

THE FEEDING ECOLOGY OF NECTARIVOROUS BIRDS IN  
THE NATAL DRakensBERG

by  
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## PREFACE

This study was carried out in the Department of Zoology, University of Natal, Pietermaritzburg, under the supervision of Professor Gordon Lindsay Maclean. The research is the original work of the author unless otherwise stated.

Graig Daniels

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## SUMMARY

Although the community ecology of nectarivorous birds has been widely studied, little work of this sort has been done on the Sunbirds (Nectariniidae) and Sugarbirds (Promeropidae). I investigated aspects of nectarivory and ornithophily in the Cathedral Peak area of the Natal Drakensberg over the annual cycle. Four species of nectarivorous birds occurred in the study area: Gurney's Sugarbird Promerops gurneyi, Malachite Sunbird Nectarinia famosa, Greater Doublecollared Sunbird N. afra and Lesser Doublecollared Sunbird N. chalybea. These birds relied on eight species of ornithophilous plants for 98% of their nectar supplies. Nectar-feeding by birds other than predominantly nectarivorous ones was also investigated.

The ornithophilous flowers exhibited a wide range of form, but were generally typical of the ornithophilous pollination syndrome. The nectarivorous bird guild showed a considerable range of bill lengths, and in many cases bill length was shorter than the corolla length of the flowers visited for nectar. However, with few exceptions, all species were capable of extracting nectar from all the plant species. Lesser Doublecollared Sunbirds removed less nectar from Aloe arborescens flowers and were never seen to visit Phygelius aequalis flowers. Greater Doublecollared and Malachite Sunbirds pierced the base of the long, tubular corolla of P. aequalis to extract the nectar. Despite this illegitimate method of feeding, the birds played a major part in the pollination of this plant.

Nectar concentration varied from 11,4% in Greyia sutherlandii to 24,4%<sup>h</sup> in Leonotis leonurus; five of the eight important nectars had concentrations of 19-25%, which appears to be the optimal concentration for nectar uptake by sunbirds. Plants with weak nectars tended to produce larger volumes of nectar, which attracted occasional nectar-feeding birds as well as nectarivorous ones. The concentrations of amino acids in all the nectars were low; the birds obtained the bulk of their protein requirements from the arthropods which they included in their diets.

The nectarivorous birds were important in pollinating the plants they visited; this was clear in all the plants investigated except Protea caffra which may self-pollinate in the absence of bird or insect pollinators.

The syndrome of ornithophily is discussed with reference to floral morphology and nectar quality. Comparisons are drawn with ornithophilous plants visited by other nectarivorous bird groups reported in the literature.

The main way in which ornithophilous plants shared the available pollinators was through the staggering of flowering seasons, so that there was a succession of flowering peaks throughout the year. Those plants whose flowering times overlapped tended to avoid interspecific pollen transfer by using different pollen-deposition sites on the birds. Nectar production in all plants was matinal. There was, therefore, no

daily temporal partitioning of the pollinator resources by the plants.

Although the different bird species showed preferences for the nectar of some plants, they were catholic in their feeding. The smaller species - Lesser Doublecollared and Greater Doublecollared Sunbirds - were better able to use small, scattered nectar resources such as those of Aloe saponaria. In contrast to many other studies of nectarivorous birds, however, the larger species rarely maintained strict feeding territories at the richer nectar sources, and interspecific aggression was not common and occurred inconsistently. Previous studies of coexistence in nectarivorous birds have shown interspecific aggression to be important in the organization of the guild. In this study the birds even appeared to form mixed-species foraging flocks at times at L. leonurus, the nectar of which was highly sought by all species.

Malachite Sunbirds and, to some extent, Gurney's Sugarbirds migrated from the study area during the winter, probably to the lowlands of Natal. This was in response to reduced nectar and arthropod supplies in the Drakensberg from May to August, combined with the drop in temperatures. Greater Doublecollared Sunbirds occurred in steady numbers throughout the year and may be better able to cope with the extreme cold in winter.

All four nectarivorous bird species fed on arthropods to provide protein, fat, mineral and other nutritional requirements not available in sufficient quantities in nectar. More arthropods

were available in summer, and arthropod-foraging by the birds increased just before the breeding season when nectar availability was lowest. The birds ingested quite large amounts of pollen, particularly from L. leonurus and the proteas; they also swallowed the perianth hairs which were abundant in the protea florets. These items might play a role in the nutrition of the birds, although their ingestion may have been incidental.

## LIST OF CONTENTS

	page
PREFACE	i
ACKNOWLEDGEMENTS	ii
SUMMARY	iii
LIST OF CONTENTS	vii
LIST OF TABLES	xi
LIST OF FIGURES	xii
CHAPTER 1: BACKGROUND AND STUDY AREA	1
1.1 INTRODUCTION	1
1.2 STUDY AREA	3
1.3 NECTARIVOROUS BIRDS	5
CHAPTER 2: ORNITHOPHILY AND NECTARIVORY	9
2.1 INTRODUCTION	9
2.2 METHODS	13
2.2.1 <u>Bird and flower morphologies</u>	13
2.2.2 <u>Nectar production</u>	13
2.2.3 <u>Feeding activity of the birds</u>	17
2.2.4 <u>Nectar quality</u>	18
2.2.4.1 Concentration	18
2.2.4.2 Sugars present	19
2.2.4.3 Amino acids	20
2.2.5 <u>The importance of the bird as pollinators</u>	21



2.3	RESULTS	23
2.3.1	<u>Bird and flower morphologies</u>	23
2.3.2	<u>Nectar production</u>	32
2.3.3	<u>Feeding activity of the birds</u>	36
2.3.4	<u>Nectar quality</u>	39
2.3.5	<u>The importance of the birds as pollinators</u>	39
2.4	DISCUSSION	41
2.4.1	<u>Flower colour and presentation</u>	41
2.4.2	<u>Flower morphology and nectar robbing</u>	42
2.4.3	<u>Bird feeding morphology, flower morphology</u> <u>and nectar concentration</u>	45
2.4.4	<u>Nectar-sugar composition</u>	58
2.4.5	<u>Amino acids in nectar</u>	62
2.4.6	<u>Nectar -energy reward, pattern of</u> <u>production and pollinator activity</u>	63
2.4.7	<u>The importance of the birds in pollination</u>	66
2.4.8	<u>Some concluding remarks</u>	70

### CHAPTER 3: COMMUNITY ORGANIZATION:

	NECTAR AVAILABILITY TO AND ITS EXPLOITATION BY BIRDS	71
3.1	INTRODUCTION	71
3.2	METHODS	78
3.2.1	<u>Flowering phenology</u>	78
3.2.2	<u>Plant abundance and total nectar</u> <u>availability</u>	78
3.2.3	<u>Bird-population index</u>	80

3.2.4	<u>The birds' feeding preferences</u>	80
3.2.5	<u>Pollen loads carried by the birds</u>	81
3.2.6	<u>Foraging at Leonotis leonurus</u>	84
3.3	RESULTS	85
3.3.1	<u>Flowering phenology</u>	85
3.3.2	<u>Plant abundance and total nectar availability</u>	85
3.3.3	<u>Flowering overlap, pollen loads and site of pollen deposition on the pollinators</u>	89
3.3.4	<u>Nectarivorous bird populations</u>	93
3.3.5	<u>Feeding preferences</u>	93
3.3.6	<u>Incidence of aggression</u>	99
3.3.7	<u>Foraging at Leonotis leonurus</u>	99
3.4	DISCUSSION	102
3.4.1	<u>How do the ornithophilous plants share the available pollinators?</u>	102
3.4.2	<u>How do the birds share the available nectar resources?</u>	108
3.4.3	<u>Nectar availability and fluctuations in nectarivorous bird populations</u>	123
3.4.4	<u>Why do Malachite Sunbirds migrate in winter?</u>	129
3.4.5	<u>Some concluding remarks</u>	132

CHAPTER 4: THE IMPORTANCE OF ARTHROPODS IN THE DIETS OF THE NECTARIVOROUS BIRDS	135
4.1 INTRODUCTION	135
4.2 METHODS	137
4.2.1 <u>Arthropod availability</u>	137
4.2.2 <u>Bird foraging behaviour</u>	137
4.2.3 <u>Faecal samples</u>	138
4.3 RESULTS	139
4.3.1 <u>Arthropod availability</u>	139
4.3.2 <u>Bird foraging behaviour</u>	139
4.3.3 <u>Faecal samples</u>	142
4.4 DISCUSSION	145
4.4.1 <u>The value of arthropods to nectarivorous     <u>birds</u></u>	145
4.4.2 <u>Other items in the birds' diets</u>	150
4.4.3 <u>Concluding remarks</u>	153
REFERENCES	154

## LIST OF TABLES

	page
1.1 Habitats defined in the study area	6
2.1 The "Histidine Scale"	22
2.2 Weights, culmen and wing lengths and bill shapes of the nectarivorous birds	24
2.3 Weights, culmen and wing lengths and bill shapes of occasional nectar-feeding birds	25
2.4 Floral characteristics of the ornithophilous plants	28
2.5 Residual nectar volumes after visits by birds	31
2.6 Sugar constituents and sugar and amino acid concentrations in nectars	37
2.7 Seed-sets in pollination experiments	40
2.8 Sucrose/hexose ratios of nectars from flowers pollinated by different bird groups	59
2.9 Nectar-sugar production in flowers pollinated by different animal groups	65
3.1 Plant nectar-sugar production, density, clumping and "potential energy value"	87
3.2 Flowering overlap and site of pollen deposition	90
3.3 Percentage of pollen loads on birds carried on the forehead/crown and chin/throat	91
3.4 Seasonal pollen loads carried by birds	92
3.5 Nectar-feeding preferences of the birds	98
3.6 Aggressive encounters among nectarivorous birds	100
4.1 Contents of faecal samples	143

## LIST OF FIGURES

	page
1.1 The study area	4
1.2 Climate of the study area	7
2.1 The ornithophilous flowers	26
2.2 Cumulative daily nectar production in flowers	33
2.3 Comparison of two methods of measuring nectar production	35
2.4 Nectar-feeding activity in relation to nectar production at <u>A. arborescens</u> and <u>L. leonurus</u>	38
3.1 Scanning electron micrographs of pollen grains	83
3.2 Ornithophilous-plant flowering phenologies	86
3.3 Nectar-sugar availability in each month	88
3.4 Monthly bird-population indices and nectar availability	94
3.5 Bird populations and nectar availability in each habitat	95
3.6 Correlation between nectar availability and bird numbers	97
3.7 Foraging activity of the different bird species at <u>L. leonurus</u>	101
4.1 Monthly arthropod availability and incidence of arthropod-foraging by birds	140
4.2 The percentage arthropod-foraging by the different bird species	141
4.3 Photomicrograph of a faecal sample containing large numbers of pollen grains and protea-perianth hairs	144

CHAPTER 1  
BACKGROUND AND STUDY AREA

1.1 INTRODUCTION

Nectarivorous birds have been widely studied by zoologists. Their comparatively restricted diet consisting largely of floral nectar and the wide occurrence of avian nectarivores provide excellent opportunities to investigate complex and often controversial topics such as competition, community structure, resource partitioning, optimal foraging and plant-animal coevolution.

Most previous ecological work has been done on hummingbirds (Trochilidae) of the New World (e.g. Stiles 1975, 1980; Feinsinger 1976, 1978, 1980; Wolf et al. 1976; Snow & Snow 1980; Kodric-Brown et al. 1984; Feinsinger et al. 1985; and references therein). The other nectarivorous bird groups have received less attention. Aspects of the ecology of the Australian honeyeaters (Meliphagidae) have been investigated by, for example, Ford & Paton (1977); Ford (1979, 1983), Paton (1980, 1985), Collins & Briffa (1982, 1983a, 1983b), Pyke (1983) and Collins & Spice (1986). Similar studies have been made of the honeycreepers (Drepanididae) of the Hawaiian Islands (e.g. Baldwin 1953; Carpenter 1976a; Carpenter & MacMillen 1976; Carothers 1982; Pimm & Pimm 1982).

The sunbirds (Nectariniidae) of Africa, southeast Asia, the East Indies, the Philippines and Australia, and the sugarbirds (Promeropidae, a family of two species endemic to southern Africa) have been the subjects of few community studies. Recent ecological investigations have looked at pollination roles (Mostert et al. 1980; Frost & Frost 1981; Collins 1983a), and the energetics or foraging behaviour of either individual bird species (Wolf 1975; Mostert et al. 1980; Collins 1983b) or several coexisting species (Cheke 1971a; Gill & Wolf 1975a, 1975b, 1977, 1978, 1979; Frost & Frost 1980; Wooller 1982; Collins 1983c). These studies have, however, been conducted at particular nectar sources or over short periods. Pettet (1977) examined the seasonal occurrence of nectarivorous birds in relation to the flowering phenologies of nectariferous plants in Nigeria. The work of Rebelo et al. (1984) and Siegfried & Rebelo (1986; and references therein) in South Africa dealt with the pollination syndromes and flowering phenologies of selected nectariferous plants, and the occurrence and abundance of nectarivorous birds in relation to these in Mountain Fynbos through the year. As far as I am aware, there has been no intensive study of a guild (Root 1967) of avian nectarivores in Africa which has incorporated a concomitant investigation of nectar production and floral morphology of all the important ornithophilous plants in the community over the annual cycle.

I set out to make such an investigation of a guild of nectarivorous birds in the Natal Drakensberg. The area promised to be interesting because of the high altitude and its associated

extreme climate, and the coexistence of a small number of nectarivorous bird species in the Nectariniidae and the Promeropidae. Initial observations showed there to be a wide morphological diversity of flowers producing nectar used by birds with a range of body size and bill length. My objectives were to examine the following interrelated aspects over the annual cycle:

- (a) the morphology of the birds and the flowers they tapped for nectar;
- (b) the characteristics of nectar production and quality in flowers visited by birds;
- (c) the role of nectarivorous birds as pollinators;
- (d) availability of nectar and patterns of its use by birds;
- (e) fluctuations in the populations of nectarivorous birds;
- (f) the importance of arthropods in the diets of the nectarivorous birds.

## 1.2 STUDY AREA

The study was conducted around the Ukhahlamba Research Station situated at the head of Mike's Pass in the Cathedral Peak area of the Natal Drakensberg (29°00'S; 29°15'E) (Fig. 1.1). The study area covered 720 ha and incorporated the foothill region of the Drakensberg known as the Little Berg. Altitude ranged from 1380 m to 1880 m. No detailed observations were made above 1880 m, although the escarpment rises to over 3000 m in the southwest. Field work was done from 1 May 1985 to 31 April 1986.



