +1.18
M = 0.83 F +4.75

ii. Wing length
r=0.986 ($p<0.05$)
F = 1.00 M - 3.3
M = 0.96 F + 5.6

iii. Tail length
r=-0.637 (ns)
F = -0.10 M + 61.7
M = -4.20 F + 293

iv. Bill length
r=-0.218 (ns) - regression not shown

v. Tarsus length
r=0.412 (ns)
M = 0.34 F + 12.0
F = 0.50 M + 9.1


i.
28
26
24
24
26
28
ii.
74
73
75
76
FEMALE MEASURE
iii.
56.5
56.0
55.5
57.0
58.0
59.0
iv.
16.0
15.8
15.6
15.6
15.7
15.8
v.
18.4
18.0
17.6
18.0
18.4
18.8
MALE MEASURE

shown in Figure 5.14. Significant correlations were found for wing lengths only, and a test of homogeneity indicated that the correlation coefficients were, in fact, heterogeneous ($\chi^2_{(4)}$=10.01, $p<0.05$).

Interpopulation correlations (Table 5.6) were strong for tarsus length-body weight and wing length-tail length in both sexes. For females, significant correlations were found between wing length and body weight, and wing length and tarsus length; for males, the correlation between tail length and body weight was also significant. Male and female wing lengths are plotted against tail length in Figures 5.15 and 5.16 respectively using data from all localities. The regression coefficients for the two sexes are not significantly different ($t=0.482$, 73 d.f., $p>0.50$).

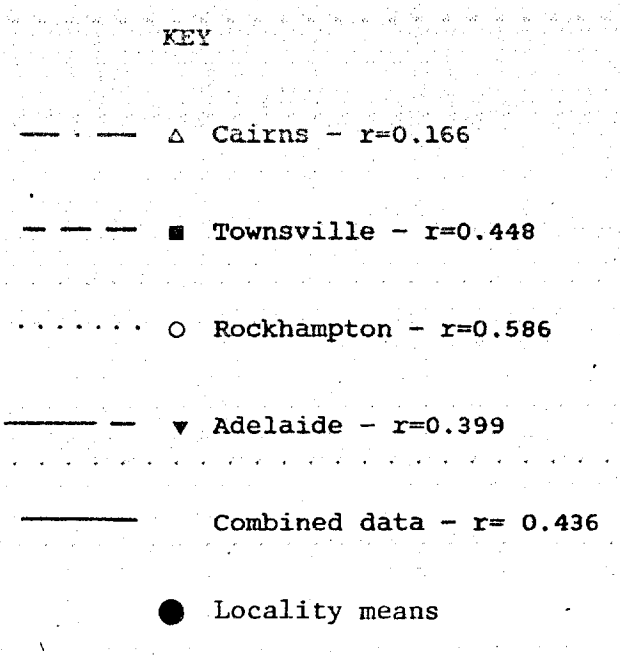
(d) Sexual dimorphism

Sexual dimorphism was evident only in wing length and tail length (Tables 5.1 and 5.7). Relative to body mass, as indicated by tarsus length or the cube root of body weight, the wing and tail were disproportionately longer in males than in females. Geographic variation in sexual dimorphism occurred only in body weight and tail length, though the dimorphism of individual characters was not ordered in the same way between localities. Geographic variation in sexual dimorphism is illustrated in Figure 5.17. Mahalanobis distance was greatest for specimens from Cairns and least for those from Rockhampton. The proportion of linear variables required to effectively separate the sexes varied between localities (Table 5.8). At all localities wing length was included in the discriminant function; it was the only discriminating variable used for specimens from Rockhampton.

Table 5.6: Interpopulation correlations of size characters in house sparrows. Arrangement of the matrix is the same as for Figures 5.4 and 5.5.

Character	Weight	Wing	Tail	Bill	Tarsus
Weight	-	-0.024	-0.355	0.182	0.626
Wing	0.354	-	0.562	0.047	-0.155
Tail	0.336	0.488	-	-0.043	-0.291
Bill	-0.139	0.022	0.100	-	-0.004
Tarsus	0.456	0.466	0.196	0.099	-

Figure 5.15 Plot of wing length versus tail length for male house sparrows



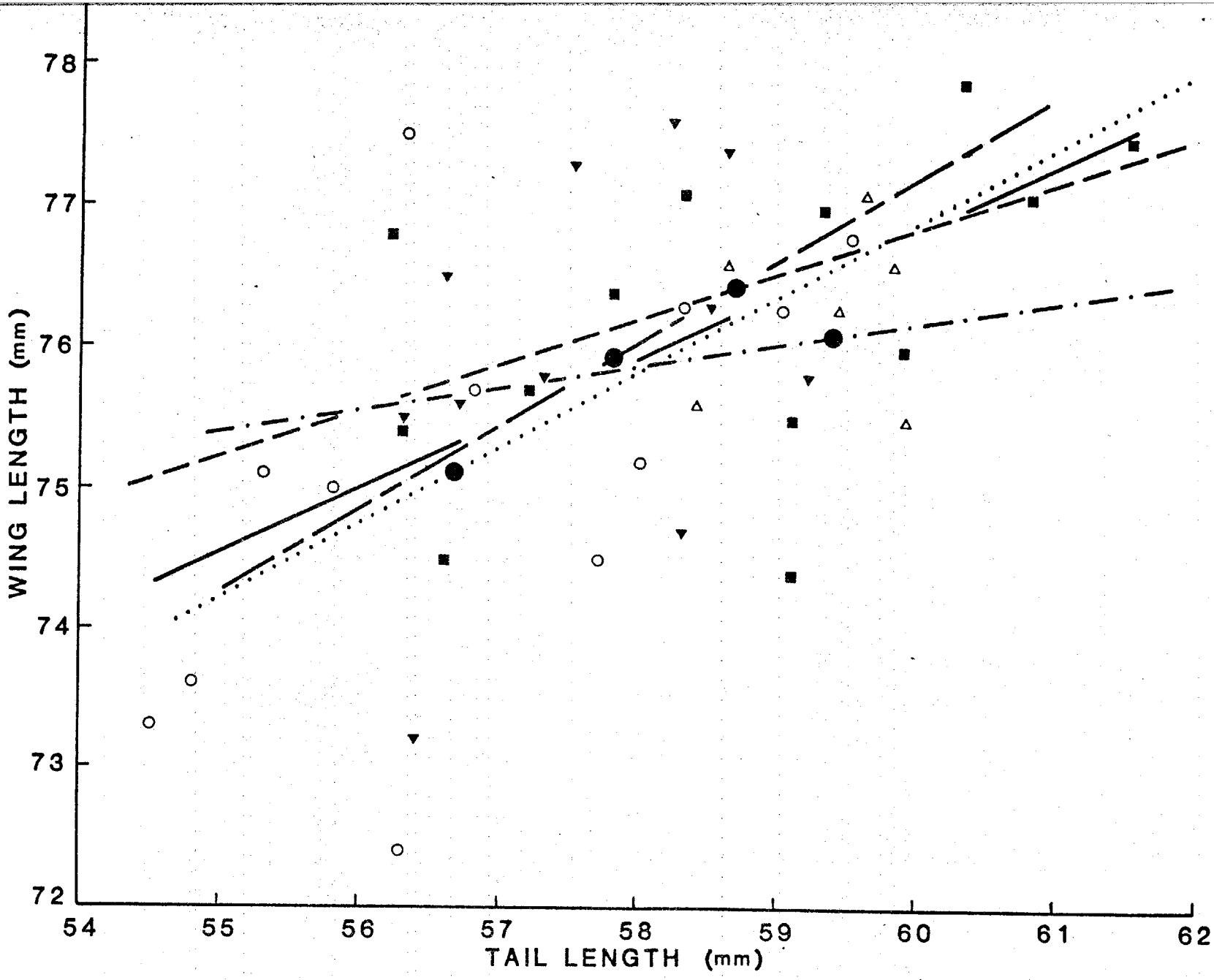
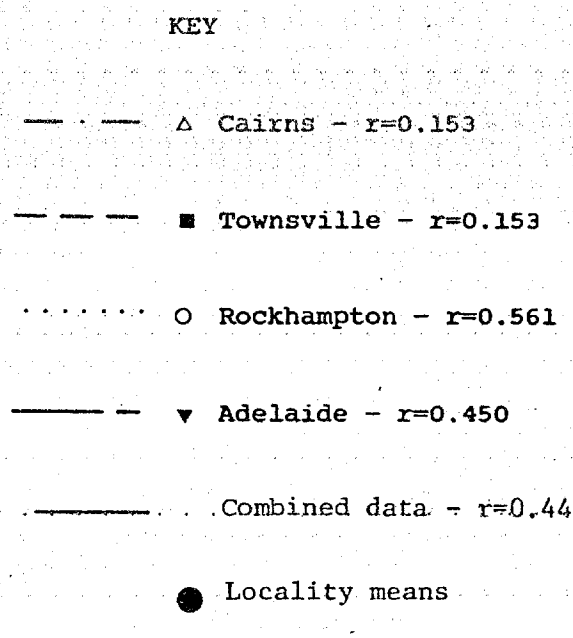

78
77
76
75
74
73
72
WING LENGTH (mm)
54
55
56
57
58
59
60
61
62
TAIL LENGTH (mm)

Figure 5.16 Plot of wing length versus tail length for female house sparrows



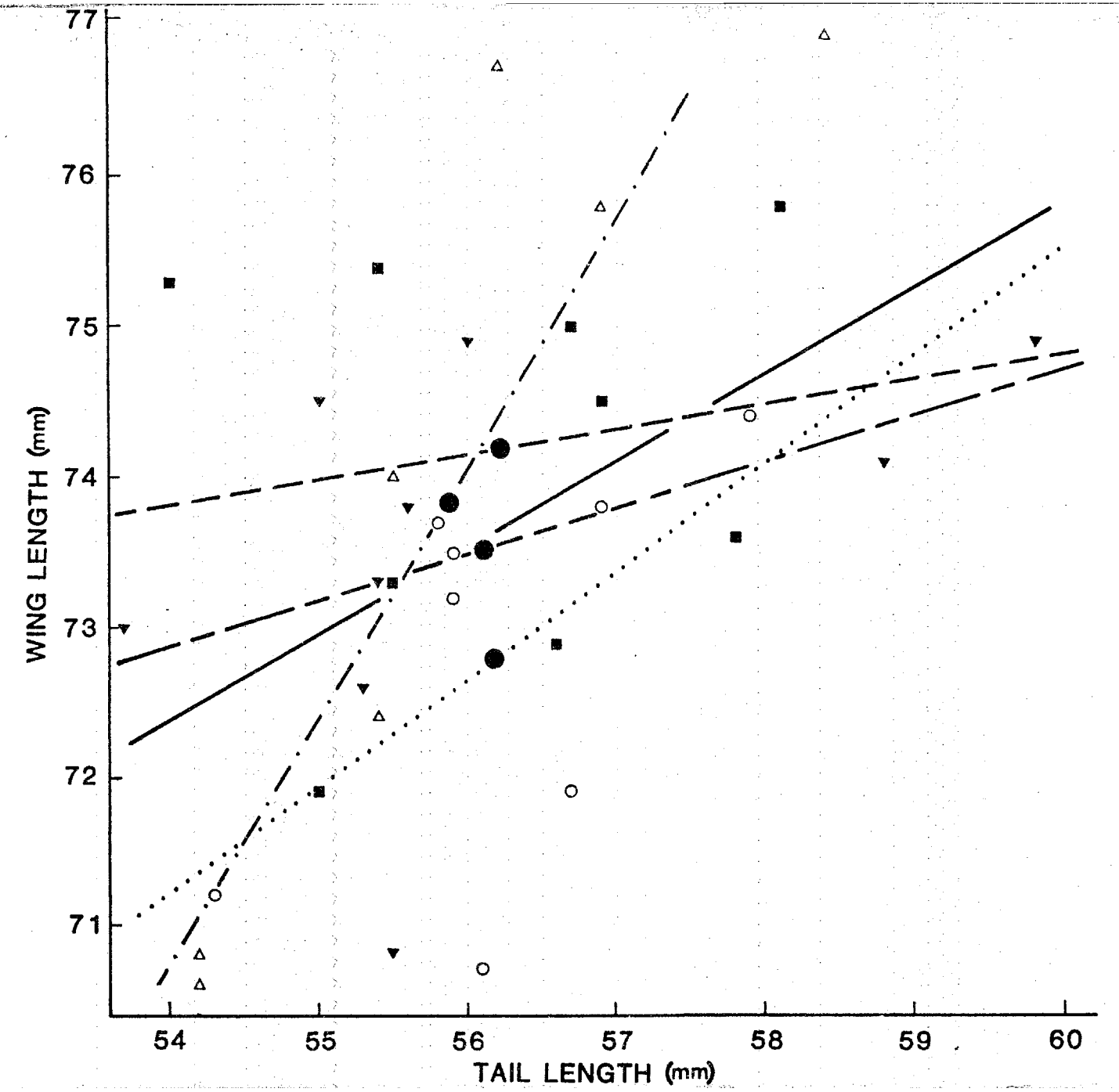

77
76
75
74
73
72
71
WING LENGTH (mm)
54
55
56
57
58
59
60
TAIL LENGTH (mm)

Table 5.7: Sexual dimorphism in size in house sparrows from Cairns, Townsville, Rockhampton and Adelaide.

(a) Combined data

Character	Mean difference[a] Absolute	Percentage
Wing length	2.32	3.15
Tail length	1.87	3.33
Bill length	-0.09	0.59
Tarsus length	0.16	0.91
Weight	0.21	0.79
Cube-root of weight	0.008	0.26

(b) Individual localities

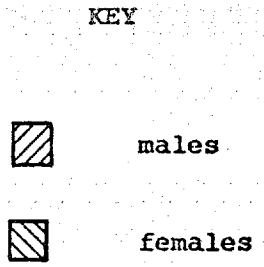
	Cairns		Townsville		Rockhampton		Adelaide	
Character	Abs	%	Abs	%	Abs	%	Abs	%
Wing	2.44	3.31	2.23	3.01	2.34	3.21	2.43	3.30
Tail	3.42	6.12	2.44	4.34	0.67	1.19	1.48	2.64
Bill	-0.20	-1.25	0.13	0.82	-0.20	-1.76	0.21	1.35
Tarsus	-0.23	-1.25	0.18	1.01	0.45	2.49	0.25	1.39
Weight	-0.09	-0.35	0.13	0.52	1.21	4.60	-0.39	-1.38
D^2	25.32		5.11		2.61		4.03	

[a]Absolute differences are male minus female; percentages are absolute difference divided by smaller mean.

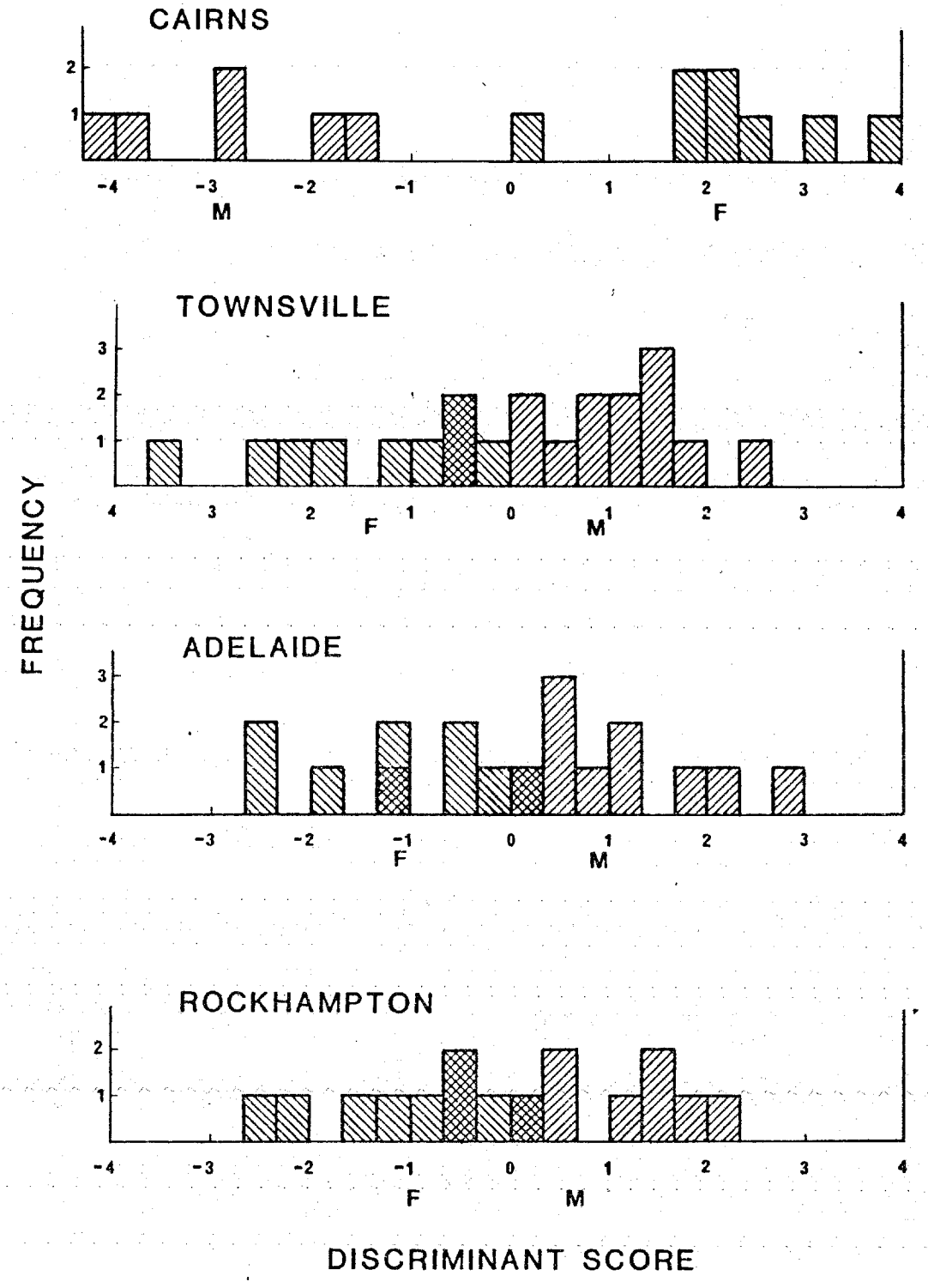
Table 5.8: Relative influence of linear variables in discriminating between males and females at different localities. Comparison of discriminant function coefficients.