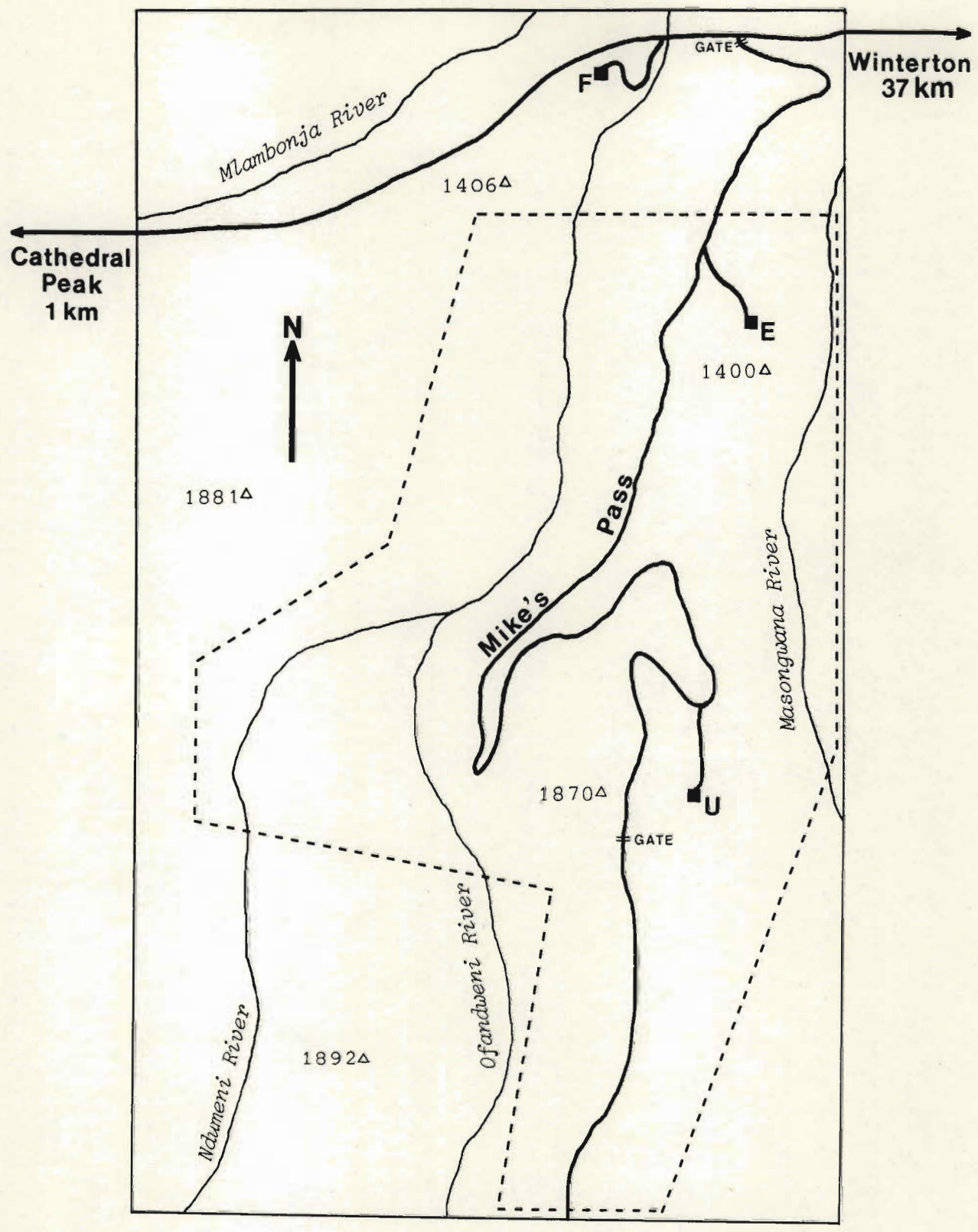


FIGURE 1.1 The study area near Cathedral Peak, Natal.

- study area boundary
- roads
- ~ rivers
- 1400Δ altitude (m)
- U Ukhahlamba Research Station
- E Education Centre
- F Forest Station
- Scale : 4 cm = 1 km

A detailed account of the plant ecology of the area has been given by Killick (1963). For some aspects of my work I divided the study area into five habitat types, descriptions of which appear in Table 1.1. The divisions between the habitats were sometimes indistinct and transects were confined to areas that were considered typical of the habitat descriptions.

Temperature and rainfall data (Fig. 1.2) were obtained from the meteorological station at Cathedral Peak Forest Station at an altitude of 1360 m. Most rainfall in the study area occurs during the summer months from October to April. Very little rain falls during the winter (May to September) and air temperatures are low over this period, with minimum temperatures often below 0°C, particularly in July.

### 1.3 NECTARIVOROUS BIRDS

Throughout this work I use the term nectarivorous bird to refer to a species which feeds predominantly on nectar. Species of birds other than nectarivorous ones which sometimes feed on nectar are referred to as occasional nectar-feeders.

Cyrus & Robson (1980) record the presence of five species of nectarivorous birds at some time of the year in the Cathedral Peak area. These are the Malachite Sunbird Nectarinia famosa, Greater Doublecollared Sunbird N. afra, Lesser Doublecollared Sunbird N. chalybea, Black Sunbird N. amethystina (Nectariniidae)

TABLE 1.1

Habitats defined in the study area at Cathedral Peak, the proportion of the study area they constituted, and the length of the transect in each.

Habitat	Altitudinal range (m)	Description (see Killick 1963)	Proportion of study area	Transect length (m)
Lower grassland	1380-1420	Lower-lying grassland areas dominated by <u>Themeda triandra</u> and with some Boulder Bed Scrub.	0,17	1400
<u>Protea caffra</u> savanna	1400-1740	<u>Protea caffra</u> stands in <u>Themeda triandra</u> grassland, with some Boulder Bed Scrub.	0,17	1140
Forest	1440-1680	<u>Podocarpus latifolius</u> forest.	0,06	1100
Sandstone cliffs	1600-1720	Cave Sandstone Scrub, with much <u>Halleria lucida</u> and <u>Protea roupelliae</u> .	0,25	3040
Little Berg grassland	1740-1880	Areas of subalpine <u>Themeda triandra</u> grassland on top of the Little Berg, with some <u>Leucosidea sericea</u> scrub.	0,35	2000

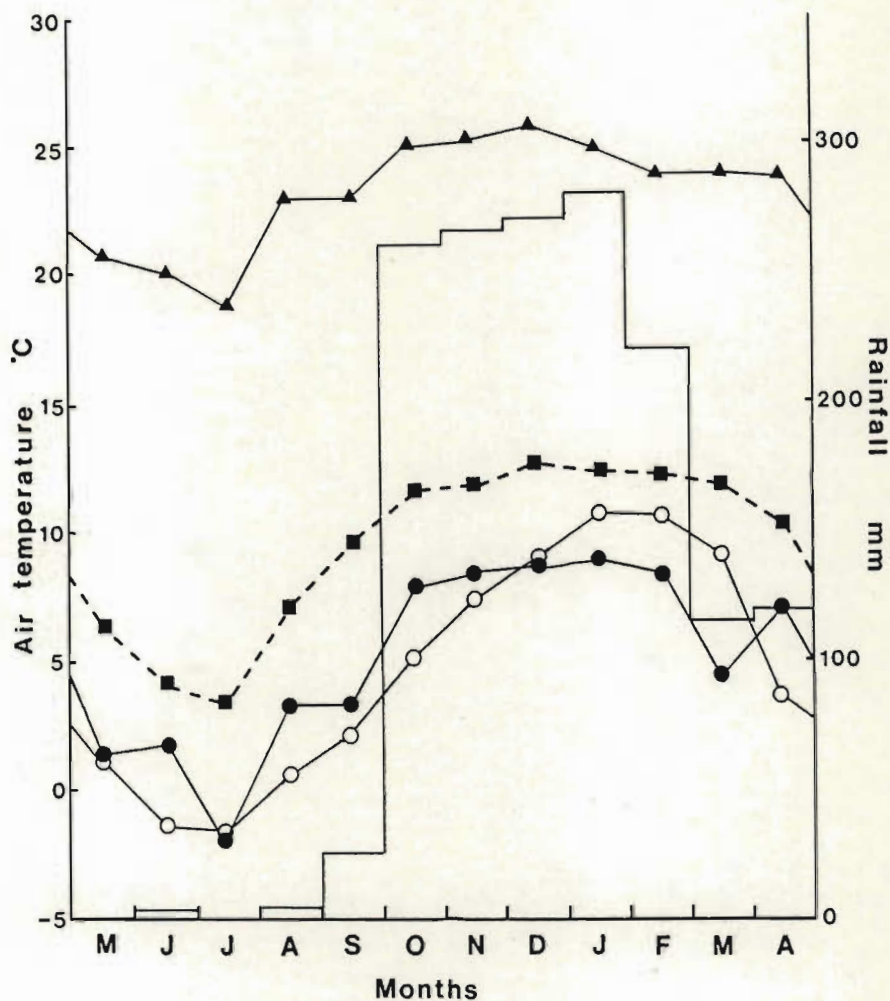


FIGURE 1.2

Air temperatures (line graphs - see below) and rainfall (histogram) at Cathedral Peak Forest Station near the study area at an altitude of 1360 m for the months May 1985 to April 1986.

- |                         |   |
|-------------------------|---|
| ▲—▲ Mean daily maximum  | ●—● Lowest minimum                            |
| ■--■ Mean daily minimum | ○—○ Lowest minimum<br>(mean for last 7 years) |

and Gurney's Sugarbird Promerops gurneyi (Promeropidae). Gurney's Sugarbird occurs only in some highland regions of Southern Africa and is listed as "meriting careful monitoring" in the South African Red Data Book - Birds (Brooke 1984). Black Sunbirds were seen only twice during the study and are thus not included in this work.

Occasional nectar-feeding by other bird species was also investigated.

## CHAPTER 2

## ORNITHOPHILY AND NECTARIVORY

## 2.1 INTRODUCTION

By specializing in a method of pollination, a plant species can increase the efficiency of pollination and can more certainly ensure cross-pollination. The specialized pollinator has its needs specifically catered for and is less likely to have to compete with other pollinators for its reward (see discussions in Faegri & van der Pijl 1979; Snow 1981; Feinsinger 1983a).

Plants have evolved structural and physiological adaptations, especially in the flower, to facilitate particular modes of pollination such as ornithophily (bird-pollination), entomophily (insect-pollination), anemophily (wind-pollination) etc. These specializations, or pollination syndromes, have been well documented (e.g. Vogel 1954; Proctor & Yeo 1973; Faegri & van der Pijl 1979; Jones & Little 1983; Real 1983; Siegfried & Rebelo 1986; and references therein). Ornithophilous flowers are generally vividly coloured, often red, lack a "landing platform" and odour, and have a tough flower wall and stiff or fused staminal filaments. The flower is usually tubular or brush-like, with deep-seated nectar. Passerine pollinators generally require a perch near the flowers, which tend to face towards the perch, often upwards. Hummingbird-flowers (i.e. those largely pollinated by hummingbirds) usually face out or down into free space, giving access to the hovering birds. Nectarivorous birds have variously

elongated, often decurved bills and specialized tongues for the efficient extraction of nectar from coevolved ornithophilous flowers (Skead 1967; Grant & Grant 1968; Snow 1981; Carothers 1982; Waser 1983a).

Ornithophilous plants yield large energy rewards when compared to those produced by insect-pollinated flowers, in return for an increased proportion and distance of outcrossing promoted by the relatively large size and therefore high mobility of avian pollinators (Heinrich & Raven 1972; Heinrich 1975; Brown et al. 1978; Cruden et al. 1983). Energy reward per flower is regulated by a balance in nectar volume and concentration. This may be influenced by factors such as the size, morphology and foraging behaviour of the birds and efficiency of uptake and assimilation of nectar by them, and by the morphology, abundance and distribution of flowers, nectar viscosity, ambient temperature, and avoidance of attracting other pollinator groups (Hainsworth 1974; Hainsworth & Wolf 1976; Gass & Montgomerie 1981; Kingsolver & Daniel 1983; Montgomerie 1984; Tamm & Gass 1986).

The major solute constituents of nectar are the sugars sucrose, glucose and fructose (Wykes 1952; Percival 1961). Baker & Baker (1983) have found relationships between nectar sugar composition and pollinator group. Hummingbird-flowers tend to have high sucrose/hexose ratios (i.e. sucrose-rich nectar) and passerine bird-flowers low sucrose/hexose ratios (i.e. glucose- and/or fructose-rich nectars). In the field and laboratory

hummingbirds have been shown to prefer sucrose-rich nectars (Hainsworth & Wolf 1976; Stiles 1976; Baker & Baker 1983).

Baker & Baker (1973a, 1973b, 1980, 1986) have also reported the presence of free amino acids in most nectars. Bird-nectars, particularly those of the Old World, tend to have relatively low concentrations of amino acids, probably because all nectarivorous birds include arthropods in their diets to provide their main source of protein (see Chapter 4). In laboratory experiments Hainsworth & Wolf (1976) found that hummingbirds did not prefer, and even rejected, nectars with amino-acid concentrations above those usually encountered by the birds in the wild. Baker & Baker (1973a) detected proteins in only three out of 266 nectars examined, and those were in bee-flowers.

Further specialization may occur within a pollination syndrome. A plant species, or a group of plant species, may coevolve morphologically and physiologically in close association with one or several species of pollinator with complementary adaptations in morphology and behaviour. Several elegant examples of this close coevolution between plants and avian nectarivores involve correlations between corolla and bill lengths, nectar rewards, and bird body sizes and foraging strategies (e.g. Snow & Snow 1972, 1980; Stiles 1975; Feinsinger 1976, 1983a; Wolf *et al.* 1976; Brown & Bowers 1985).

There are, however, relatively few examples of very narrow specialization with, for example, one plant species being pollinated by only one coadapted pollinator in ornithophily



(Feinsinger 1983a). Extreme specialization has disadvantages: the pollinator and plant cannot occur separately, and adversity for one is adversity for both. Less specialized pollinators, on the other hand, could have other nectar sources available, and less specialized plants several potential pollinators (see Faegri & van der Pijl (1979), Snow (1981) and Feinsinger (1983a) for more thorough discussions).

Coevolutionary specialization is also open to exploitation by unspecialized nectar robbers which extract the nectar illegitimately (i.e. without fulfilling the pollination role, usually by piercing the corolla; legitimate use of nectar is nectar removal by a pollinator in the manner most likely to effect pollination). Illegitimate nectar-removal is a common phenomenon, and occurs among both nectarivorous and occasional nectar-feeding birds (e.g. see Skead 1967; Snow & Snow 1980; Inouye 1983). Ornithophilous flowers are often equipped to ward off nectar-thieving with a tough protective flower wall, calyx or bracts (Snow 1981; Inouye 1983).

I investigated some of these morphological and physiological aspects of ornithophily in the Drakensberg; little work of this nature has been done on bird-plant associations in Africa, particularly in investigating aspects of nectar production and quality. A knowledge of these is essential in studying how nectariferous plants and nectarivores interact in a community.

## 2.2 METHODS

### 2.2.1 Bird and flower morphologies

Nectarivorous birds were trapped throughout the study period using mist nets. Each bird was identified, colour-ringed, and its weight, and wing and culmen lengths recorded. The degree of curvature of the bill was measured on a scale of 1-10, where 1 represents no curvature and 10 has an angle of  $90^\circ$  between tangents at the base and the tip of the bill.