	Cairns	Townsville	Rockhampton	Adelaide
Wing	1.564	0.628	1.000	0.981
Tail	-2.203	0.598	-	-
Bill	0.853	-0.364	-	0.365
Tarsus	-	0.480	-	-
% correctly classified	100	87.0	80.0	90.0

Figure 5.17 Histograms of discriminant scores, showing geographic variation of sexual dimorphism



"M" and "F" indicate mean discriminant scores for males and female respectively


CAIRNS
TOWNSVILLE
ADELAIDE
ROCKHAMPTON
FREQUENCY
DISCRIMINANT SCORE
M
F

5.3.3 Correlations with climatic variables -

(a) Seasonal correlations

Correlation coefficients between mean body weight and mean maximum and minimum temperatures for each month are shown in Table 5.9. For both Townsville and Adelaide, none of these correlations are significant.

(b) Geographic correlations

Correlations between the morphological variables and 12 climatic variables are shown in Table 5.10. For male body weight, wing length, bill length and tarsus length, and female wing length, tail length and tarsus length, none of the correlations was significant. Female body weight was significantly correlated with maximum winter and minimum summer temperatures only. Tail length in males was positively correlated with mean 3 p.m. relative humidity and negatively correlated with elevation. Female bill length was highly positively correlated with minimum and maximum summer temperatures, maximum winter temperature, and average maximum temperature, and negatively correlated with elevation.

Regressions of body weight (W=grams) on latitude (°L) had the equations $W=0.16°L + 22.6$ ($F=14.08$, 1x41 d.f., $p<0.01$) for males and $W=0.18°L+22.0$ ($F=18.98$, 1x32 d.f., $p<0.01$) for females. These equations were used to predict body weight at other latitudes for which banding data were available - comparisons are shown in Table 5.11. In all cases, predicted values were close to the values obtained from banding records.

(c) Sexual dimorphism

The Mahalanobis distance measure was highly correlated with rainfall and minimum winter temperature ($p<0.15$), indicating that

Table 5.9: Correlations between body weight and monthly climatic data[a]

	Townsville		Adelaide	
	Male	Female	Male	Female
Male	-	0.523	-	0.028
Female	0.523	-	0.028	-
Minimum	0.230	-0.139	-0.150	-0.476
Maximum	0.229	-0.222	-0.133	-0.486

[a]Townsville, weather data for June, 1982
Adelaide, from Bureau of Meteorology (1975)

Table 5.10: Correlation coefficients of linear variables, weight and Mahalanobis distance measure with climatic variables. Significant correlations are in bold face (n=4). Abreviations as per Table 2.1

(a) Males

	D^2	Weight	Wing	Tail	Bill	Tarsus
RAIN	0.899	-0.756	0.469	0.821	0.120	-0.238
MINW	0.835	-0.867	0.610	0.894	0.283	-0.427
MAXW	0.468	-0.834	0.190	0.510	-0.129	-0.165
MINS	0.443	-0.861	0.228	0.525	-0.083	-0.217
MAXS	0.314	-0.648	-0.105	0.244	-0.403	0.100
HUM9	0.727	-0.514	-0.027	0.430	-0.386	0.227
HUM3	0.758	-0.842	0.887	0.997	0.660	-0.726
AMIN	0.608	-0.903	0.381	0.687	0.051	-0.307
AMAX	0.383	-0.760	0.054	0.384	-0.255	-0.051
LATIT	-0.571	0.861	-0.280	-0.607	0.054	0.214
LONGIT	0.013	-0.400	-0.406	-0.104	-0.626	0.320
ELEV	-0.687	0.940	-0.819	-0.956	-0.569	0.712

(b) Females

	Weight	Wing	Tail	Bill	Tarsus
RAIN	-0.659	0.439	-0.739	0.752	0.655
MINW	-0.725	0.600	-0.640	0.757	0.494
MAXW	-0.960	0.257	-0.220	0.995	0.257
MINS	-0.974	0.300	-0.186	0.991	0.207
MAXS	-0.903	-0.030	-0.098	0.980	0.251
HUM9	-0.651	-0.043	-0.603	0.836	0.728
HUM3	-0.528	0.866	-0.587	0.469	0.294
AMIN	-0.926	0.426	-0.363	0.948	0.322
AMAX	-0.949	0.128	-0.145	0.999	0.236
LATIT	0.935	-0.329	0.329	-0.975	-0.332
LONGIT	-0.776	-0.311	0.163	0.859	0.092
ELEV	0.703	-0.831	0.468	-0.634	-0.216

Table 5.11: Predicted body weight for various localities, compared with actual weight obtained from banding schedules

	Predicted		Actual for May-July (sample-size indicated)	
	M	F	M	F
Sydney (34°S)[a]	28.0	28.1	26.6 (4)	-
Mount Nelson, Tas. (43°S)[b]	29.5	29.7	30.7 (2)	29.4 (1)
Hobart, Tas. (43°S)[c]	29.5	29.7	28.4 (5)	27.1 (7)
Canberra (35.3°S)[d]	28.2	28.4	28.3 (4)	-

[a] from specimens in Australian Museum
[b] J.G.K. Harris (unpublished data - A.B.B.S.)
[c] N. Tolman (unpublished data - A.B.B.S.)
[d] R.A. Tilt (unpublished data - A.B.B.S.)

sexual dimorphism is greater from areas with warmer winters and higher rainfall.

5.4 Discussion

5.4.1 Seasonal variation -

(a) Body weight

Seasonal weight changes in house sparrows from Townsville and Adelaide are compared in Figure 5.18 with weight changes in English birds (Oxford: O'Connor, 1973). House sparrows in England gained weight progressively from mid-summer to mid-winter due to increased fat storage on the body. Males lost weight in mid-autumn and spring as a result of decreasing fat reserves; this decrease was due to increased sexual displays and growth of reproductive organs. In females, spring weight loss resulting from the decrease in fat reserves was more or less offset by the increase in size of the ovary and oviduct as breeding commenced; females lost weight in autumn since the gonads did not develop during this period - even though the birds were involved in sexual displays and nest-building.

House sparrows in Adelaide followed this general pattern of weight variation; however, there were some differences: (1) in Adelaide, male sparrows did not gain weight in winter - during this period they dropped to their minimum weight for the year; (2) variation in female weight over the year was greater in Adelaide than at Oxford; (3) females reached their maximum weight in mid-winter in Adelaide rather than in early autumn. While data collected in Townsville do not yet include the summer months, the pattern of weight variation followed here was similar to that in

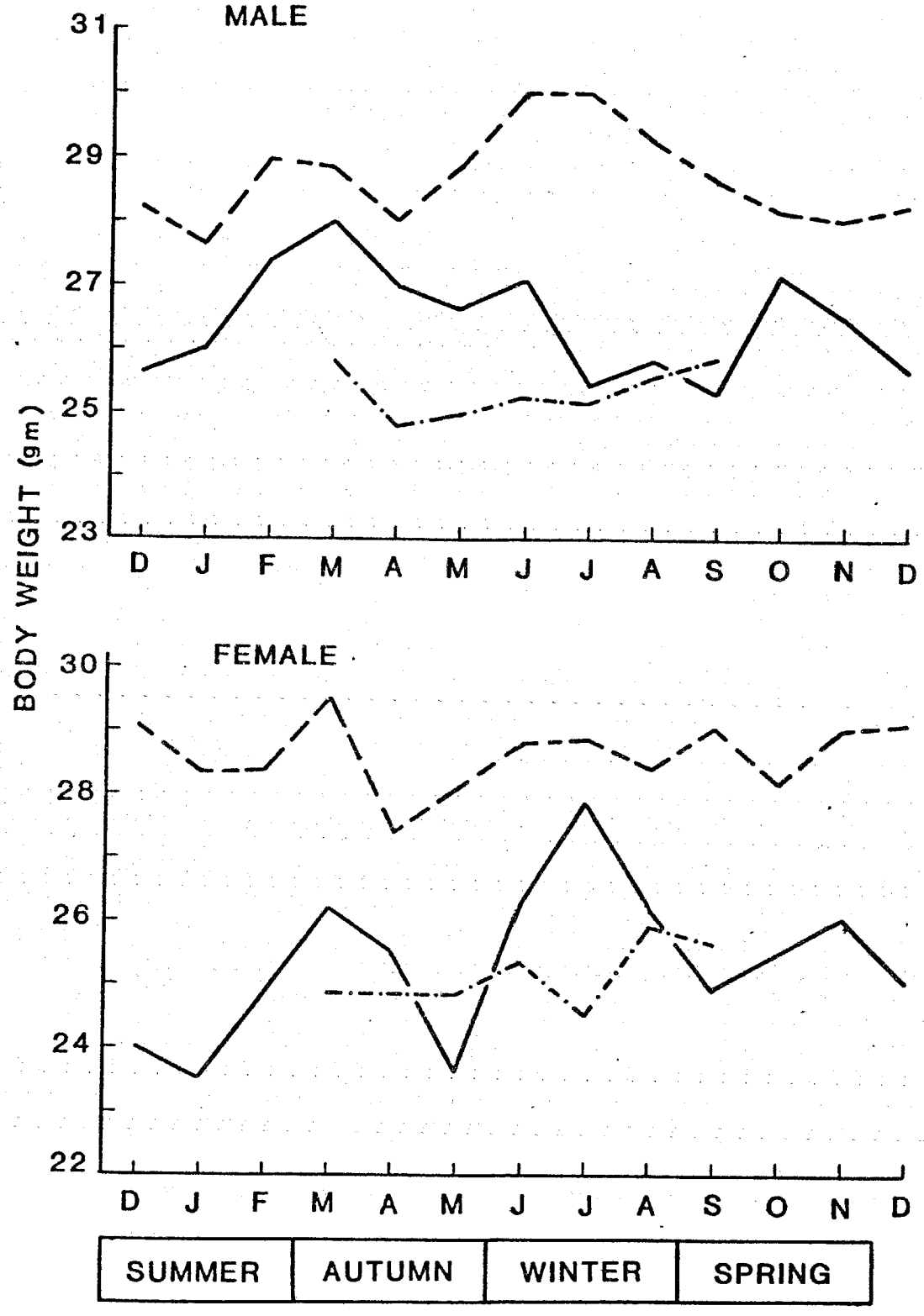
Figure 5.18 Comparison of seasonal variation of body weight in Townsville with that in temperate regions

Localities:

— — Oxford, England (O'Connor, 1973)

——— Adelaide (Jenkin, unpublished data)

—·— Townsville


MALE
31
29
27
25
23
BODY WEIGHT (gm)
D J F M A M J J A S O N D
FEMALE
30
28
26
24
22
D J F M A M J J A S O N D
SUMMER
AUTUMN
WINTER
SPRING

Adelaide; however, there was less variation between the months in Townsville than in temperate areas. In spring, birds from Townsville and Adelaide were similar in weight, but the weights in England were always larger than those found in Australian birds.

The degree of sexual dimorphism displayed by English birds varied throughout the year. From late autumn to early spring males were heavier than females; however, at other times of year females were heavier than males. In Adelaide, males were heavier than females for 10 months of the year, females becoming heavier in late winter and early spring. In Townsville, the sexes were almost identical in weight from mid-autumn to early spring, but males were slightly heavier in early autumn, indicating that annual variation in weight in Townsville sparrows may follow the same pattern as in Adelaide. The low correlation between body weight and average monthly temperature in Australian house sparrows suggests that the Australian populations for which adequate data are available are not subjected to the low temperatures required for the production of large amounts of insulative body fat.

(b) Feather variables

Seasonal variation in wing length of birds from Townsville and Hobart (Tolman, unpublished data) is compared in Figure 5.19 with that of house sparrows in Czechoslovakia (Folk and Novotny, 1970). These data indicate that the wing remiges developed until the end of winter, attaining their maximum length in early spring. In subsequent months, the remiges were gradually worn off at the tips, this process culminating at the end of summer when the mean wing length attained the minimum value. During this period the males started to moult and their average wing length increased as new

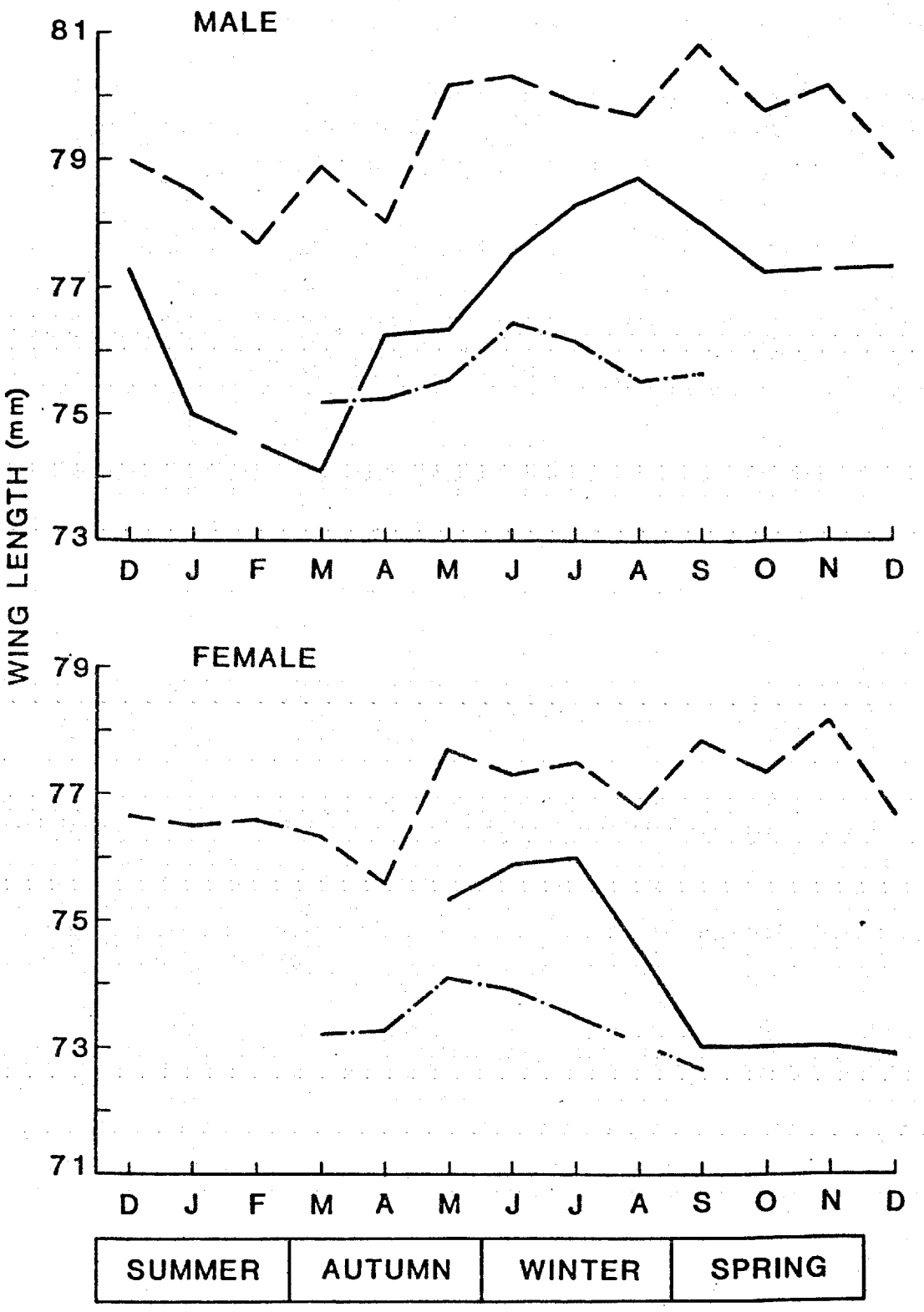
Figure 5.19 Comparison of seasonal variation of wing length between localities

Localities:

— — Czechoslovakia (Folk and Novotny, 1970)

——— Hobart (Tolman, unpublished data)

— · — Townsville


MALE
81
79
77
75
73
WING LENGTH (mm)
D J F M A M J J A S O N D
FEMALE
79
77
75
73
71
D J F M A M J J A S O N D
SUMMER
AUTUMN
WINTER
SPRING

remiges grew. The wing length of females decreased rapidly during the breeding season (spring) due to their remiges becoming damaged by incubation. After breeding there was a slight decrease until mid-autumn when the minimum was reached. The primary feathers were replaced by late autumn and the wing length increased abruptly. Females were thus about a month behind males in moulting.

Australian house sparrows followed this pattern closely, though female wing lengths decreased earlier in the year than did those in Czechoslovakia. In Townsville, wing length decreased from June in both sexes - two months earlier than in Hobart.

Tail length in Hobart and Townsville sparrows followed similar trends to those shown by wing length. In Hobart (Figure 5.20), tail moult of males began in February and by June the rectrices had reached their maximum length. During spring there was a slight decrease in length, but it was not until February that tail length decreased significantly as feathers were dropped and moult occurred. In contrast, the tail length of females decreased soon after June and by December had dropped by 10% due to wear occurring during incubation. As for the cycle of wing moult, Townsville birds were one or two months ahead of Hobart birds in the tail moult cycle.