A typical flower of each plant species commonly tapped for nectar by birds was examined and drawn. The effective corolla length of 20 fresh flowers was measured using calipers. The effective corolla length was the distance from the base of the nectary to the point at which the corolla or other floral structure restricted the insertion of a bird's head further into the flower. Notes were made on curvature of the corolla, if any, coloration, scent, nature of the peduncle, the natural position of flowers on the plant, and possible features to deter nectar-robbing.

### 2.2.2 Nectar production

The volume, concentration and pattern of nectar secretion in flowers commonly visited by nectarivorous birds were examined. All measurements of nectar production were made in clement weather. 5- and 10- $\mu\text{l}$  graduated micro-capillary pipettes were

used to measure nectar volume. A temperature-compensated sucrose refractometer was used to measure nectar concentration (% = weight of solute/weight of solution x 100; also sometimes called Brix).

Inflorescences or groups of flowers were covered with 2-mm nylon mesh at 17h00 the evening before measurement in order to exclude the birds, and the volumes and concentrations of the nectar in a sample of flowers recorded. At 07h00 the next day, and every 2 h till 17h00, nectar volume and concentration readings were taken from the protected flowers to establish the pattern of nectar production throughout the day. The mean volume and concentration for each interval were converted to mg sucrose equivalents by changing the refractometer concentration readings to g/l (i.e. weight of solute/volume) and multiplying by the nectar volume (Bolten et al. 1979).

Only Greyia sutherlandii nectar production was successfully measured from the intact flower. The flowers of the other plant species studied had to be destroyed in order to extract the nectar and consequently nectar production could not be followed in individual flowers. This meant that large samples of flowers were required because of considerable variation in nectar volumes within each sample, mostly because of differing ages and residual nectar volumes of individual flowers (see Cruden & Hermann (1983) for other factors which can cause such variation).

Despite using as large a sample size as time would allow, the results were very variable. A method that was either non-

destructive or which could sample more flowers more quickly was required. Towards the end of the study the latter approach was attempted by water-extraction of nectar from large numbers of flowers; I tried this on Leonotis leonurus and Protea roupelliae.

Five samples of 100 protected L. leonurus flowers were taken every 2 h and placed in screw-top jars with 100 ml of distilled water. A sample of 10 protected P. roupelliae inflorescences was taken every 2 h; each inflorescence was placed in a jar with 200 ml of water. In both cases a drop of wetting agent was added to each jar to reduce water-surface tension. Samples were immersed for 20 min and gently agitated by inversion every 5 min. The resulting solutions were filtered through Whatman No. 1 filter paper and 20 ml stored in a vial for analysis in the laboratory. A little Thiomersal (BDH product No. 30416) was added to each vial to prevent microbial breakdown of sugars in the samples.

Establishment of the concentration of sugars in a known volume of water and subtraction of initial readings allowed extrapolation to the amount of sugar produced per flower or inflorescence over a time interval. A knowledge of the concentration of the nectar produced (far less variable than nectar volume per flower) enabled calculation of nectar volumes.

The amount of water used to extract the nectar was determined by experiment. The samples had to be fully immersed, but the use of too much water resulted in sugar concentrations too weak to measure (see below). A rough guide for the measurement of nectar

production in ornithophilous flowers by the method described here is to use 100-200 ml of water for every 100 flowers.

In the laboratory the concentration of reducing sugars present in the samples was determined by the sensitive Nelson modification of the Somogyi method (Marais et al. 1966). The determination uses four reagents:

Reagent A: anhydrous sodium carbonate (25 g), sodium potassium tartrate (25 g), sodium bicarbonate (20 g) and anhydrous sodium sulphate (200 g) dissolved and made up to 1000 ml with distilled water.

Reagent B: copper sulphate pentahydrate (30 g) dissolved in 150 ml distilled water to which 4 drops of concentrated sulphuric acid were added; the solution was made up to 200 ml with distilled water.

Reagent C: one part Reagent B mixed with 25 parts Reagent A just before use.

Reagent D: ammonium molybdate (25 g) dissolved in 450 ml distilled water; 21 ml of concentrated sulphuric acid were slowly added with stirring; sodium arsenate heptahydrate (3 g) dissolved in 25 ml distilled water was added; the solution was made up to 500 ml with distilled water and incubated at 37° for 24 h in a foil-wrapped flask.

Before doing the determinations proper a dilution series of the sample solutions was made to establish if, and to what extent, dilution was necessary to remain within the accurate range of the colour reaction.

The determination procedure was as follows. 1 ml of sample solution was added to 1 ml of Reagent C in a folin tube and heated in a boiling water-bath for 20 min. After cooling in a cold water-bath, 1 ml of Reagent D was added and each tube agitated until the evolution of CO<sub>2</sub> ceased. After 10 min the test solutions were made up to 25 ml with distilled water and their absorbances read at 520 nm in a spectrophotometer against a distilled water blank given the same treatment as the samples.

The spectrophotometer readings were converted to sugar concentrations (mg/l) using a d-glucose standard curve. These were then used to calculate the total amount of reducing sugar extracted in the water and thus mg reducing sugar produced per flower or inflorescence over the time interval (subtracting the readings for previous time intervals).

### 2.2.3 Feeding activity of the birds

The nectar-feeding activity of birds was monitored at L. leonurus (for one day) and Aloe arborescens (for two days). A group of each of these plants was watched from 05h00 to 18h00, and the frequency of foraging visits related to the pattern of nectar production. At A. arborescens, the foraging rate, or average time a bird took to extract the nectar from flowers, was

calculated by recording the number of flowers probed and the duration of each foraging bout (Wolf et al. 1976). The total number of visits made to the clumps and the time of each visit were noted. At L. leonurus foraging activity was monitored by counting the number of nectarivorous birds seen feeding in the clump under observation every 15 min through the day.

At Halleria lucida, L. leonurus and A. arborescens, feeding birds were chased away and the nectar residue in the flowers they had probed measured with capillary tubes in order to ascertain the efficiency of nectar removal by the birds. The volumes in adjacent flowers were also measured to ensure that the residual measurements were valid, i.e. that the flowers were not likely to have been empty or low in nectar before the visit.

#### 2.2.4 Nectar quality

##### 2.2.4.1 Concentration

As mentioned, total sugar concentration was measured with a temperature-compensated refractometer. The instrument used was an Atago No. 1 with a range 0-32%. Where nectar concentration exceeded 32% or the sample was of insufficient volume to make an accurate reading, known volumes of nectar were diluted with known volumes of distilled water and readings thus facilitated were used to calculate the actual concentrations.

#### 2.2.4.2 Sugars present

The main sugars present in the nectars fed upon by birds were qualified and quantified using descending paper chromatography. 0.5  $\mu\text{l}$  of fresh undiluted and diluted (1:1 and 1:2 with water) nectar was spotted on Whatman No. 1 chromatography paper immediately after extraction from the flower in the field. 0.5  $\mu\text{l}$  of a standard solution containing 2% each of glucose, fructose and sucrose was also spotted on each paper. The solvent used was n-propanol:ethyl acetate:water (14:4:2 by volume) (Baker & Baker 1983). The papers were run for 72 h, allowing the solvent front to run off the end of the paper.

Once removed from the tank and dried, the chromatograms were dipped in a developing reagent consisting of two solutions mixed just before use: solution A was 75 mg oxalic acid in 15 ml ethanol; solution B was 150 mg p-aminobenzoic acid in 25 ml chloroform and 2 ml acetic acid. Once the papers were again dry they were placed in an oven and heated at 110°C for 20 min. This caused pentose sugars to show a red-brown colour and other sugars brown (Baker & Baker 1983).

When viewed under ultraviolet light all sugars fluoresced green and the sugar spots were outlined in pencil. Baker & Baker (1983) eluted their sugar spots and used a fluorometer and standards to quantify the sugars present. As I had no access to a fluorometer I used spot areas to quantify the sugars: Fisher et al. (1948) showed that sugars could probably be quantified in



paper chromatography in this way, using regressions made from standard solutions. This was found to work well. As an index to spot area, the outlined spots were photocopied onto a standard paper, cut out and weighed to 0,1 mg. Standard regression curves were constructed using known solutions of glucose, fructose and sucrose, spotted and treated in the same way as the nectar samples. The regressions were logarithmic and had  $r^2$  values of 0,99, 0,97, and 0,99 for the glucose, fructose and sucrose curves respectively. Tests of known solutions showed the method to be accurate to an average of 4,6% (never exceeding 10%) over the robust range of the logarithmic curve (5-70  $\mu$ g sugar).

The sucrose/hexose ratio (by weight) was computed for each nectar (Baker & Baker 1983). I used Baker & Baker's terminology in which a ratio of 0,5 represents a "balanced nectar";  $>0,999$  is "sucrose-dominated"; 0,5-0,999 is "sucrose-rich"; 0,1-0,499 is "hexose-rich"; and  $<0,1$  is "hexose-dominated".

#### 2.2.4.3 Amino acids

The total concentration of free amino acids in nectar samples was determined by the method described by Baker & Baker (1973a, 1980). This is based on a colour development using ninhydrin. In my tests I placed 5  $\mu$ l of fresh nectar on Whatman No. 1 filter paper. Once dry, 8  $\mu$ l of 0,2 % ninhydrin in acetone was placed on the same spot. After 24 h this was visually compared with a colour-development scale made from standard histidine solutions treated in the same way: the "Histidine Scale". The scale from

0-10 represents concentrations of 0-25 mM (Table 2.1). The colours of the "Histidine Scale" were found to fade quite quickly and a colour photograph true to the scale was used in the field. Nectar spots were also tested for the presence of proteins using brom-phenol blue stain (Baker & Baker 1973a).

#### 2.2.5 The importance of the birds as pollinators

Young unopened inflorescences or groups of buds of each of the ornithophilous plant species were caged to exclude potential animal pollinators before and while the flowers were open. I used three treatments: (1) inflorescences covered with 2-mm "insect mesh" to exclude both birds and insects; (2) inflorescences covered with 20-mm "bird mesh" to exclude birds but allow access to most insects (only butterflies were seen to be deterred by these exclosures but these insects rarely visited the plants under investigation); and (3) nearby inflorescences of similar age were inconspicuously marked and left exposed as the natural controls. Between 5 and 10 inflorescences were subjected to each treatment and the seed-set (or fruit-set) in 20-100 flowers in each inflorescence was counted (see results for sample sizes for the different plant species). I used seed-set as indicating levels of pollination because it was easily counted; pollination can occur, however, without the subsequent seed-set, as a result, for example, of nutrient limitations (Horn 1962). The differences in the results of treatments were compared using one-way analysis of variance (ANOVA) and the Student-Newman-Keuls test.

TABLE 2.1

The "Histidine Scale" and associated aqueous histidine (free amino acid) concentrations (Baker & Baker 1973a, 1980).

Score on "Histidine Scale"	Histidine concentration (M x 10 <sup>3</sup> )
0	<0,049
1	0,049
2	0,098
3	0,195
4	0,391
5	0,781
6	1,563
7	3,125
8	6,250
9	12,500
10	25,000

## 2.3 RESULTS

### 2.3.1 Bird and flower morphologies

The four nectarivorous bird species in this study: the Malachite Sunbird Nectarinia famosa, Greater Doublecollared Sunbird N. afra, Lesser Doublecollared Sunbird N. chalybea and Gurney's Sugarbird Promerops gurneyi, showed a range of body size and culmen length. All had decurved bills, that of the Greater Doublecollared Sunbird slightly more so than the others (Table 2.2).

Three other species of birds were recorded taking nectar occasionally. These were the Cape White-eye Zosterops pallidus, Blackeyed Bulbul Pycnonotus barbatus and Redwinged Starling Onychognathus morio. Their characteristics are shown in Table 2.3 for comparison with the nectarivorous bird species.

I focused my studies on eight species of nectariferous plants which together accounted for 98,1% of bird nectar-feeding observations recorded during transect walks (see Chapter 3). These plants were : Leonotis leonurus (Lamiaceae), Halleria lucida, Phygelius aequalis (Scrophulariaceae), Aloe arborescens, Aloe saponaria (Liliaceae), Protea caffra, Protea roupelliae (Proteaceae) and Greyia sutherlandii (Greyiaceae). The floral morphology of these plants is illustrated in Fig. 2.1 and further described in Table 2.4.

The first five of the above plant species had well developed corolla tubes; these were sympetalous (fused) in all except A.

TABLE 2.2

Mean weights, culmen and wing lengths and bill shapes of nectarivorous bird species in the study. N = sample size. (Sketches 0,4 X life-size.)


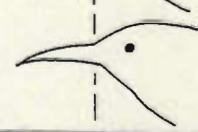

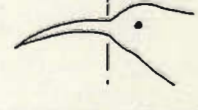






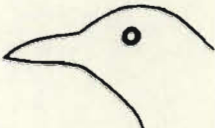
Species	N & sex	Weight g	Culmen (range) mm	Wing mm	Bill	
					Curvature	Shape
Gurney's Sugarbird	4 ♂	35,8	28,7 (28-30)	93	4	
	3 ♀	30,7	27,3 (26-28)	87	3	
Malachite Sunbird	18 ♂	18,9	33,4 (31-35)	79	4	
	11 ♀	15,0	30,7 (28-33)	74	4	
Greater Doublecollared Sunbird	14 ♂	13,0	28,5 (26-30)	67	6	
	13 ♀	11,2	26,3 (25-29)	62	5	
Lesser Doublecollared Sunbird	4 ♂	8,9	22,8 (22-24)	59	4	
	2 ♀	7,6	20,1 (20-21)	54	4	

TABLE 2.3

Mean weights, culmen and wing lengths and bill shapes of birds which occasionally fed on nectar in the study area.

N = sample size. (Sketches 0,4 x life-size.)

Species	N	Weight g	Culmen (range) mm	Wing mm	Bill shape
Cape White-eye	10	12,5	10,4 (9-11)	65	
Blackeyed Bulbul	3	42,5	16,2 (15-18)	103	
Redwinged Starling*	-	110,0	28,8 (27-30)	149	

\* Data for the Redwinged Starling taken from Maclean (1985); (the weight is an estimate).