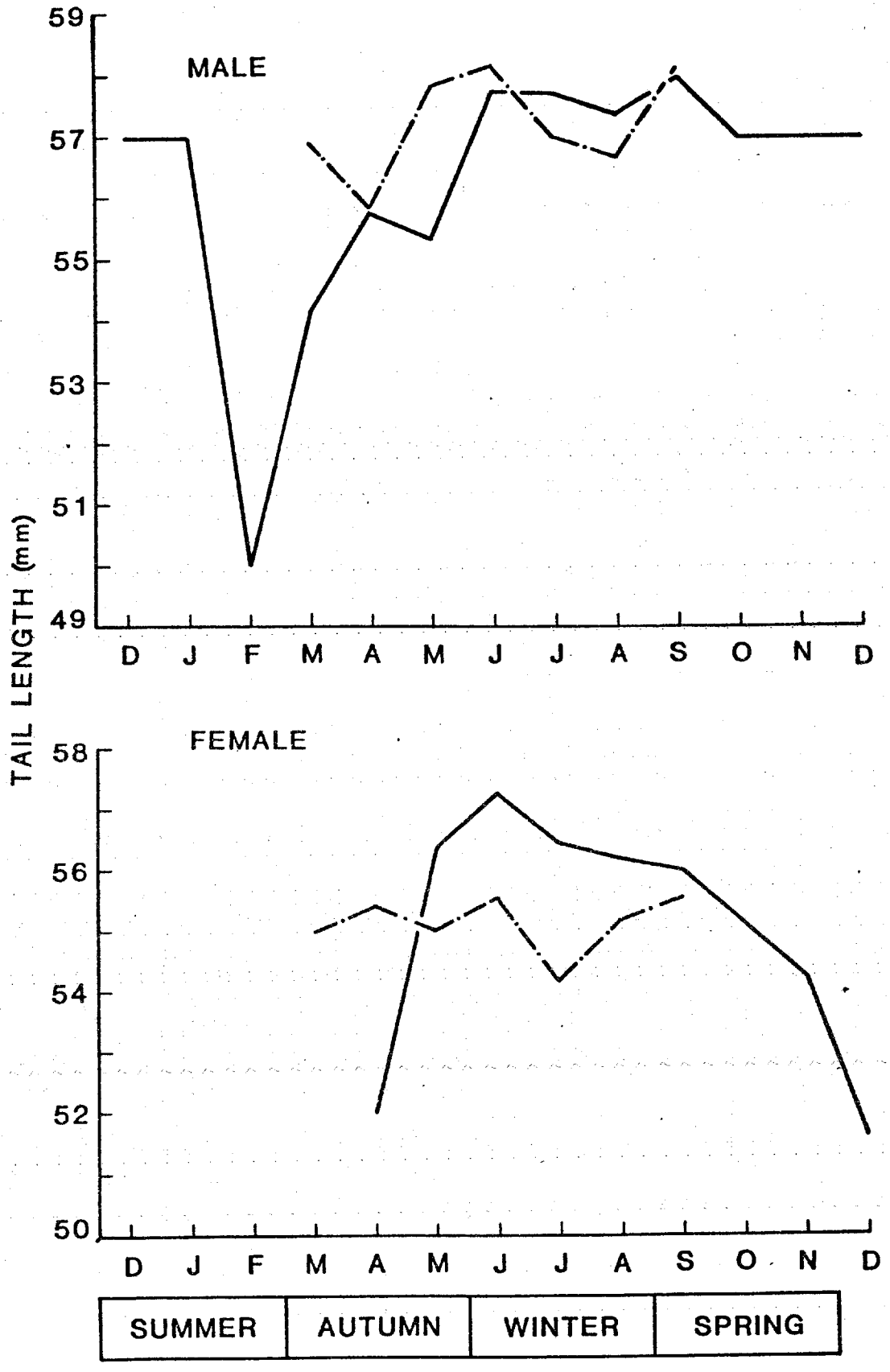
Summers-Smith (1963) states that the annual moult of house sparrows in England occurs mainly in the period July to mid-October (mid-summer to mid-autumn), a period corresponding to January to mid-April in Australia. The data presented here suggest that sparrows in tropical Australia moulted in January and February, while those in temperate Australia moulted from February. In southern Australia the last clutches of eggs for the breeding season were laid in late December and early January. Therefore, the

Figure 5.20 Comparison of seasonal variation of tail length between localities

Localities:

——— Hobart (Tolman, unpublished data)

—·— Townsville


MALE
FEMALE
TAIL LENGTH (mm)
59
57
55
53
51
49
58
56
54
52
50
D J F M A M J J A S O N D
SUMMER
AUTUMN
WINTER
SPRING

parents were not free of the young until the end of January, and moult was delayed until then. In Townsville, the heavy rainfall experienced in December and January may curtail the breeding season and cause an early moult. Many studies of avian reproductive periods do, in fact, emphasize that breeding stops during or begins after that part of the year when the rains are the heaviest (Moreau, 1950; Thomson, 1950; Voous, 1950), and studies in tropical India indicate that the house sparrow there ceases all reproductive activity during the period of monsoons in December and may begin again for a short period in February (Naik and Mistry, 1973).

New feathers produced at the moult serve to reduce the extent of male markings on the body. The reduction of these markings has been recorded from Europe (Summers-Smith, 1963) and North America (Selander and Johnston, 1967) and may be important in reducing the level of inter-male aggression at a time of year when strong social ties are important.

(c) Bill length

The house sparrow and many other birds that are largely granivorous in the winter and insectivorous in the summer exhibit seasonal changes in bill length resulting from variation in the rate of wear experienced by the constantly growing horny tip. In samples of sparrows from California, Davis (1954) found that mean bill length varied significantly throughout the year; bill length was significantly greater from late spring to mid-summer than in winter. In Germany, Steinbacher (in Selander and Johnston, 1967) found a 10% increase in bill length through the summer. Bill length remained almost constant from autumn to spring, and had lower variance in this period than in the summer. Seasonal variation was greater in

females than in males. Variation in Townsville over the whole year is probably less than that in temperate areas since insects remain a part of the diet for longer periods.

5.4.2 Geographic variation -

An obvious problem with examining geographic variation of the house sparrow over a small number of localities is that the whole range of environments in which it is found are not represented, and any geographic trends in house sparrow size and proportions may not be revealed. However, the specimens came from a large enough range over Australia to provide a basis on which to compare the variability and geographic variation of house sparrows in Australia with those in North America and Europe.

That house sparrows in Australia have undergone significant differentiation in body size is shown by the clinal variation in body weight, since body weight is a good indicator of general size (Amadon, 1943), provided that weights are taken from specimens collected at the same time of year. Since all samples used here were collected in June and July, the seasonal changes shown in Section 5.3.1 do not need to be accounted for.

The regression of body weight on latitude exemplifies the ecogeographic rule of Bergmann, which describes adaptive trends in body size as they relate to problems of heat flow and temperature regulation (Mayr, 1963). Johnston and Selander (1964) found that a regression of male body weight on latitude had the equation W=24.1 + 0.12°L for localities north of southern Texas (25°N); this equation is in agreement with the regression obtained in Section 5.3.2. In Europe, the regressions of weight on latitude are: W=16.2 + 0.29°L

(males) and W = 16.8 + 0.26°L (females) (Pinowski and Myrcha, 1977). These regressions are slightly different from those found in Australia and North America. Body weight shows more latitudinal variation in Europe than in North America and Australia (Table 5.12).

Since body weight varies seasonally and throughout the day (Pinowski and Myrcha, 1977), most studies on the validity of Bergmann's rule for birds use wing length as an indication of general body size, since "wing load" necessitates a fairly close correlation between wing length and body weight (Mayr, 1956). In the sample examined here, variation in wing length between localities was not highly significant. In males, 11.4 per cent of the variability was due to locality effects; in females only 0.5 per cent was attributable to locality (Table 5.2). Similarly, tarsus and bill lengths and female tail length showed only small amounts of variability which were attributable to locality. The small amount of geographic variation in tail and wing lengths is ordered in the opposite direction to body weight and agrees with the "latitude effect" described by Snow (1954): "with the same winter temperatures, wing length tends to be greater at lower latitudes than it is at higher latitudes" (p.21). This effect is generally hidden when a large number of localities are used in studies of geographic variation, and is implicated here since the four localities sampled have minimum winter temperatures of about the same value (Table 2.1).

Measures of interlocality variability in North American house sparrows have approximately the same values as those found in Australia (Johnston and Selander, 1971, 1973); however, these

Table 5.12: House sparrow body weights at various latitudes in Australia, North America (Johnston and Selander, 1964) and Europe (Pinowski and Myrcha, 1977)

Latitude	Australia		North America	Europe	
(°N or S)	M	F	M	M	F
10	24.2	23.8	25.3	19.1	19.4
20	25.8	25.6	26.5	22.0	22.0
30	27.4	27.4	27.7	24.9	24.6
40	29.0	29.2	28.9	27.8	27.2
50	30.6	31.0	30.1	30.7	29.8
60	-	-	-	33.6	32.4

measures are less than for European birds. Johnston and Selander (1973) found that wing length, tail length and bill length were especially constrained in geographic variation in American samples. A possible cause for such modest interlocality variability is that there was a restriction on available variability in the birds making up the inoculum samples of the 1860s. Such a restriction could be due to low variance in the inocula, owing to chance trapping effort (the Founder effect - Mayr, 1940), or to restricted variation in the source itself (low variance in the populations from which the inocula originated). Since the number of sparrows introduced in the 1860s was in the hundreds (Ryan, 1906), and came from only a few localities in England, the latter is more likely.