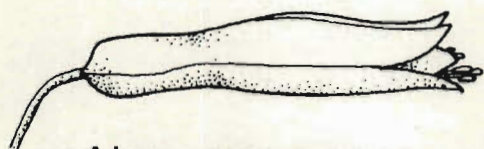




Halleria lucida X1,4



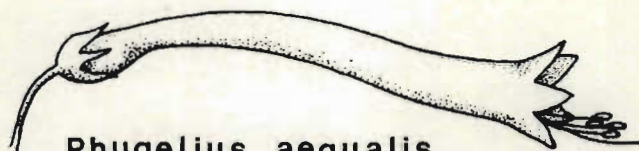
Leonotis leonurus X1,4



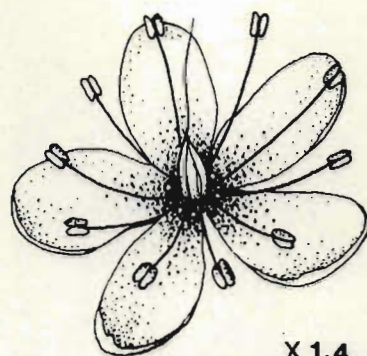
Aloe arborescens X1,4



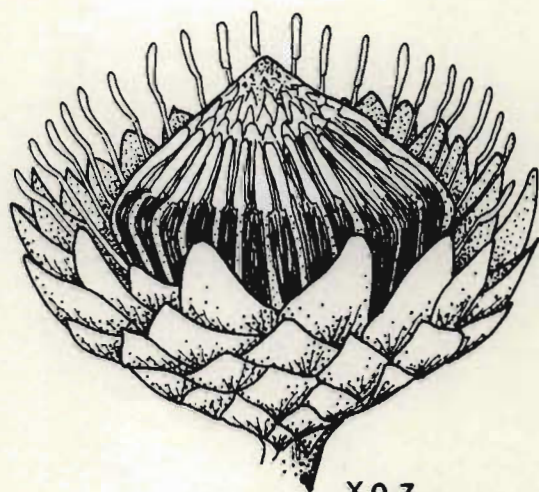
Aloe saponaria X1,4



Phygelius aequalis X1,4



X1,4  
Greyia sutherlandii



X0,7  
Protea caffra



X0,7  
Protea roupelliae



TABLE 2.4

Floral characteristics of the eight main plant species visited by birds for nectar.

Species	Flower type	Effective corolla min-mean-max (mm)	Corolla <sup>1</sup> curvature	Colour	Scent <sup>2</sup>	Orientation	Nature of peduncle
<u>Halleria lucida</u>	tubular	27-29,6-32	4-5	red	none	out/down	long, flexible
<u>Leonotis leonurus</u>	tubular	23-26,0-31	5-6	orange	none	out	short, stiff
<u>Aloe arborescens</u>	tubular	28-34,1-37	0	red	none	down	long, flexible
<u>Aloe saponaria</u>	tubular	36-37,2-41	2-3	orange to red	none	down	long, flexible
<u>Phygelius aequalis</u>	tubular	35-40,2-44	5	red	none	down	long, flexible
<u>Greyia sutherlandii</u>	cup	0	-	red	none	all <sup>3</sup>	short, stiff
<u>Protea caffra</u>	brush <sup>4</sup>	5-15*	-	pink	sweet	up	short, stiff
<u>Protea roupelliae</u>	brush <sup>4</sup>	25-45*	-	pink to red	none	up	short, stiff

1 measured as for the culmen of birds

2 human assessment!

3 ovoid inflorescence with flowers facing up, down and out

4 the form of the pseudanthial inflorescence

\* subjective estimate (depends on the age of the inflorescence, position in the inflorescence, pressure the bird exerts, etc.)

arborescens in which it was polypetalous. The proteas had a brush-like inflorescence, with the enclosing bracts and crowding of the flowers creating an effective corolla. The flower of G. sutherlandii was an open cup-shape, which gave almost any nectarivore access to its nectar. In tubular flowers, the corolla was curved in a way similar to that found in the nectarivorous birds' bills. Only in A. arborescens was there no curvature, but here polypetally made the corolla quite flexible. The flowers of most of these species were red or pink; some were orange (Table 2.4). Lack of scent is typical of ornithophilous flowers, and in this study only P. caffra had a scent detectable to my nose.

All the tubular flowers faced outwards or downwards, and all except L. leonurus had a long flexible peduncle. The protea heads opened upwards. G. sutherlandii flowers faced in all directions, forming an ovoid inflorescence (Table 2.4).

Although some species of birds showed preferences for the nectars of particular plants, they were remarkably catholic in their feeding (see Chapter 3), taking the nectar from flowers with a wide diversity of size and form.

I tried to compare foraging rates of Greater Doublecollared Sunbirds, Lesser Doublecollared Sunbirds and Gurney's Sugarbirds at A. arborescens flowers by recording the number of flowers visited and the length of the foraging bout. The average handling times per flower for the three species were 10,8 s,

6,7 s and 8,7 s (n = 166, 61 and 40) respectively; but the results were very variable and there were no significant differences ( $t$ -test:  $P > 0,1$ ). Measurement of the residual volume of nectar in flowers after visits by different bird species feeding at A. arborescens, H. lucida and L. leonurus (Table 2.5) showed a significant difference in the abilities of the birds to extract nectar only in the case of the Lesser Doublecollareds at A. arborescens flowers. This bird removed significantly less nectar from these flowers than the other nectarivorous bird species which visited them.

With its long corolla tube, P. aequalis almost completely prevented legitimate feeding at its flowers by the nectarivorous birds of this study. The plant's most common visitor was the Greater Doublecollared Sunbird, and yet this bird had to slit the corolla to reach the nectar in the flower. The corollas of all open flowers were pierced, usually in two or three places, and even the Malachite Sunbirds seemed to prefer using these slits to legitimate feeding. Greater Doublecollared Sunbirds left a mean nectar residue of only  $0,61 \mu\text{l}$  (n = 16) in the P. aequalis flowers visited in this manner.

Cape White-eyes, with their short sharp beaks, pierced H. lucida flowers at the base of the corolla to get at nectar. However, only 6,8% of the flowers were found to be pierced, and the birds observed seemed to spend far more time foraging for insects near the flowers than in nectar-feeding.

TABLE 2.5

Residual nectar volumes in flowers measured immediately after feeding visits by nectarivorous birds. Figures in parentheses show sample sizes.

Flowers visited	Nectar residue ( $\mu\text{l}$ ) after visit by			
	Gurney's Sugarbird	Malachite Sunbird	Greater Doublecollared Sunbird	Lesser Doublecollared Sunbird
<u>H. lucida</u>	-	0,35 (27)	0,58 (61)	-
<u>L. leonurus</u>	-	0,41 (50)	0,35 (48)	0,22 (21)
<u>A. arborescens</u>	0,19 (12)	-	0,24 (27)	6,16 <sup>*</sup> (14)

\*Significantly different ( $t$ -test,  $P < 0,05$ ) from other species at the same flowers.

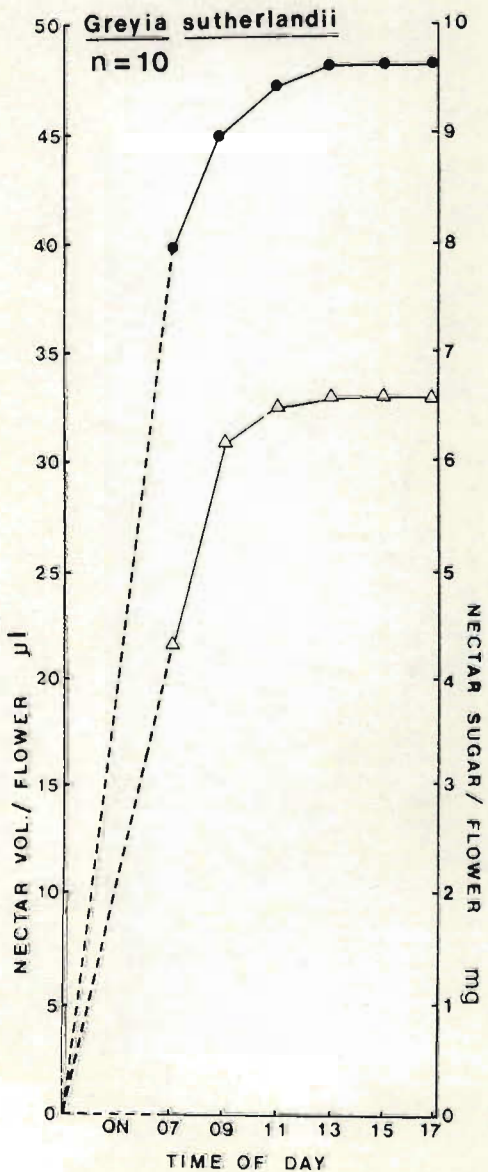
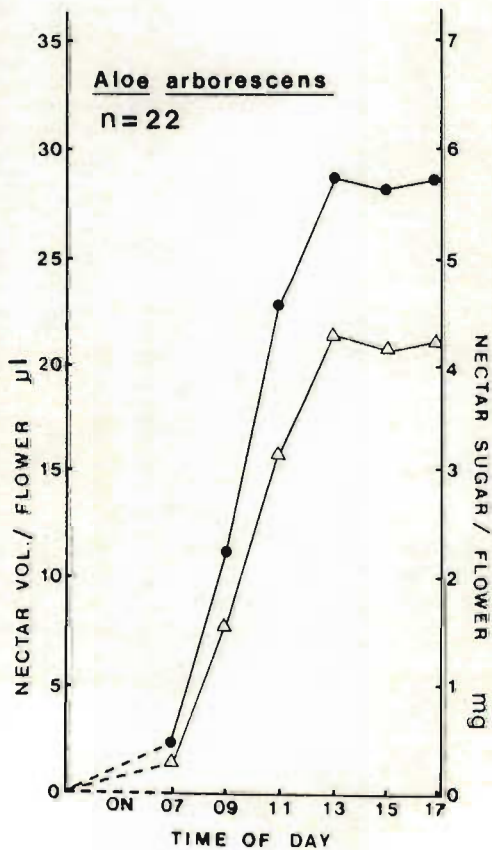
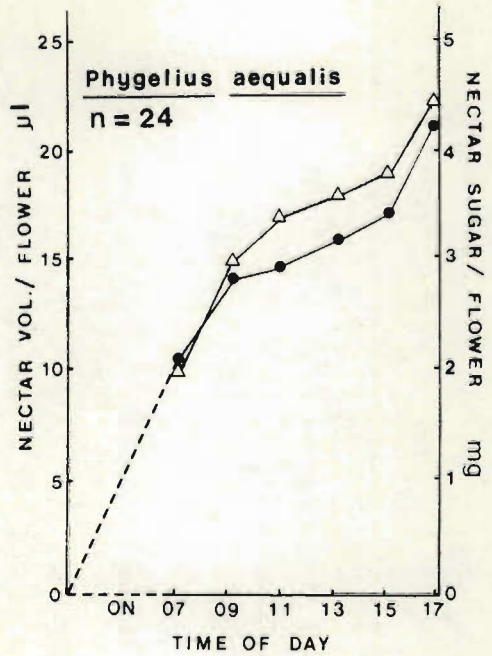
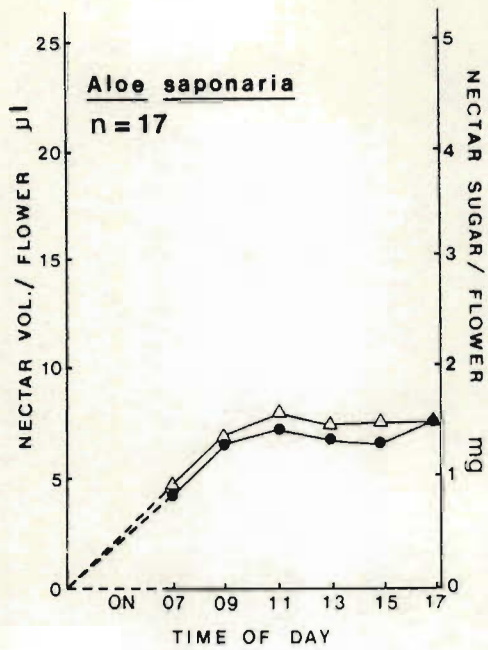
Cape White-eyes, Blackeyed Bulbuls and Redwinged Starlings were all seen visiting G. sutherlandii, A. arborescens and P. caffra for nectar. At the first two plant species this was done legitimately. At A. arborescens, however, white-eyes took nectar by inserting the bill between the petals at the base of the corolla; starlings and, in particular, bulbuls crushed the base of the flower between their mandibles. In this way bulbuls did much damage to A. arborescens inflorescences in the Podocarpus forest. It must be noted that some or all visits of occasional nectar-feeders to P. caffra may have been to feed on the insects common in these flower-heads, rather than on nectar. Visits to G. sutherlandii were common, particularly by Redwinged Starlings, and were undoubtedly made to feed on this plant's copious nectar.

### 2.3.2 Nectar production

Most of the eight plant species important to the avian nectarivores started secreting nectar early in the morning, reaching a maximum accumulation between 11h00 and 13h00 (Fig. 2.2). Nectar production before 07h00 was regarded as overnight production. Most of this "overnight" production usually occurred between 05h00 and 07h00, although the exact pattern of production between 17h00 and 07h00 was not elucidated.

Results of nectar-sugar production measured by the water-extraction method (Method B) are shown and compared with the usual capillary-tube procedure (Method A) in Fig. 2.3. In L. leonurus Method B gave a similar amount and pattern of sugar production to Method A, but with more accuracy because of the





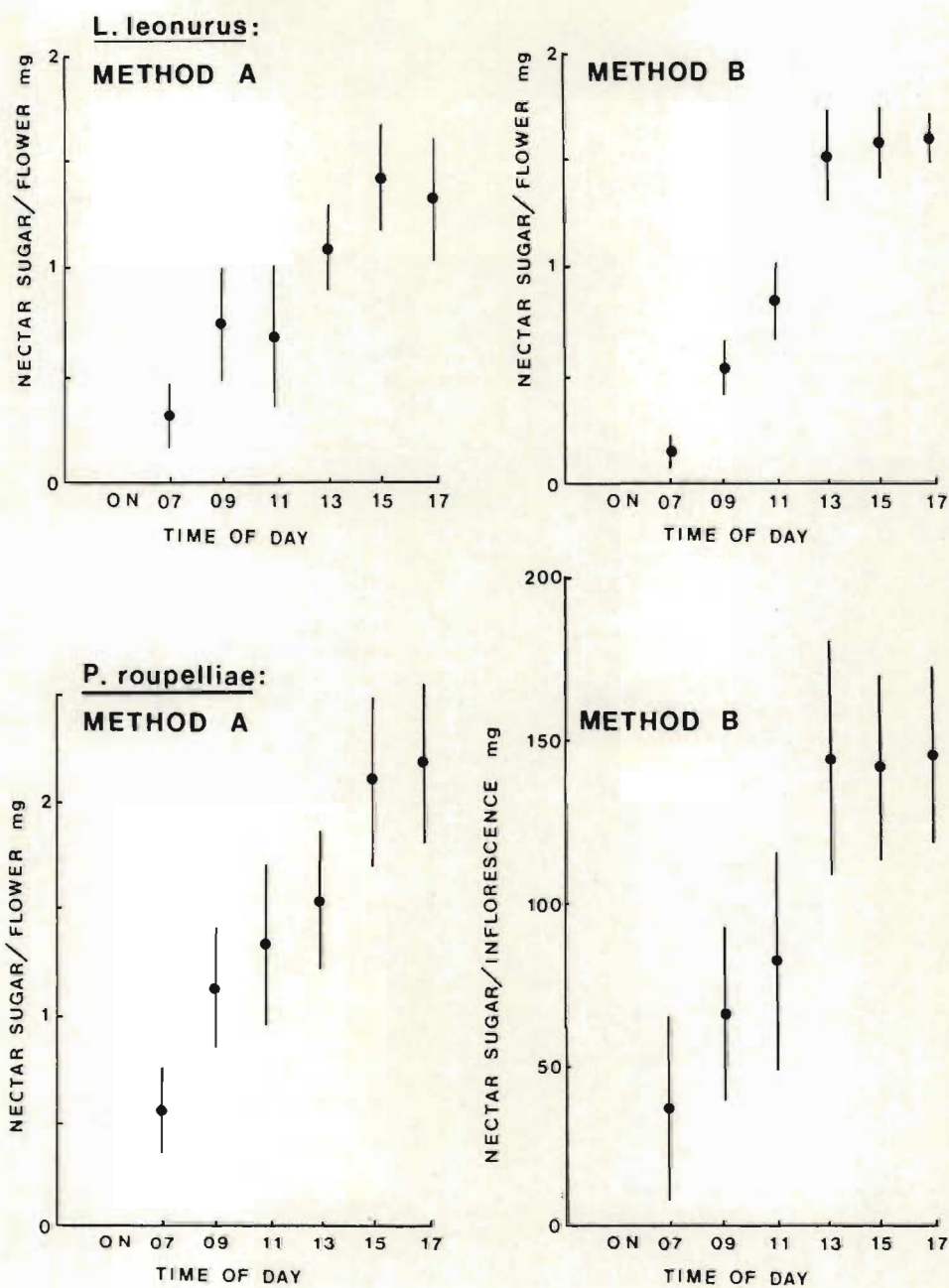


FIGURE 2.3 Comparison of the two methods used to determine nectar production in *L. leonurus* and *P. rouPELLIAE*. Method A is by removal of nectar with capillary tubes; Method B is by extraction with water. Vertical bars represent 95% confidence limits.