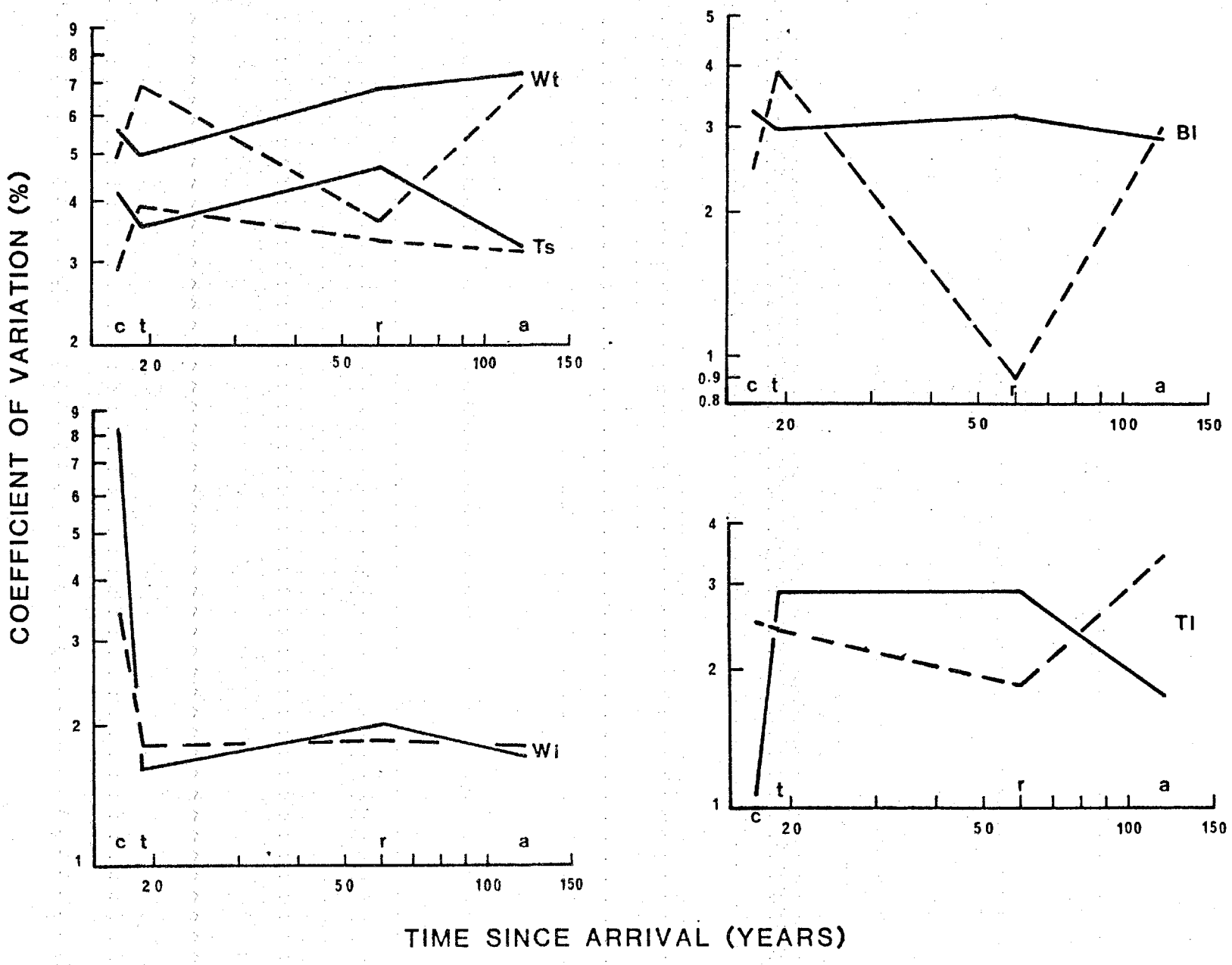
While interlocality variation is smaller in Australia and North America than in Europe, the average levels of interpopulation variability are approximately the same. Comparison of samples of Australian sparrows with those from England and North America (Tables 5.2 and 5.13) reveal no differences in average level of intrapopulation variability. Lack (1940) found no greater variability in wing length and bill length in North American house sparrow populations than those in England and Germany (a further source of North American introductions) and concluded that, if there was a phase of increased variability following introduction then it was confined to a brief period when the populations were rapidly expanding and adapting to new environmental conditions. Coefficients of variation of the linear measures and body weight are plotted in Figure 5.21 against the length of time since initial colonisation for each locality. The wing length of sparrows in Cairns (colonised 1964) had high coefficients of variation while

Table 5.13: Intrapopulation variability in size in house sparrows from North America (including the Hawaiian Islands and Bermuda) and England (from Selander and Johnston, 1967)

Character	Mean coefficient of variation	
	Males	Females
(1) Wing length		
North America	1.88	1.88
England	2.28	1.90
(ii) Tail length		
North America	2.60	2.80
Europe	2.54	2.44
(iii) Bill length		
North America	3.79	3.87
England	3.62	4.41
(iv) Tarsus length		
North America	3.62	3.68
England	3.62	4.41
(v) Body weight		
North America	5.82	5.96
Europe	6.01	5.92

Figure 5.21 Change in coefficient of variation of measured characters with time since arrival at locality.

Wt - body weight
Wi - wing length
Tl - tail length
Bl - bill length
Ts - tarsus length


COEFFICIENT OF VARIATION (%)
Wt
Ts
Bl
Wi
Tl
c t
r
a
20
50
100
150
TIME SINCE ARRIVAL (YEARS)

birds in other localities had coefficients which were lower - though, as shown in Table 5.3, this difference was not significant. Coefficients of variation of weight and tail length increased with time after introduction, while tarsus length and bill length remained relatively constant. Females from Rockhampton were unusual in having a coefficient of variation of bill length of less than one per cent. The relationship between variability in the population and the time it has been established requires further study, particularly in populations at the expanding edge of the species' range.

The homogeneity of correlation coefficients between the different localities indicates that the same characters tended to covary in each population. Using 18 localities and larger sample sizes, Selander and Johnston (1967) found that all character pairs were significantly correlated, with the strongest correlations between wing length and tail length. In Australian sparrows, the strongest correlations were between body weight and tarsus length, and between wing length and tail length for each sex. While the same pairs of characters tended to covary at each locality, the regression equations varied from locality to locality as shown in Figure 5.16 for females. Figure 5.15 crudely shows geographic variation in feather length in males and indicates that the relationship between wing length and tail length for males was similar for the four localities. In this case, a regression analysis using locality means yielded a similar result to that using individual measurements. In contrast, the heterogeneity in the female sample resulted in a different regression equation since tail length in females did not vary geographically.

Intersexual correlations and regressions of locality means (Figure 5.14) show that for body weight and wing length the size of females can be predicted from that of males and vice versa with some accuracy. Because female tail length does not vary geographically there is poor intersexual correlation between the locality means for this character. Similarly, bill length and tarsus length covariation between the sexes is minimal since geographic variation is non-significant and the variation present is ordered in a random fashion (Figures 5.12 and 5.13). House sparrows from North America (Selander and Johnston, 1967) had significant intersexual correlations for each character.

The average level of sexual dimorphism in size calculated for Australian sparrows closely approximated that of North American sparrows (Selander and Johnston, 1967); males are 2-3% larger than females in body weight and feather length characters, similar in size of bill and about 1% larger than females for tarsus length.

Sexual dimorphism in body parts may be attributed to Darwinian sexual selection (Johnston and Selander, 1973); sexual differences in wing length and tail length relative to body mass are presumably related to behavioural differences. The long term maintenance of sexual dimorphism in size appears to be largely genetic in birds (Lande, 1980) and any changes in the amount of dimorphism between locality samples are therefore the result of adaptation to local conditions. However, because size is a polygenic character (including both sex-linked and autosomal loci), there is a tendency for a significant part of each new generation to be of intermediate size relative to parents (Falconer, 1960). Johnston and Selander (1973) found that significant sexual dimorphism did occur in house

sparrows of high and mid-latitude populations and that this sexual dimorphism became stronger after periods of high mortality in winter. Johnston and Fleischer (1981) demonstrated that intraspecific fighting for feeding rights was probably responsible for a frequency-dependent mortality pattern that significantly enhanced the degree of sexual size dimorphism in a population. Because the severity of winter varies geographically sexual size dimorphism is also expected to vary in this way. Greater dimorphism is thus expected in sparrows at higher latitudes with vigorous winters and lesser sexual differences at lower latitudes; this holds for North American and European populations but not for those from South America (Johnston and Selander, 1973). In the samples collected in Australia sexual dimorphism is larger in sparrows from the tropics and smaller in the temperate localities; this is similar to the pattern found in the South American samples of Johnston and Selander (1973). The small sexual differences found in Rockhampton sparrows is probably due to the fact that the sample was collected from around a zoological garden where food was plentiful throughout winter. Colder than normal winters in Cairns and Townsville in 1982 (Chapter Two) may have contributed to the high level of sexual dimorphism found in sparrows from these localities.

Bill length and tarsus length were the only variables of those measured that did not exhibit conspicuous geographic or sexual variation. However, these characters are also the features which are most variable between individuals within populations (Table 5.2); this variability is closely tied to width of feeding niche (Rothstein, 1973). Hamilton and Johnston (1978) found that while bill size was not subject to conspicuous geographic variation in

mean value, the variance of bill size over the sample localities was correlated significantly with latitude if the sexes were combined; they related reduction of variance at low latitudes to increased competition (and therefore decreased niche width). At higher latitudes competition was reduced and the variance of bill size increased, indicating an increase in niche width. In the Australian samples, the correlation between variance of bill length and latitude was not significant ($r=-0.115$, 2 d.f., $p>0.05$). In addition, variances of bill length were homogeneous for the samples suggesting that niche widths of Australian house sparrows in winter were the same at each locality. Intrapopulation coefficients of variation of bill length in Australian house sparrows were less than those in North American house sparrows (Selander and Johnston, 1967) but were about the same as those found by Baker (1980) in New Zealand stocks. This lowered amount of variation is probably the result of a genetically restricted founding stock.

CHAPTER SIX

GENERAL DISCUSSION

The foregoing discussions and studies of the house sparrow in other parts of its range have revealed that it is a most "adaptable" bird. Several aspects of this adaptability are characteristic of colonising species in general (Mayr, 1965). However, the house sparrow and other commensal granivores have characteristics which have allowed them to expand their ranges dramatically with the spread of man from the centres of indigenous agriculture (Johnston and Klitz, 1977). Specific characteristics of the house sparrow as a colonising bird species include:

(1) The basic evolutionary adjustment of associating with man in a commensal relationship; this relationship has allowed the house sparrow to follow man gradually to new areas of the world without regard for the natural habitat of the region.

(2) The capacity for complex size adaptation. Significant north-south clinal variation occurs in Australia, North America and Europe, though the selective agencies of this variation are not yet understood. This size adaptation represents adaptation to local climatic conditions.

(3) The capacity for rapid character modification. Large variance in character variables permits rapid response to selection for change in size, proportions etc. Populations of house sparrows in Australia and North America have only half as much interlocality variance as the European

populations, but this variability has developed in about 130 years, a much shorter period than the 10000 years since house sparrows moved into western Europe with man.

(4) The capacity for long-distance dispersal. Populations of house sparrows produce individuals which are capable of moving away from their birth-place. This inherent ability for dispersal means that new habitat is being regularly monitored.

With the combination of these factors and the additional assistance of deliberate transport by man the house sparrow has now become widespread from the tropics to the Arctic Circle in Eurasia and its range is gradually expanding to these regions in North America. In Australia and New Zealand, the house sparrow is found from the southern-most to the northern-most points. Clearly, the sparrow is subjected to a wide variety of climatic conditions and must have needed to adapt to these climates as it followed its host into them.

The slow rate of spread into the tropical regions of Australia suggests that the house sparrow did require some time before it became adapted to the conditions encountered there. However, movement into the tropics generally requires few physiological changes for birds since the thermoregulatory devices which evolved with flight were developed in this region (King and Farner, 1964). The major thermoregulatory problems encountered by house sparrows in the tropics would be heat-induced, rather than cold-induced, and the common mechanisms such as panting, gular fluttering and temporary hyperthermia are adequate for coping with these problems. These are augmented by a battery of behavioural thermoregulatory devices as

described in Section 4.4.3. In a study of latitudinal trends in the metabolic adjustments of the house sparrow over its range in North America, Kendeigh and Blem (1974) concluded that "there is no reason, as far as bioenergetics is concerned, why the house sparrow should not eventually spread through the American subtropics and tropics" (p.185).

The delay in reaching North Queensland from the south may also be explained by movement of the house sparrow inland rather than along the coastal route (Chapter Three), though the reasons for this inland movement and the sudden rapid spread throughout the region would require further study.

Long-term studies of the population dynamics of the house sparrow in tropical regions would also prove useful in filling in some of the gaps in our knowledge of a bird species which has supplied much needed information on the evolution, population dynamics and physiology of birds in general.

BIBLIOGRAPHY

Aldrich, J.W. and J.S. Weske. 1978. Origin and evolution of the eastern house finch population. *Auk.* **95**: 528-536.

Alexander, W.B. 1958. The spread of the sparrow. *Emu.* **58**: 335-336.

Amadon, D. 1943. Bird weights as an aid in taxonomy. *Wilson Bull.* **55**: 164-177.

Amoroso, E.C. and F.H.A. Marshall. 1960. External factors in sexual periodicity, in A.S. Parkes (Ed.). *Marshall's Physiology of Reproduction*, vol. 1, part 2. pp. 707-831. Longmans, London.

Aschoff, J. and D. von Holst. 1960. Schlafplatzflüge der Dohle, *Corvus monedula* L. *Proc. 12th Intern. Ornith. Congr., Helsinki.* p. 55.

Ashford, R.W. 1978. First record of house sparrow for Papua New Guinea. *Emu.* **78**: 36.

Baker, A.J. Morphometric differentiation in New Zealand populations of the house sparrow (*Passer domesticus*). *Evolution.* **34**: 638-653.

Baker, A.J. and A. Moeed. 1979. Evolution in the introduced New Zealand populations of the common myna, *Acridotheres tristis*. *Can. J. Zool.* **57**: 570-584.

Baker, J.R. 1938. The relationship between latitude and breeding seasons in birds. *Proc. Zool. Soc. London.* 108: 557-582.

Barrows, W.B. 1889. *The English Sparrow (Passer domesticus) in North America*. U.S. Dept. of Agriculture. Washington.

Beimborn, D.A. 1967. *Population ecology of the English sparrow in North America*. M.S. Thesis, Univ. of Wisconsin at Milwaukee.

Bravery, J.A. 1970. Birds of the Atherton Shire, Queensland. *Emu.* **70**: 49-63.

Bureau of Meteorology. 1975. *Climatic Averages, Australia*. Metric Edition. Aust. Govt. Publ. Serv., Canberra.

Calhoun, J.B. 1947. The role of temperature and natural selection in relation to the variations in size of the English sparrow in the United States. *Am. Nat.* **81**: 203-228.

Cameron, R.J. 1982. *Year Book, Australia*. No. 66, 1982. Australian Bureau of Statistics, Canberra.

Caughley, G. 1977. *Analysis of Vertebrate Populations*. John Wiley and Sons, London.

Chisholm, A.H. 1919. Introduced birds in Queensland. *Emu*. *14*: 126-134.

Chisholm, A.H. 1926. Editor's note. *Emu*. *25*: 277.

Chisholm, E.C. 1926. Birds introduced into New South Wales. *Emu*. *25*: 276-279.

Christian, C.S., S.J. Paterson, R.A. Perry, R.O. Slatyer, G.A. Stewart and D.M. Traves. 1953. Survey of the Townsville - Bowen region, North Queensland, 1950. *C.S.I.R.O. Land Res. Series*. *2*: 1-87.

Condon, H.T. 1962. A handlist of the birds of South Australia. *South Australian Ornithologist*. *23*: 86-151.

Counsilman, J.J. 1974. Waking and roosting behaviour of the Indian myna. *Emu*. *74*: 135-148.

Dang, H.R. and S.S. Guraya. 1978. Testis growth and regression in harmful birds in the Punjab in relation to some environmental factors. *Aust. J. Zool*. *26*: 39-45.

Darlington, P.J., Jr. 1957. *Zoogeography: the geographic distribution of animals*. John Wiley and Sons, New York.

Davis, J. 1954. Seasonal changes in bill length of certain passerine birds. *Condor*. *56*: 142-149.

Dyer, M.I., J. Pinowski and B. Pinowska. 1977. Population dynamics, in Pinowski, J. and S.C. Kendeigh (Eds.). *Granivorous birds in ecosystems. International Biological Program 12*. pp. 53-105. Cambridge University Press, Cambridge.

Falconer, D. 1960. *Introduction to Quantitative Genetics*. Oliver and Boyd, Edinburgh.

Folk, C. and I. Novotny. 1970. Variation in body weight and wing length in the house sparrow, *Passer domesticus* (L.), in the course of a year. *Zoologicke Listy*. *19*: 333-342.

Frith, H.J. and J.L. McKean. 1975. Races of the spotted turtledove, *Streptopelia chinensis* (Scopoli), in Australia. *Aust. J. Zool*. *23*: 295-306.

Gill, H.B. 1970. Birds of Innisfail and hinterland. *Emu*. *70*: 105-116.

Grinnell, J. 1919. The English sparrow has arrived in Death Valley: an experiment in nature. *Am. Nat*. *43*: 468-473.

Guthrie, T.H. 1971. House sparrows crossing the Tweed River. *Aust. Bird-Watcher*. *4*: 77-78.

Hamilton, S. and R.F. Johnston. 1978. Evolution in the house sparrow. VI. Variability and niche width. *Auk.* **95**: 313-323.

Hammer, M. 1948. Investigations on the feeding habits of the house sparrow (*Passer domesticus*) and the tree sparrow (*Passer montanus*). *Dan. Rev. Game Biol.* **1**: 1-59.

Horton, H. 1976. *Around Mount Isa.* University of Queensland Press, St. Lucia.

Jenkins, C.F.H. 1959. Introduced birds in Western Australia. *Emu.* **59**: 201-207.

Johnston, R.F. 1976. Estimating variation in bony characters and a comment on the Kluge-Kerfoot Effect. *Occ. Pap. Mus. Nat. Hist., Univ. of Kansas.* **53**: 1-8.

Johnston, R.F. and R.C. Fleischer. 1981. Overwinter mortality and sexual size dimorphism in the house sparrow. *Auk.* **98**: 503-511.

Johnston, R.F. and W.J. Klitz. 1977. Variation and evolution in a granivorous bird: the house sparrow, in Pinowski, J. and S.C. Kendeigh (Eds.). *Granivorous birds in ecosystems. International Biological Program 12.* pp. 15-51. Cambridge University Press, Cambridge.

Johnston, R.F. and R.K. Selander. 1964. House sparrows: rapid evolution of races in North America. *Science.* **144**: 548-550.

Johnston, R.F. and R.K. Selander. 1971. Evolution in the house sparrow. II. Adaptive differentiation in North American populations. *Evolution.* **25**: 1-28.

Johnston, R.F. and R.K. Selander. 1973. Evolution in the house sparrow. III. Variation in size and sexual dimorphism in Europe and North and South America. *Am. Nat.* **107**: 373-390.

Kalmbach, E.R. 1940. Economic status of the English sparrow in the United States. *U.S. Department of Agriculture, Technical Bulletin.* **711**.

Keast, A. 1959. The Australian environment, in Keast, A., R.L. Crocker and C.S. Christian (Eds.) *Biogeography and ecology in Australia.* Junk, The Hague.

Kendeigh, S.C. 1969. Tolerance of cold and Bergmann's rule. *Auk.* **86**: 13-25.

Kendeigh, S.C. and C.R. Blem. 1974. Metabolic adaptation to local climate in birds. *Comp. Biochem. Physiol. A.* **48**: 175-187.

Keve, A. 1976. Some remarks on the taxonomic position of the tree sparrow introduced into Australia. *Emu*. *76*: 152-153.

Kikkawa, J. and Y. Yamashina. 1966. Breeding of introduced black swans in Japan. *Emu*. *66*: 377-381.

King, J.R. and D.S. Farner. 1964. Terrestrial animals in humid heat: birds, in *Handbook of Physiology*, Section 4. pp. 603-624 American Physiological Society, Washington.

Lack, D. 1940. Variation in the introduced English sparrow. *Condor*. *42*: 239-241.

Lack, D. 1947. The significance of clutch-size, parts 1 and 2. *Ibis*. *89*: 302-352.

Lack, D. 1948. The significance of clutch-size, part 3. *Ibis*. *90*: 24-45.

Lande, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution*. *34*: 292-307.