large sample size and the speed which this method allowed. The pattern of sugar production was similar for both methods in P. roupelliae, although the amounts cannot be compared because I used Method A on separate flowers and Method B on whole inflorescences. Both methods gave very variable results for P. roupelliae, but this would be expected because of the small sample sizes, particularly in Method B of only 10 inflorescences which varied in age and size. Method B may be useful in future nectar-production studies, particularly when sampling of large numbers of individual flowers in a short time is required.

G. sutherlandii and A. arborescens produced the largest nectar volumes per flower and had low nectar concentrations (Fig. 2.2; Table 2.6). Total sugar reward per flower varied from 1,3 mg sucrose/day in L. leonurus to 6,7 mg sucrose/day in G. sutherlandii (see Table 3.1, p 87).

### 2.3.3 Feeding activity of the birds

Patterns of pollinator activity at A. arborescens and L. leonurus followed the rate of nectar production quite closely; foraging commenced soon after nectar production started and increased in intensity as the rate of nectar production increased, but in a delayed fashion, with the birds' foraging responding to changes in nectar production in the previous time interval in the plots (Fig. 2.4).

TABLE 2.6

Sugar concentrations, sugar constituents and sucrose/hexose ratios, and amino acid concentrations of the nectars of the eight major plant species attracting nectar-feeding birds. ND = not detected.

Species	Nectar concentration % min.-mean-max.	Nectar-sugar composition				Amino-acid concentration: mean on the "Histidine scale"
		% glucose	% fructose	% sucrose	sucrose/hexose ratio	
<u>H. lucida</u>	19,2-21,3-25,9	19	40	41	0,69 = sucrose-rich	1,25
<u>L. leonurus</u>	22,6-24,4-25,4	31	34	35	0,54 = sucrose-rich	2,20
<u>A. arborescens</u>	11,6-13,2-14,4	39	47	14	0,16 = hexose-rich	4,75
<u>A. saponaria</u>	16,4-19,6-22,0	37	45	18	0,22 = hexose-rich	5,33
<u>P. aequalis</u>	16,2-19,7-23,0	30	33	37	0,59 = sucrose-rich	0,45
<u>G. sutherlandii</u>	09,4-11,4-17,6	45	55	ND	0,00 = hexose-dominated	2,63
<u>P. caffra</u>	11,4-12,5-14,0	45	55	ND	0,00 = hexose-dominated	3,50
<u>P. roupelliae</u>	13,2-19,5-22,5	42	50	08	0,09 = hexose-dominated	0,55
Mean	17,7	36	45	19	0,29 = hexose-rich	2,58

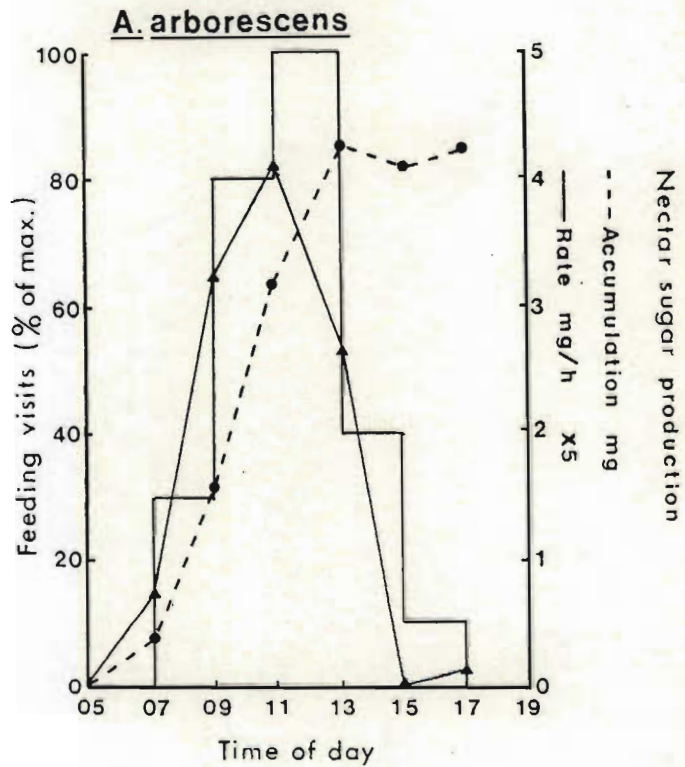
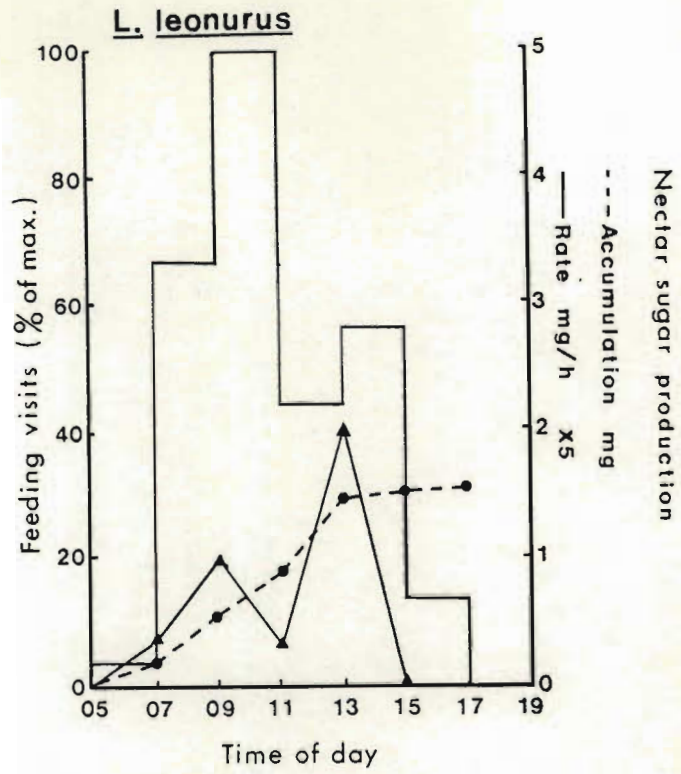


FIGURE 2.4

Nectar-feeding activity of birds (histograms) at A. arborescens and L. leonurus in relation to patterns of daily nectar-sugar production. (Broken lines indicate cumulative nectar-sugar and solid lines indicate the rate of nectar-sugar production per flower)

#### 2.3.4 Nectar quality

Mean nectar concentration ranged from 11,4% in G. sutherlandii to 24,4% in L. leonurus; the plants which produced the smaller nectar volumes generally had more concentrated nectars (Fig. 2.2; Table 2.6). Most nectars were high in glucose and fructose, with a mean sucrose/hexose ratio of 0,29 for the plants in this study, although three species - H. lucida, L. leonurus and P. aequalis - were classified as sucrose-rich according to the terminology of Baker & Baker (1983).

Amino-acid concentrations were generally low in the nectars, with an average of 2,58 on the "Histidine Scale". The amino-acid concentrations were not sufficient to influence significantly the refractometer measurements of nectar-sugar concentrations (Inouye et al. 1980). No proteins were detected in any of the nectars.

#### 2.3.5 The importance of the birds as pollinators

In all the plant species investigated, except P. caffra, the exposed inflorescences had significantly greater seed-set than those in cages which excluded birds ("bird mesh") and both birds and insects ("insect mesh") (Table 2.7). There was no significant difference between the two caged treatments in any of the plant species. P. caffra was the only plant which showed no significant difference between any of the treatments and if anything it had a higher seed-set in inflorescences enclosed to exclude all animal pollinators. I have no data for such experiments on A. saponaria because the exclusion cages were destroyed by baboons.

TABLE 2.7

The seed-sets under different treatments to selectively exclude potential pollinators of the plant species studied. N = number of inflorescences in each treatment; n = number of flowers examined for seed-set from each inflorescence. F = F-value for the one-way analysis of variance (ANOVA) on the original data. Where this proved significant each pair combination of treatments was tested (Student-Newman-Keuls test) to establish which were significantly different (\* $P < 0,05$ ; \*\* $P < 0,01$ ).

Species	N	n	% seed-set in treatments			F	Degrees of freedom
			birds and insects excluded	birds excluded	exposed		
<u>H. lucida</u>	8	20	8,7	16,3	52,5**	24,7	2, 21
<u>L. leonurus</u>	10	20	5,0	6,5	41,0**	19,3	2, 27
<u>A. arborescens</u>	5	100	47,8	47,0	73,0**	7,3	2, 12
<u>P. aequalis</u>	8	20	3,1	6,9	40,0**	43,4	2, 21
<u>G. sutherlandii</u>	5	40	5,2	5,0	15,6*	5,5	2, 12
<u>P. caffra</u>	10	30	27,0	21,7	25,7	0,2	2, 27
<u>P. roupelliae</u>	6	40	0,8	1,7	8,8**	22,4	2, 15

## 2.4 DISCUSSION

### 2.4.1 Flower colour and presentation

There is a distinct tendency for colours of ornithophilous flowers to be at the red end of the colour spectrum (Skead 1967; Grant & Grant 1968; Miller & Miller 1971; Faegri & van der Pijl 1979; Rebelo & Siegfried 1985). The ornithophilous flowers in this study were mostly red, with some pink and orange. Although this trend is clear, the reasons for it are not. Work on hummingbirds has shown that the birds have no colour preferences and are sensitive to a wide range on the colour spectrum (Miller & Miller 1971; Miller et al. 1985). Waser (1983a) suggested that colour serves as an advertisement, and that the floral nectar reward is the ultimate attractant; the birds learn to associate colour advertisement and its position with reward (Miller et al. 1985), and reward alone seems to dictate their flower preferences (McDade 1983). Certainly the nectarivorous birds of this study were observed taking nectar from many different coloured flowers, often in gardens near the study area (see also Skead 1967; Rebelo et al. 1984). Perhaps red flowers contrast most sharply with green foliage. This subject is a much debated one and there are as yet no clear answers (see also Bené 1941; Grant 1966; Raven 1972; Goldsmith 1980; Welker 1984; Rebelo et al. 1985). Work on nectarivorous bird groups other than hummingbirds is needed, and may help to interpret this phenomenon.

Unlike many hummingbird-plants (Grant & Grant 1968; Faegri & van der Pijl 1979), the ornithophilous plants in this study provided the birds with a perch near their flowers. In the proteas the whole inflorescence served as the perch. The individual flowers of H. lucida arose straight from the branches and trunk. The other species had sturdy stems supporting the inflorescence to act as a perch. It is for this reason that sunbird- and sugarbird-plants are generally thick-stemmed and perennial (see also Siegfried et al. 1985).

In the plant species of this study in which the flowers hung downwards, the peduncle was long and flexible and the birds were able to manipulate the tubular flower easily to the desired angle. This was particularly important in a plant like H. lucida where the perch was often above the pendulous flowers. In those plants which had a stiff peduncle (see Table 2.4) the flowers were fixed in a position suitable for extraction of nectar in relation to the perch provided. Consistency in perch-position and flower arrangement, such as that found in L. leonurus and A. arborescens, would increase the birds' rate and thoroughness of foraging and enhance the fidelity of pollen transfer. This would apply particularly to L. leonurus with its consistent flower orientation.

#### 2.4.2 Flower morphology and nectar robbing

In the plants with fixed flower positions (i.e. with a short stiff peduncle) the nectar was protected by thick fleshy bracts subtending the inflorescence (proteas), or an extended calyx (L.

leonurus), and crowding of the flowers in the inflorescence. Only G. sutherlandii had no protection, but its weak nectar probably deterred illegitimate insect visitors (see p 55).

In all the tubular flowers of this study (except in L. leonurus with its fixed flower position, calyx and crowding) the corolla was the main nectar-protecting feature (Roubik 1982). The corollas were long and tough and, in all but A. arborescens, sympetalous. Another protective feature may have been that they all had long flexible peduncles which would make corolla-piercing, particularly by birds, difficult because there is little against which to brace the flower. These features might explain why Cape White-eyes had pierced only 6,8% of H. lucida flowers for nectar, and preferred to search among the flowers and in the mouths of corollas for small insects; in this way they may play a part in pollination. It is interesting, though, that Greater Doublecollared Sunbirds were very aggressive towards Cape White-eyes, often chasing them away from H. lucida, suggesting that there was some competition between these species.

In my study P. aequalis was visited almost entirely by Greater Doublecollared Sunbirds which were never seen to take nectar in the legitimate manner at this plant. This was probably because their bills were not long enough for them to reach the nectar from the mouth of the corolla. Malachite Sunbirds also visited these flowers, usually in the way the Greater Doublecollared Sunbirds did: by inserting the bill into a slit in the corolla. This plant seems to have attempted to protect its nectar from



nectar robbers with so long a corolla that legitimate removal of nectar is impossible, or less worthwhile, at least for the birds in the study area. A similar situation was found by Greig-Smith (1980) in a study of the Seychelles Sunbird N. dussumieri: in eight out of 26 plants visited by the birds nectar removal was solely by piercing the long corollas.