Lavery, H.J. and P.M. Johnson. 1968. Mammals and birds of the Townsville district, North Queensland. 2. Birds. *Qld. J. Agric. Anim. Sci*. *25*: 243-254.

Lavery, H.J., D. Seton and J.A. Bravery. 1968. Breeding seasons of birds in north-eastern Australia. *Emu*. *68*: 133-147.

Lofts, B. and R.K. Murton. 1973. Reproduction in birds, in Farner, D.S. and J.R. King (Eds.). *Avian Biology*, vol. 3. pp. 1-107. Academic Press, New York.

Long, J.L. 1972. Introduced birds and mammals in Western Australia. *Agric. Prot. Board, West. Aust. Tech. Ser*. *1*: 1-30.

Long, J.L. 1981. *Introduced birds of the World*. Reed, Sydney.

MacMillan, B.W.H. 1981. Food of house sparrows and greenfinches in a mixed farming district, Hawkes Bay, New Zealand. *N.Z. J. Zool*. *8*: 93-104.

Mayr, E. 1940. Speciation problems in birds. *Am. Nat*. *74*: 249-278.

Mayr, E. 1956. Geographical character gradients and climatic adaptation. *Evolution*. *10*: 105-108.

Mayr, E. 1963. *Animal Species and Evolution*. Harvard Univ. Press, Cambridge, Mass.

Mayr, E. 1965. The nature of colonization in birds, in Baker, H.G. and G.L. Stebbins (Eds.) *Genetics of Colonizing Species*. Academic Press, New York.

Moreau, R.E. 1931. An Egyptian sparrow roost. *Ibis. Ser. 13. 1*: 204-208.

Moreau, R.E. 1950. The breeding seasons of African birds, 1. Land birds. *Ibis. 92*: 223-267.

Naik, R.M. and L. Mistry. 1973. Breeding season and reproductive rate of *Passer domesticus* (L.) in Baroda, India, in Kendeigh, S.C. and J. Pinowski (Eds.). *Productivity, population dynamics and systematics of granivorous birds*. pp. 133-140. PWN - Polish Scientific Publishers, Warszawa.

Nautical Almanac, 1982. H.M.S.O., London.

Nero, P.W. 1951. Pattern and rate of cranial "ossification" in the house sparrow. *Wilson Bull. 63*: 84-88.

Nie, N.H., C.H. Hull, J.G. Jenkins, K. Steinbrenner and D.H. Bent. 1975. *SPSS: Statistical Package for the Social Sciences*. Second Edition. McGraw-Hill, New York.

Niles, D.M. 1973. Geographic and seasonal variation in the occurrence of incompletely pneumatized skulls in the house sparrow. *Condor. 75*: 354-356.

Nix, H. 1979. Vertical 'hawking' by both native and introduced species in Canberra. *Canberra Bird Notes 4*: 20-21.

North, C.A. 1973. Movement patterns of the house sparrow in Oklahama. *Ornithol. Monogr. 14*: 79-91.

O'Connor, R.J. 1973. Patterns of weight change in the house sparrow, *Passer domesticus* (L.), in Kendeigh, S.C. and J. Pinowski (Eds.). *Productivity, population dynamics and systematics of granivorous birds*. pp. 111-125. PWN - Polish Scientific Publishers, Warszawa.

Pinowska, J. and A. Myrcha. 1973. Biomass and production rates, in Pinowski, J. and S.C. Kendeigh (Eds.). *Granivorous birds in ecosystems. International Biological Program 12*. pp. 107-126. Cambridge University Press, Cambridge.

R.A.O.U. 1964. Queensland Branch. Circular No. 84, June.

Robbins, C.S. 1973. Introduction, spread and present abundance of the house sparrow in North America. *Ornithol. Monogr. 14*: 3-9.

Rolls, E.C. 1969. *They all ran wild*. Angus and Robertson, Sydney.

Rothstein, S.I. 1973. Relative variation of avian morphological features: relation to the niche. *Am. Nat. 107*: 769-799.

Ryan, C.S. 1906. On European and other birds liberated in Victoria: Presidential address. *Emu*. *5*: 110-119.

Sage, B.L. 1957. Remarks on the taxonomy, history and distribution of the house sparrow introduced into Australia. *Emu*. *57*: 349-352.

Selander, R.K. and R.F. Johnston. 1967. Evolution in the house sparrow. I. Intrapopulation variation in North America. *Condor*. *69*: 217-258.

Serventy, D.L. and H.M. Whittell. 1976. *Birds of Western Australia*. University of Western Australia Press, Perth.

Snow, D.W. 1954. Trends in geographical variation in the Palearctic members of the genus *Parus*. *Evolution 8*: 19-28.

Sokal, R.R. and F.J. Rohlf. 1981. *Biometry*. Second Edition. W.H. Freeman and Company, San Francisco.

Southern, H.N. 1945. The economic importance of the house sparrow, *Passer domesticus* (L.): A review. *Ann. Appl. Biol*. *32*: 57-67.

Stidolph, R.H.D. 1922. A strange nesting place. *Emu*. *22*: 75.

Storr, G.M. 1973. List of Queensland birds. *Spec. Publs. West. Aust. Mus*. *5*.

Summers-Smith, D. 1963. *The House Sparrow*. Collins, London.

Tarr, H.E. 1950. The distribution of foreign birds in Australia. *Emu*. *49*: 189-198.

Thomson, A.L. 1950. Factors determining the breeding seasons of birds: an introductory review. *Ibis*. *92*: 173-184.

Thomson, G.M. 1922. *The Naturalization of Animals and Plants in New Zealand*. Cambridge University Press, London.

Threadgold, L.T. 1960. A study of the annual cycle of the house sparrow at various latitudes. *Condor*. *62*: 190-201.

Trezise, F. 1964. Untitled. *The Bird Observer*. *388*: 4.

Voous, K.H. 1950. The breeding seasons of birds in Indonesia. *Ibis*. *92*: 279-287.

Wheeler, W.R. 1967. The birds of Cairns, Cooktown and the Atherton Tablelands. *The Australian Bird-watcher*. *3*: 55-76.

Will, R.L. 1973. Breeding success, numbers and movements of house sparrows at McLeansboro, Illinois. *Ornithol. Monogr*. *14*: 60-78.

Witherby, H.F., F.C.R. Jourdain, N.F. Ticehurst and B.W. Tucker. 1938. *The Handbook of British Birds*. vol. 1. Crows to firecrest. H.F. and G. Witherby, Ltd, London.

APPENDIX

(a) Scientific names of birds listed in Table 1.1

Ostrich	*Struthio camelus*
Mute swan	*Cygnus olor*
Mallard	*Anas platyrhynchos*
Cattle egret	*Ardeola ibis*
California quail	*Lophortyx californicus*
Common pheasant	*Phasianus colchicus*
Feral pigeon	*Columba livia*
Spotted turtledove	*Streptopelia chinensis*
Laughing turtledove	*S. senegalensis*
Skylark	*Alauda arvensis*
Red-whiskered bulbul	*Pycnonotus jocosus*
Red-vented bulbul	*P. cafer*
Blackbird	*Turdus merula*
Song thrush	*T. philomelos*
European goldfinch	*Carduelis carduelis*
European greenfinch	*C. chloris*
House sparrow	*Passer domesticus*
Tree sparrow	*P. montanus*
Nutmeg mannikin	*Lonchura punctulata*
White-winged whydah	*Euplectes albonotatus*
Common starling	*Sturnus vulgaris*
Indian myna	*Acridotheres tristis*
House crow	*Corvus splendens*

(b) The sparrows and their near relatives

The sparrows belong to the Order Passeriformes and are a sub-family of the weaver-finches as shown below (after Summers-Smith, 1963):

ORDER Passeriformes

FAMILY Ploceidae

(Weaver-finches)

Sub-family Passerinae | Ploceinae | Estrildinae

Genera:		Distribution:		
Plocepasser	(4 spp.)	Africa		
Pseudonigrita	(2 spp.)	Africa		
Montifringilla	(7 spp.)		Asia	Europe
Petronia	(5 spp.)	Africa	Asia	Europe
Histurgops	(1 sp.)	Africa		
Philetairus	(1 sp.)	Africa		
Sporopipes	(2 spp.)	Africa		
Passer	(15 spp.)	Africa	Asia	Europe
		Introduced: Australasia		
			N. and S. America	

(c) The species of the genus *Passer*, their primary zoogeographic affinity, and their sympatry with primitive agricultural man (from Johnston and Klitz, 1977)

Ethiopian species

Tropical African agricultural region

P. griseus (Vieillot), the grey sparrow

P. iagoensis (Gould), the rufous sparrow

P. luteus (Lichtênstein), the golden sparrow

P. eminibey (Hartlaub), the chestnut sparrow

Other regions

P. melanurus (Müller), the cape sparrow

P. simplex (Lichtênstein), the desert sparrow

P. castanopterus (Blyth), the Somali sparrow

Palearctic species

Near Eastern agricultural region

P. domesticus (L.), the house sparrow

P. hispaniolensis (Temminck), the Spanish sparrow

P. montanus (L.), the tree sparrow (part)

P. moabiticus (Tristram), the scrub sparrow

Other regions

P. ammodendri (Gould), the Saxual sparrow

P. pyrrhonotus (Blyth), the Sind jungle sparrow

Oriental species

Eastern Chinese agricultural region

P. rutilans (Temminck), the cinnamon sparrow

P. montanus (L.), the tree sparrow (part)

Southeast Asian agricultural region

P. flaveolus (Blyth), the olive-crowned sparrow

P. montanus (L.), the tree sparrow (part)