In the absence of Greater Doublecollared Sunbirds, Malachite Sunbirds may feed legitimately at P. aequalis, but in my observations they preferred to use the slits made by the smaller birds. In 77% of visits in which I recorded their foraging behaviour, Greater Doublecollared and Malachite Sunbirds probed the slits from behind the flower and no pollen transfer could take place; 23% probed slits from in front of the flower in which case the stamens often contacted the birds' breast feathers. This probably effected some pollination. The rough treatment of the flowers by the foraging birds could also bring about pollination if P. aequalis is self-fertile (Inouye 1983). Pollinator-exclusion experiments with this plant indicated that about 83% of the 40% seed-set was as a result of bird visitation (Table 2.7). So even seemingly illegitimate nectar-removal probably does somehow play an important part in the pollination of P. aequalis. A further point is that P. aequalis flowers in some other parts of the Drakensberg (e.g. Garden Castle) were found to have shorter corolla tubes than those in this study, but I have not made observations of nectar-feeding or investigated seed-set in these areas.

### 2.4.3 Bird feeding morphology, flower morphology and nectar concentration

Elegant partitioning of nectar resources among coexisting avian nectarivores has often been linked with close correlations in flower and bird morphologies, particularly concerning variations in corolla and bill length (Snow & Snow 1972, 1980; Colwell 1973; Stiles 1975; Feinsinger 1976, 1983a; Wolf et al. 1976; Brown & Bowers 1985).

This study revealed a lack of such clear partitioning (see Chapter 3): nectarivorous bird species with diverse bill lengths fed on the nectars of flowers with a wide range of morphology and, notably, effective corolla lengths. All four bird species, for example, fed legitimately and voraciously on the nectar of H. lucida which was certainly out of the reach of the bills of Lesser Doublecollared Sunbirds, and probably of those of Greater Doublecollared Sunbirds and Gurney's sugarbirds as well. The picture of a straightforward correspondence between bill length and corolla length, often indicated by the literature, is undoubtedly an oversimplification.

In the hand, the nectarivorous birds in this study were all capable of protruding their tongues well past the tip of the bill. This was a very rapid movement. Such protrusibility of the tongue is widely known in sunbirds and hummingbirds (Skead 1967; Hainsworth 1973; Schlamowitz et al. 1976; Hainsworth & Wolf 1979). The nectar-feeding mechanisms of sunbirds and hummingbirds (and probably sugarbirds - see tongue morphologies

in Skead (1967)) are very similar and show striking convergence. The birds rely largely on licking (moving the tongue in and out) to take up nectar. Most of the nectar ingested by this process is via the twin grooves of the tongue, and it seems to be taken in purely by capillary flow (Hainsworth 1973; Schlamowitz et al. 1976; Ewald & Williams 1982; Montgomerie 1984). The brush-like tip of the birds' tongues accounts for less than 10% of the nectar uptake per lick (Ewald & Williams 1982), whereas white-eyes appear to rely solely on their brush-tongues to imbibe nectar (Skead 1967; Moreau et al. 1969).

Thus, protrusion of the tongue extends the feeding reach of a bird. This must explain, for example, how Lesser Doublecollared Sunbirds (culmen length 22,8 mm) were able to feed legitimately on the nectars of H. lucida (corolla length 29,6 mm) and A. arborescens (corolla length 34,1 mm).

It has been shown, however, that increasing corolla length linearly reduces nectar uptake by a given bird (Hainsworth 1973; Schlamowitz et al. 1976; Kingsolver & Daniel 1983; Montgomerie 1984). This reflects a reduction in "lick volume". Thus to have a bill as long as, or longer than, the corolla is an advantage in that uptake rate is increased. Curvature of the bills of nectarivorous birds may also enhance nectar-uptake rates: this appears to be the case for honeycreepers (Carothers 1982). The bill-corolla correlations observed by some studies are thus in many cases reflections of optimal feeding relations and not necessarily exclusive ones. (It is interesting that there is a

positive correlation between culmen length and the rate of uptake of a set nectar in the absence of a corolla (Montgomerie 1984). This probably also relates to increased tongue length and therefore "lick volume". It thus appears to be an advantage to have a long bill, irrespective of flower morphology.)

The importance of such optimization of intake rates is difficult to gauge. Intake rates have been established for the Bronze Sunbird Nectarinia kilimensis (15-17 g) at varying corolla lengths (Schlamowitz et al. 1976). There was a reduction from an intake of 26,7  $\mu\text{l/s}$  at a corolla length of 20 mm, to 18,1  $\mu\text{l/s}$  at a corolla length of 30 mm (which was probably just longer than the birds' bill length: the authors did not state the culmen length of their study birds; this was taken to be a mean of 28 mm (Maclean 1985)). Unfortunately Schlamowitz et al. (1976) did not conduct experiments with corollas longer than this. Hainsworth (1973) found maintenance of a linear fall-off in the rate of nectar uptake from corollas much longer than the bill length for hummingbirds (e.g. Blackchinned Hummingbird Archilochus alexandri), although uptake was still possible from a corolla of over twice the bill length (assuming the culmen length of 20 mm for the Blackchinned Hummingbird given elsewhere in Hainsworth (1973)). At twice the bill length, uptake by this tiny bird of 3,3 g was about 4  $\mu\text{l/s}$ . Fitting a straight line to the data of Schlamowitz et al. (1976) gave a more rapid drop in uptake rate with an increase in corolla length, with uptake still possible at just over 1,5 times the bill length. However, even at a corolla length of 1,5 times the bill length the uptake would be about 3,5

$\mu\text{l/s}$ . These crude extrapolations suggest that much of the birds' time would be spent moving between flowers and that flower spacing, rather than intake time, would be important since nectar removal seems rapid even at corolla lengths greater than the bill length.

I tried to compare the foraging rates of the different bird species at A. arborescens flowers (p 29). The results showed great variability, with no significant differences among the three bird species examined. The results were, however, very inaccurate - partly because the birds seemed to "waste" a lot of time during foraging bouts. They also did not forage continuously: less than 75% of their time in view was spent on nectar-feeding activity. This could have been for many reasons, but suggests that handling time may not always be as important to these animals (with their high-quality food) as some researchers seem to imply by the importance they attribute to intake rates (e.g. Carothers 1982; Kingsolver & Daniel 1983; Tamm & Gass 1986: see later discussion).

More important was the amount of nectar removed from a flower with a long corolla by birds with differing bill lengths. Of the combinations of bird-plant visits I investigated (Table 2.5), only the Lesser Doublecollared Sunbird visiting A. arborescens showed a significant difference from other species in its ability to extract nectar. Nearly all the nectar was removed from flowers in the other bird-flower combinations. The reason for this must be that the corolla of A. arborescens (34,1 mm long) is longer than the feeding reach of the Lesser Doublecollared

Sunbirds, preventing these birds from removing all of the nectar. At L. leonurus flowers (26 mm long) the Lesser Doublecollared Sunbirds could remove as much as, or even a little more than, the other bird species. It would thus appear that the feeding reach of these birds is between 1,1 and 1,5 times the culmen length - rather less than for hummingbirds. This may invalidate the rough extrapolations I made earlier (p 47) for intake rates at long corollas from the sunbird data of Schlamowitz et al. (1976).

Nectar-energy reward is a function of both nectar volume and nectar concentration. The obviously high energy requirements of large endothermic pollinators (Cruden et al. 1983) probably led Percival (1974) to state that bird-nectars are relatively concentrated. Baker (1975) and Pyke & Waser (1981) dispute this statement. Baker (1975) amassed data on nectar concentrations of hummingbird-flowers. He found means of 22-24% for various areas (range 12-34%) compared with means of 30-48% for bee-flower nectars. The passerine-pollinated flowers in my study had nectars with a mean concentration of 17,7% (range 11,4-24,4%), somewhat lower than the hummingbird-flower data. This could be caused by many factors, but, if it is a general trend, it would not be surprising because hummingbirds are generally smaller birds and hover frequently when foraging: their energy demands (by weight) are thus larger than those of sunbirds (Lasiewski 1963) and higher nectar concentrations may be necessary to sustain them. In the Cape, however, Siegfried & Rebelo (1986) found nectar concentrations of 18,3-29,6% in ten sunbird- and

sugarbird-pollinated Erica species, which gives a range similar to that of hummingbird-nectars.

Nectar concentration affects the rate of uptake by the birds (Hainsworth 1973; Schlamowitz et al. 1976; Collins et al. 1980; Montgomerie 1984) because of an exponential increase in viscosity of the nectar with increasing concentration and the consequential reduction in rate of capillary flow (Baker 1975).

Heyneman (1983) and Kingsolver & Daniel (1983) used models to predict optimal nectar concentration for hummingbirds, and (to some extent) sunbirds, based on the birds' feeding morphology and behaviour. They concluded that optimal sugar concentrations were 20-25% sucrose for maximum sugar flux (energy intake) for a continuous capillary flow system. Kingsolver & Daniel (1983) contended, however, that the licking action of hummingbirds and sunbirds describes discontinuous flow, i.e. nectar is not taken up in a continuous stream by this process: the stream is broken with each licking cycle. The optimum nectar concentration under these conditions would be 35-40% sucrose. Thus large nectar volumes per flower, which require many licks, may be expected to have these higher nectar concentrations to maintain optimal rate of uptake. Small nectar volumes which could be taken up in one lick would be better represented by the continuous model and could be expected to have concentrations of 20-25% (Kingsolver & Daniel 1979, 1983).

In the flowers of my study the nectar concentration ranged from 11,4 to 24,4% (Table 2.6). Five of the eight nectars were

between 19 and 25%. These would fit well into Kingsolver & Daniel's (1983) model only if the volumes of nectar could be taken up in a single licking cycle (i.e. by continuous flow). The nectar volume production of these flowers was 5-20  $\mu\text{l}$ /day. Whether or not the volume in a flower could be taken up in one licking cycle would depend on the time of day, previous visitation, corolla, bill and tongue lengths, etc., but would often exceed one "lick's worth". Schlamowitz et al. (1976) found lick volumes for N. kilimensis of 4-12  $\mu\text{l}$ , but Ewald & Williams (1982) criticized analysis of film taken at 18 frames/s, as it was in these determinations. Ewald & Williams (1982) used 70 frames/s in studies on hummingbirds and found that licking rates were up to five times greater than Hainsworth (1973) had found using 18 frames/s. This suggests that the lick-volume results of Schlamowitz et al. (1976) are probably greatly over-estimated.

Furthermore, Kingsolver & Daniel's (1983) model does not hold for the larger volumes. G. sutherlandii has the largest nectar volume and the weakest nectar concentration - less than a third of that predicted. It is possible that Kingsolver & Daniel's presumption that licking entails discontinuous flow is incorrect for sunbirds: it is not known how the tongue is "emptied" in sunbirds once a load has been taken up. If this allowed continuous flow, or if some slight suction were involved, as Liversidge (in Skead 1967) suggested, then the optimal concentration would remain at the 20-25% predicted by the continuous models. Schlamowitz et al. (1976) stated that suction was impossible for sunbirds and hummingbirds because of the open



nature of their lingual grooves. They did suggest, however, (and for reasons other than those being discussed) that "For the sunbirds, the extension of the groove over the entire length of the tongue could allow for movement of nectar back into the throat in a continuous stream..."; it would seem that this is a plausible idea.

Further, Kingsolver & Daniel's (1983) ideal of 35-40% nectar concentration for large nectar volumes is inconsistently encountered in nature. They claimed that their "predictions are consistent with present evidence on the nectar concentrations in flowers visited by hummingbirds." They gave several references to support this statement (Baker 1978; Bolton & Feinsinger 1978; Baker, I. & Baker, H. G. 1982; Pyke & Waser 1981; Feinsinger et al. 1982), but many data in the same references and in others (Baker 1975; Hainsworth & Wolf 1972a, 1976) do not support their model.

Yet another point is that these models are unrealistic because they measure optima for the birds, but do not consider the plants. For example, large volumes of very concentrated nectar would be energetically costly for a plant to produce. And such production would reduce pollen flow through a reduction in the number of feeding visits by the pollinator; plants must find a balance between reward size and spacing which keeps their pollinators healthy but moving. Large volumes of concentrated nectar would encourage indolence unless, as is the case in those plants that do support the model, flowers are few and scattered.

What of the very low nectar concentration of G. sutherlandii? This flower has no effective corolla as defined on p 13. As discussed earlier, this would allow of rapid nectar uptake, and although the optimum for the nectarivorous birds may still be as Kingsolver & Daniel (1983) predicted, this and other factors will be influencing nectar concentration. For example, G. sutherlandii attracted large numbers of occasional nectar-feeding birds, as well as nectarivorous ones, and these undoubtedly play a role in pollination of the plant. It is not clear exactly how birds like bulbuls and starlings take up nectar, but their tongue structures are certainly very different: none contains the twin grooves of sunbird and sugarbird tongues. Kingsolver & Daniel's (1983) model cannot thus apply. Such birds seem to need large nectar-volumes in order to take up nectar (Cruden & Hermann-Parker 1977; Cruden & Toledo 1977): the three species of plant visited by these large occasional nectar-feeders had the most dilute nectars and among the largest nectar volumes (see also Oatley & Skead 1972; Jacot Guillarmod et al. 1979). All the plant species in this study which attracted starlings and bulbuls had very little or no sucrose in their nectars - a feature common in "oriole/starling" flowers (Cruden et al. 1983). Are these plants catering to attract these large pollinators? I believe this is the case at least in G. sutherlandii, judging by its massive nectar-volume and flower production, floral morphology and regular visitation by both occasional nectar-feeding and nectarivorous birds.

Clearly the models of Heyneman (1983) and Kingsolver & Daniel (1979, 1983) are unavoidably simplistic: nectar concentration relies on a vast number of variables.

Another interesting aspect concerning nectar concentration is that of nectar viscosity and its dramatic increase with a decrease in temperature (Baker 1975). The high altitude of my study area and concomitant lower temperatures would make weaker nectars easier to take up. It would be interesting to compare the nectar concentrations of plants such as H. lucida, L. leonurus and A. arborescens from this study with those of the same species growing in lowland areas of Natal. Some hummingbird-flower studies have shown a distinct pattern of decreasing nectar concentrations with increasing altitude and latitude (Hainsworth & Wolf 1972b; Hainsworth 1973; Pyke & Waser 1981; Cruden et al. 1983). However, the nectar concentrations of L. leonurus in this study were very similar to those found by Frost & Frost (1980) for this species on the coast of Natal.

A further factor encouraging low nectar concentrations might be the metabolic water requirements of the birds, but Calder (1979) and Calder & Hiebert (1983) have shown that even under hot, dry conditions hummingbirds take in enough water in their nectar-feeding to meet their metabolic demands; indeed, diuresis often occurs (Calder & Hiebert 1983). I did not observe nectarivorous birds drinking during my study, and reports of drinking for sunbirds are not common (Skead 1967). In any case they are capable of drinking free water and there was never any shortage of this in the study area.

I thought that nectar concentration might affect assimilation efficiency by the birds, and that this could influence the quality of nectar. Chromatographic analysis of the cloacal fluid from three Greater Doublecollared Sunbirds, two Malachite Sunbirds and a Gurney's Sugarbird revealed no traces of reducing sugars. This method of detection was sensitive down to  $<0,42 \mu\text{g}$ . Thus in the  $1 \mu\text{l}$  of fluid spotted there was less than  $0,42 \mu\text{g}$  reducing sugar, or  $<0,42 \text{ g/l}$ . In the case of the Greater Doublecollared Sunbirds, one was caught while feeding extensively on G. sutherlandii, one on H. lucida and one on L. leonurus. No sugars were detected in any of the cloacal fluid samples. This means roughly that less than  $0,42 \text{ g/l}$  was escaping assimilation in each case, despite the differences in concentrations of the nectars consumed. Thus, very approximately, over 99% of nectar-sugar consumed was assimilated in all three cases (assuming that the birds had not been drinking water and that they had a regular water excretion). In laboratory experiments with hummingbirds (Hainsworth 1974) and honeyeaters (Collins & Morellini 1979), the birds had assimilation efficiencies of 97->99%, with no relationship to the concentration of nectar supplies. It thus appears that nectar concentration does not affect the amount of sugar assimilated, although it could affect passage time.

Competition with other pollinators has also been implicated as influencing the concentration of nectar produced by plants. Bolten & Feinsinger (1978) predicted that ornithophilous flowers with nectar accessible to bees would have lower concentrations

than nectars exclusively reached by hummingbirds. They based their hypothesis on the apparent preferences of bees for the more concentrated nectars and the possibility that lower concentrations deter them from illegitimately visiting more open flowers. Their data supported their hypothesis and there was a significant positive correlation between nectar concentration and corolla length.

A similar pattern was found by Hainsworth & Wolf (1972a) and Wolf et al. (1976). Pyke & Waser (1981), however, found that this trend was inconsistent with their compilation of data; but I think their averaging of such a wide range of information has probably obscured trends which may be clearer on a more local scale. My data are few, but do support this hypothesis. More open flowers did tend to have less concentrated nectar, and, while bees showed little interest in G. sutherlandii nectar, which they could easily have reached, they were often observed trying to squeeze into H. lucida flowers, apparently in a bid to reach the nectar.

An important consideration ignored in nearly all discussions of nectar concentration is the effect of rainfall. In my study area there is an average of 105 raindays a year (Tyson et al. 1976). After a heavy rainfall the nectar concentration in the open flowers of G. sutherlandii fell to a mean of 1,2% ("normal" = 11,4%), with a concomitant rise in nectar volume. By contrast, after the same storm, H.lucida, with its fused corolla and out-or down-facing flowers, had a nectar concentration of 20,0% ("normal" = 21,3%) after the same storm. A sympetalous corolla

tube also moderates the effects of evaporation: G. sutherlandii flowers (protected from birds) had a nectar concentration of 17,6% at the end of a dry day, compared with 10,4% for freshly secreted nectar. Again, by contrast, H. lucida nectar rose in concentration by only 2,4% over the same period. Southwick et al. (1981) found evaporation to have a strong effect on the nectar concentrations in open entomophilous flowers.

Assuming that the concentration of nectar secreted is constant throughout the day, such a stabilization of concentration afforded by a tubular corolla must surely be an important function of this floral character. This could be particularly important in flowers which produce more concentrated nectar because a slight rise in concentration would cause a sharp increase in viscosity (Baker 1975; Montgomerie 1984) which could vitiate the birds' feeding. The low concentration of nectar produced by G. sutherlandii may even be in compensation for its lack of corolla, anticipating daily concentration by evaporation. One might expect plants with cup-shaped flowers to flower in the dry season to avoid nectar dilution by rainwater. This did not appear to occur, however, probably because flowering season depends on many factors (see Chapter 3), and the opposite effect of evaporation is most prevalent when the effects of rain would be lowest (April-September).

In food-choice experiments, Hainsworth & Wolf (1976), Stiles (1976) and Tamm & Gass (1986) showed that nectar concentration was the major factor influencing hummingbird food choice. The

birds took the most concentrated food in preference tests using nectar concentrations below 45-55% (see Tamm & Gass 1986), despite lower efficiency of energy intake. Lower nectar concentration requires increased volume intake per energy gain and thus increased weight of the bird, causing higher foraging costs (DeBenedictis et al. 1978; MacMillen & Carpenter 1977). This is probably more important in hummingbirds, with their small size and expensive hovering during foraging (DeBenedictis et al. 1978). Crop volume is a limiting factor in hummingbird foraging (Hainsworth & Wolf 1972b) and this is probably also important. Limitation would be a direct function of crop volume and nectar-concentration. Although no work of this nature has been done on sunbirds or sugarbirds, such factors probably influence nectar concentration preferences in these bird as well.

#### 2.4.4 Nectar-sugar composition

Baker & Baker (1979, 1983) have shown that there is a relationship between the proportions of sucrose, glucose and fructose in a flower's nectar and its pollinator-type. Hummingbird-nectars tend to be high in sucrose (high sucrose/hexose ratios), and passerine bird-nectars low in sucrose (Table 2.8).

My data support their conclusions insofar as there were no sucrose-dominated nectars in my study and most were either

TABLE 2.8

Percentages of bird-nectars in each of the four sugar-ratio categories, arranged according to the plants' bird pollinator group; extracted from Baker & Baker (1983). N = number of nectars analyzed in each group.

Bird group	Hexose-dominated	Hexose-rich	Sucrose-rich	Sucrose-dominated	N
Sunbirds	69	26	6	0	35
Honeyeaters	82	18	0	0	22
Honeycreepers	83	17	0	0	6
Hummingbirds	0	13	32	55	140
This study	38	25	38	0	8



hexose-dominated or hexose-rich, the mean for all the nectars being hexose-rich (Table 2.6). However, three (38%) were sucrose-rich, and Siegfried & Rebelo (1986) found three of the four nectars of sunbird-pollinated Erica species which they investigated to be sucrose-dominated. By contrast, only 6% of sunbird-nectars in the data of Baker & Baker (1983) were sucrose-rich or sucrose-dominated. These discrepancies may stem from the small number of nectars examined in my study and that of Siegfried & Rebelo (1986), but suggest that many more sunbird-nectars should be analyzed before the findings of Baker & Baker (1983) can be confirmed.

Baker & Baker (1983) suggested that hummingbirds prefer sucrose-rich nectars because of a "taste" for sucrose in these birds, developed during their original coevolution with bee-flowers which also have high-sucrose nectars. However, Watt et al. (1974) have pointed out that the production of oligosaccharides like sucrose is more costly to plants than secreting monosaccharides; possibly for this reason, most nectars are hexose-rich rather than sucrose-rich (Baker & Baker 1983). That hummingbird-nectars are consistently sucrose-rich and that the birds strongly prefer sucrose-rich nectars (Hainsworth & Wolf 1976; Stiles 1976) suggests that the dominance of sucrose is important, and is not only because of a "taste" for this disaccharide.

There have been no reasons suggested for this. I thought that a sucrose solution may have lower viscosity than glucose or

fructose solutions of equal concentration, and thus enhance uptake rates by birds. However, if anything, sucrose solutions are slightly more viscous (Montgomerie et al. 1984). The answer may lie in the efficiency and rapidity of absorption and assimilation of different sugars and their physiological deployment. Related to this, and possibly affecting water balance, is the observation by Watt et al. (1974) that a solution of oligosaccharides (e.g. sucrose) will exert a lower osmotic pressure than one with an equal concentration of monosaccharides (e.g. glucose or fructose). This would seem to fit with the question of water balance and nectar-feeding mentioned earlier. Hummingbirds, while feeding on nectar, incur large excesses of water (Calder 1979; Calder & Hiebert 1983). The osmotic pressure of the blood will be lower if sucrose has been absorbed from the gut rather than glucose and fructose with the same energy value, since sucrose has about twice the calorific value per molecule (Baker & Baker 1983). The lower osmotic pressure of sucrose per energy gain would reduce water absorption and make water excretion less costly; Calder & Hiebert (1983) described hummingbirds as suffering from "internal flooding", and, unless osmotic work is done to retain body salts, the birds would need almost total replacement of these daily. The small size, high metabolism and foraging costs of hummingbirds would make such considerations very important, and hummingbird-plants may have been impelled to produce the costly sucrose-rich nectar. This theory depends, of course, on there being little or no conversion of sucrose to monosaccharides before absorption; I could find no literature on this subject for hummingbirds, but it has been

shown that both monosaccharides and disaccharides are absorbed by the gut of the domestic fowl (Bogner 1966; Fearon & Bird 1968). A study of digestion and absorption in the gut of hummingbirds and sunbirds may be very enlightening.

#### 2.4.5 Amino acids in nectar

Amino acids occur in detectable quantities in almost all nectars and there is a clear link between amino-acid concentration and pollinator-type (Baker & Baker 1973a, 1973b, 1980, 1986). Baker & Baker hypothesized that bird-nectars are likely to have low amino-acid concentrations, since nectarivory in birds appears to have arisen several times independently and yet all groups supplement their diets of nectar with arthropod food, probably as their primary protein source (Ford & Paton 1976; Baker & Baker 1986). The importance of nectar and arthropods in the diets of nectarivorous birds is discussed more fully in Chapter 4.

Average amino-acid concentrations of 3,5, 3,3 and 3,5 on the "Histidine Scale" have been recorded for sets of data on old-world bird-nectars (Table 1 in Baker & Baker 1986). Means for hummingbird-nectars (new-world) were 5,9, 4,9, 4,2, 3,3 and 4,5. The old-world values are low, as Baker & Baker (1983a, 1973b, 1980, 1986) predicted. The mean for my study of 2,6 also supports their hypothesis. They consider that the higher amino-acid concentrations in hummingbird-nectars (which are relatively

low none the less) may be the result of recent evolution of these plants from the entomophilous condition (Baker & Baker 1973a, 1980). Values for older hummingbird-flower associations in Costa Rica substantiate this, having a mean of 3,3 on the Histidine Scale (Baker & Baker 1986). Heyneman (1983) noted that even small amounts of non-sugar constituents in nectar, like amino acids, can cause large increases in viscosity and thus reduce sugar flux (energy intake). This could be another reason for the low amino-acid concentrations found in bird-nectars.

There was a tendency in this study for flowers with shorter corollas to have low nectar-sugar concentrations, large nectar volumes and higher amino-acid concentrations. This may reflect a recent evolution from entomophily to ornithophily in which G. sutherlandii seems to be at a less advanced stage, through A. arborescens, with its development of a simple polypetalous corolla (unfused), and quite large volumes of fairly dilute nectar with high amino-acid concentration, to typically ornithophilous flowers such as H. lucida, L. leonurus, and P. roupelliae with long effective corollas, smaller nectar volumes, more concentrated nectar and low amino-acid concentrations.

#### 2.4.6 Nectar-energy reward, pattern of production and pollinator activity

Although it is commonly accepted that the nectar-energy reward per flower is generally higher for larger endothermic pollinators, there are few quantitative data on the subject.

Information compiled by Cruden et al. (1983) showed that flowers pollinated by large pollinators with high energy demands (bats, birds and hawkmoths) produce a higher energy reward than flowers pollinated by "low-energy" insects (Table 2.9). Cruden et al. (1983) found a wider range and higher mean sugar reward in sunbird-flowers than I did in my study, but they are relatively close, and both are based on a rather small sample of plant species. Together with my data, the means for sunbird- and hummingbird-flowers are strikingly close when compared with the other groups. The wide range of rewards per flower within a pollination syndrome are a consequence of a host of factors, many already discussed, but most particularly that of flower density mentioned earlier in connexion with the importance of energy intake rates. This aspect is addressed in Chapter 3.

Cruden et al. (1983) found that, in general, nectar production started 1-4 h before initiation of pollinator activity, with maximum accumulation (i.e. a halt in daily nectar production) occurring at about this time. The patterns of nectar production observed in this study were typical of bird-flowers, nectar production occurring during the day. Other high-reward flowers, attracting bats and hawkmoths, produce nectar nocturnally and competition between these animals and birds hardly occurs (Baker 1961, 1973, 1978; Scogin 1980; Helversen & Reyer 1984). In the plant species at which I monitored bird visitation over the day (Fig. 2.4), the bird feeding activity more closely followed the rate of nectar production and related less clearly to maximum accumulation of nectar in the flowers. A similar trend is also

TABLE 2.9

Nectar-sugar production per flower per day in plant species grouped by pollinator class. All data extracted from Cruden *et al.* (1983), except those from this study. N = number of plant species.

Flower pollinator class	mg sugar/flower/day		N
	mean $\pm$ S.E.	range	
Bat	26,5 $\pm$ 6,4	10,2 - 43,6	5
Hummingbird	2,9 $\pm$ 0,6	0,3 - 12,0	18
Sunbird	3,4 $\pm$ 1,0	0,2 - 9,2	9
Bee	0,7 $\pm$ 0,2	0,002 - 6,2	63
Butterfly	0,4 $\pm$ 0,1	0,02 - 0,7	10
This study	3,0 $\pm$ 0,6	1,3 - 6,7	8

apparent in the data of Frost & Frost (1980) for sunbirds visiting L. leonurus (although they found a much higher nectar production and a slightly different pattern of production in the plants of their study).

I think this trend is to be expected. Both A. arborescens and L. leonurus produced very little nectar until about 07h00, at which time foraging started. It would be to the advantage of all birds to start feeding several hours after production started, when nectar rewards were high (as Cruden et al. (1983) maintained), only if all the birds started feeding at once. But, if one were to "cheat" by starting early, the whole system would collapse because selection would strongly favour the cheater. So one would expect the birds to start feeding as soon as rewards offset foraging costs, with intensity of foraging related to rate of secretion, rather than maximum accumulation of nectar as suggested by Cruden et al. (1983).

#### 2.4.7 The importance of birds in pollination

I have already discussed some of the advantages and costs of birds as pollinators. It seems that a large proportion of the seed-set in the plants I studied was effected by visiting birds (Table 2.7). Other studies have shown similar pollination roles in sunbirds, hummingbirds and honeyeaters (e.g. Cruden 1972; Linhart 1973; Brown & Kodric-Brown 1979; Young 1982; Paton & Turner 1985; Collins & Spice 1986). Only in P. caffra was the

importance of the birds as pollinators not clear. The assumption that the plants chosen for study were ornithophilous thus seems to have been largely justified. It is interesting and perhaps significant that the highest proportions of seed-set resulting from bird visitation were in those flowers with long sympetalous corollas which are particularly typical of the ornithophily syndrome (Faegri & van der Pijl 1979). These plants also had a high fidelity in the site of pollen deposition on the bird pollinators (see Chapter 3). The generally high seed-set suggests that the plants have an efficient system of partitioning pollinator resources (see Chapter 3).

The results of these enclosure experiments should be treated with some reservation, however, because the treatments did not include tests of self-compatibility and germination rates to check seed viability. Young (1982) found that exclusion of sunbirds from Lobelia spp. in Kenya did not reduce seed-set per se but greatly reduced the viability of the seeds. My data show that birds were important in increasing seed-set and it is possible that their contribution would also increase seed viability through probable outcrossing. Another factor which could have influenced the results was that the "bird mesh" may also have deterred insects from visiting the inflorescences, particularly large insects. I did see many insects entering the "bird mesh" enclosures, but visitation rates by some species could have been reduced; I did not check this possibility. The importance of insect pollination may thus have been underestimated.



Some seeds were set in all the plants in spite of treatment to exclude both birds and insects. Such pollination could have been by self-fertilization (which may reduce seed viability and certainly reduces gene flow), or by insects small enough to penetrate the mesh, or even by wind pollination. It thus seems that all the plants could set some seed in the absence of animal pollen vectors.

P. caffra presented a confusing picture from the results of the manipulations. Although there were no significant differences between the treatments, exclusion of the birds and insects gave the highest seed-set, and at 27% this is unusually high for a Protea species: members of this genus usually set less than 10% (Horn 1962). The low seed-set of many of the Proteaceae is often attributed to nutrient and water limitation rather than a shortage of pollinators (Horn 1962; Lamont et al. 1985; Paton & Turner 1985). This may have been a reason for the difference in seed-set between P. caffra and P. roupelliae, although I have no evidence that P. roupelliae grew on poorer soils. It could be that the seeds in the exposed inflorescences of P. caffra would have shown a greater viability than those (possibly self-pollinated) in the protected inflorescences, but self-pollination seems unlikely as it is uncommon in the Protea genus (Horn 1962). It has been suggested that arthropods, even very small ones, play a role in pollinating some members of the Proteaceae which were once assumed to be entirely ornithophilous (Vogel 1954; Lamont et al. 1985); if this is the case in P. caffra, tiny arthropods may well have entered the "insect-mesh" cages and pollinated the

plant. But why then does this plant seem to attract large numbers of nectarivorous birds and conform in many ways to the ornithophilous syndrome? Its massive nectar production seems wasted if the plant is pollinated by insects. Interestingly P. caffra was the only plant whose inflorescences were pale pink to white and which had a detectable odour, suggestive of entomophily. It is possible that P. caffra is either very generalized, almost opportunistic, in the way it achieves pollination (emphasizing, incidentally, the danger in strict categorization of plants into "pollination syndromes"), or it represents a transition from one syndrome to another.

However, from my observations and studies of pollen loads (see Chapter 3) it is obvious to me that the birds do play some part in pollinating P. caffra (it may be an important role, particularly in long-distance outcrossing). Insects could also pollinate P. caffra and/or it may be self-pollinating. The ultimate seed-set is probably determined by nutrient limitations and not by a lack of pollination. Further work, including self-compatibility and germination studies and examination of the effect of nutrient availability on seed-set, is needed to test these suggestions. Of particular interest would be an investigation of outcrossing rates for all the plants of this study and the roles the different pollinators play in this aspect of pollination ecology (e.g. see Heinrich & Raven 1972; Linhart 1973; Linhart & Feinsinger 1980).

#### 2.4.8 Some concluding remarks

The pollination syndrome of ornithophily displays a complexity of trends, compromises and inconsistencies. In conclusion I should point out that the plant- and bird-species assemblage in this study does not form a closed community. All the species occur elsewhere, often in very different assemblages. Each is thus the product of evolution over a wide range of conditions, and not only those prevalent in one small area selected for study. Studies that have shown close bird-plant relationships have been largely tropical, with the species sharing homogeneous and often restricted ranges.

A further consideration is that of the wide diversity of origin of ornithophilous plants (Vogel 1954; Baker & Baker 1983). Similar selective pressures will produce a gamut of response and innovation in plants, moulded by their phylogenetic predispositions and constraints.

## CHAPTER 3

## COMMUNITY ORGANIZATION:

## NECTAR AVAILABILITY TO AND ITS EXPLOITATION BY BIRDS

## 3.1 INTRODUCTION

There has been much discussion about the role that competition among flowering plants for pollinators has played in the structuring of plant communities (e.g. Levin & Anderson 1970; Poole & Rathcke 1979; Waser & Real 1979; Thompson 1981; Rathcke 1983; Waser 1983b; Waser & Fugate 1986). Waser (1983b) defines competition in this context as "any interaction in which co-occurring plant species (or phenotypes) suffer reduced reproductive success because they share pollinators".

Rathcke (1983) and Waser (1983b) identify two kinds of such competitive interaction: (1) "competition through pollinator preference" in which plant species attempt to lure the pollinators away from the other plant species; and (2) "competition through interspecific pollen transfer" whereby pollinators, in visiting different plant species, transfer pollen between them, resulting in pollen wastage and clogging of the stigmatic surface with foreign pollen. It is important to note that the second type of competition would occur even if the number of pollinators were unlimited.

There is a distinct tendency for coexisting flowering plants, particularly those closely related, to differ in the characteristics of their flowers and flowering patterns

(Heinrich 1975; Stiles 1975, 1977; Carpenter 1976a; Feinsinger 1976, 1978, 1983a; Motten 1986). If one plant were able to attract all pollinator visits away from other plants which share its pollinators, "competition through pollinator preference" (Waser 1983b) could lead to local exclusion of similar species (MacArthur 1972), ultimately giving rise to the diversity in flowering observed in plant communities. However, this diversity is more likely a product of divergence through character displacement among sympatric plant species, particularly encouraged by the effects of "competition through interspecific pollen transfer" (Levin & Anderson 1970; Waser 1977, 1978). Such divergence could be effected in two ways: (a) differences in floral morphology and reward; and (b) differences in flowering time.

Possibility (a) can be seen at two levels. The most obvious is the specialization by plants to attract a specific type of pollinator, i.e. the development of a pollination syndrome; this level of divergence was discussed in Chapter 2. Secondly, continued divergence within a syndrome in order to induce further and more specific pollinator consistency is often observed and can involve aspects of reward size and flower density (Levin & Anderson 1970; Feinsinger 1976, 1978, 1983b; Rathcke 1983; Hudson & Sugden 1984), flower height and arrangement (Feinsinger 1976; Waddington 1979), time of day over which nectar is produced (Baker 1961; Cruden et al. 1983; Opler 1983), flower coloration and structure, and pollinator learning (Levin & Schaal 1970; Snow & Snow 1980; Prendergast 1983; Waser 1983b). An important sort of

structural variation has to do with the site and fidelity of pollen deposition on the pollinator. This is determined by the position of the anthers and stigma and by the angle of approach by the pollinator, and may completely eliminate "competition through interspecific pollen transfer". So, for example, two plants could share the same pollinators but avoid such competition if one deposited its pollen on the crown of the pollinator and the other deposited its pollen on the pollinator's chin. There have been few reports of this simple but effective form of divergence in the literature on ornithophilous plants (Stiles 1975; Carpenter 1978; Brown & Kodric-Brown 1979).

The second possible route for divergence is through (b): differences in flowering times. Although many factors influence this aspect (Bawa 1983; Waser & Fugate 1986), the staggering of flowering in plant communities, particularly when plants share pollinators, has been commonly reported (e.g. Stiles 1975, 1977; Carpenter 1976a, 1976b; Waser 1976, 1978; Feinsinger 1978; Kodric-Brown & Brown 1978; Waser & Real 1979; Frankie 1980). These sequential flowering trends are particularly clear in communities with a small number of plant species vying for the attention of the same pollinator or group of pollinators (Waser 1983b).

Such a succession of flowering through the year would not only diminish competition between the plants for pollination, but would also provide a succession of nectar supplies for the pollinators, encouraging them to reside in the community and to

specialize in nectar-feeding (Baker 1973; Heithaus et al. 1975; Wolf et al. 1976; Opler 1983; Rathcke 1983).

However, the abundance of nectariferous flowers may vary considerably through the year. This has been shown in hummingbird-plant community studies by Skutch (1950), Wolf (1970), Snow & Snow (1972), Stiles (1974, 1975, 1980), Feinsinger (1976), Feinsinger et al. (1985) and many others; in honeyeater-plant communities (Ford 1979; Collins & Briffa 1982; Pyke 1983; Ford & Paton 1985); in honeycreeper-plant communities (Baldwin 1953; Carpenter & MacMillen 1976; Pimm & Pimm 1982); and sunbird- or sunbird-and-sugarbird-plant communities (Pettet 1977; Rebelo et al. 1984). These studies have tried to link aspects of avian nectarivore biology with the annual cycle of food availability.

Very few studies have, however, attempted to measure accurately the total amount of nectar available to a group of avian pollinators through the annual cycle. Most have relied only on the intensity of flowering (or worse still, the number of plant species in flower) through the year as an index of nectar availability. Such indices give an inaccurate picture of nectar-resource fluctuations. Only the studies by Gass & Montgomerie (1981), Pyke (1983) and, to some extent, Ford (1979) have combined data on the abundance, flowering intensity and nectar-sugar production per flower of each plant species in an examination of nectar availability in a community. This I attempted to do in my study.

Nectarivorous birds are often itinerant animals and "track" nectar supplies on a local and regional scale (e.g. sunbirds: Skead (1967), Pettet (1977), Greig-Smith (1980); sugarbirds: Skead (1963), Rebelo et al. (1984); hummingbirds: Wolf (1970), Wolf et al. (1976), Feinsinger & Colwell (1978), Stiles (1980), Gass & Montgomerie (1981); honeyeaters: Keast (1968), Hopper (1981), Pyke (1983), Ford & Paton (1985); honeycreepers: Baldwin (1953), Carpenter & MacMillen (1976)). Large endothermic animals, particularly birds, are highly mobile, which makes them attractive pollinators to plants: birds are able to move large distances, relative to insects, in search of nectar, and follow flowering peaks. Thus a steady flow of nectar in a community may not be as important for birds as it is for insects. Birds also have an alternative food in the form of arthropods which can tide them over periods of low nectar production; the importance of arthropod-food is discussed in Chapter 4.

How coexisting nectarivorous birds share available nectar resources has been the subject of many studies. Nectar is a simple, highly desirable and easily studied resource, making nectarivores ideal subjects in which to investigate competition and coexistence. Most of the detailed work has been done on hummingbirds (e.g. Colwell 1973; Wolf et al. 1976; Feinsinger 1976, 1978; Brown et al. 1978; Hainsworth & Wolf 1979; Snow & Snow 1980; Stiles 1980; Kodric-Brown et al. 1984; Brown & Bowers 1985; Feinsinger et al. 1985). There have also been several such studies of honeyeater communities (e.g. Recher & Abbott 1970; Recher 1971, 1977; Ford & Paton 1977; Ford 1979; Pyke 1980;



Collins & Briffa 1982; Collins et al. 1984) and of honeycreepers (e.g. Baldwin 1953; Carpenter & MacMillen 1976; Carothers 1982; Pimm & Pimm 1982). Investigations of coexistence in sunbirds and sugarbirds have been rather general in nature (Skead 1963; Skead 1967; Pettet 1977), or of short duration (e.g. Cheke 1971a; Gill & Wolf 1975a, 1975b, 1978, 1979; Wolf 1975; Frost & Frost 1980), or have been more concerned with other aspects of ornithophily (Rebelo et al. 1984; Siegfried & Rebelo 1986).

Apart from the partitioning of resources through variations in bird-flower morphology which was mentioned in Chapter 2, there are four other ways in which nectar resources are partitioned between species in nectarivorous bird communities:

(a) Habitat selection

Nectar resources in a community may be partitioned through the selection of different habitats by different bird species; this may be as a result of competition for nectar or for other reasons (Wolf 1970; Linhart 1973; Feinsinger 1976; Feinsinger et al. 1982).

(b) Temporal separation

Partitioning of nectar temporally during the day has been reported for hummingbirds (e.g. Colwell 1973; Schoener 1974; Feinsinger 1976; Wolf & Hainsworth 1977) and honeyeaters (Craig & Douglas 1984); this usually relates to the depletion of nectar resources through the day, rendering the use of the remaining nectar profitable only for different birds and different foraging

strategies. There have also been reports of interesting diurnal temporal separation in nectarivorous bumblebees (Pleasants 1983).

(c) Spatial separation

Some coexisting birds have been shown to display spatial partitioning of resources (e.g. MacArthur 1958; Willson 1970) and this has been found in some hummingbird communities at large, high-density nectar sources (Snow & Snow 1972; Colwell et al. 1974; Feinsinger 1976).

(d) Foraging strategies

Two main types of foraging strategies have been identified: (i) territorial and (ii) generalist foraging. In the territorial strategy an individual defends high-density nectar resources (usually clumps of nectariferous plants). Such interference competition relies on there being sufficient energy resources in the territory to support the owner in this highly energetic behaviour; territories may be static or shifting depending on the energy demands of the bird, intruder pressure and nectar-resource availability and replenishment in the defended areas. The generalist strategy involves the use of smaller, scattered nectar sources which are unprofitable to defend. In many cases this is also termed "trap lining" because the birds move from one small source to another, tapping nectar which has accumulated between visits (e.g. Feinsinger & Chaplin 1975; Feinsinger 1976, 1978, 1980; Kodric-Brown & Brown 1978; Feinsinger et al. 1979; Pimm & Pimm 1982; Feinsinger & Swarm 1982; Collins & Briffa 1982,

1983a; Feinsinger et al. 1985). Thus the size of a bird and the nectar-sugar reward, reward (flower) spacing on a plant, and plant density and dispersion are important in determining the ways in which birds forage, and, ultimately, the structure of nectarivorous bird communities.

## 3.2 METHODS

### 3.2.1 Flowering phenology

The pattern of flowering by plant species whose nectar was important to the birds was monitored over the year. Twenty randomly chosen plants of each species were marked and the number of live, open flowers or inflorescences on each was counted once, or sometimes twice, every month. In Halleria lucida with its many individual flowers, numbers were estimated by counting flowers in lots of 10. In the other plants, in which inflorescences were counted, the average number of flowers open per inflorescence ( $n = 10$ ) was also established. The level of flowering each month was expressed as the mean percentage of the maximum for each species.

### 3.2.2 Plant abundance and total nectar availability

The number of each of the eight important plant species was counted along 5 transects (see Table 1.1) in a strip 10 m either side of the transect line. I used a pair of 9 X 25 binoculars with a mark on the focusing ring to indicate a distance of 10 m (i.e. if a plant stem focused beyond the 10-m mark, it was

outside the transect). This method was accurate to 0,2 m. These figures were converted to plant density (no./ha) for each transect, and for the study area as a whole.

Extrapolation of data on flowering phenology and daily nectar production allowed calculation of the total nectar sugar available to the birds for each month in each habitat (g sugar/ha). In calculations of total nectar availability, the figures were weighted according to the area which each habitat contributed to the whole study area.

For each plant species, nectar-sugar production per plant (at peak flowering), overall density in the study area and a rough "clumping index" were multiplied together to give a "potential energy value". The "clumping index" was a subjective assessment of the degree to which the plants tended to grow in close conspecific aggregations. It ranged from 1-5, where 1 showed no aggregation and a very scattered distribution, and 5 represented plants which almost invariably grew in clumps.

These "potential energy values" are a rather crude assessment of the potential usefulness of a plant to all the nectarivorous bird species in the community. A more sensitive index would need to combine many other variables, such as further aspects of nectar quality, nectar-feeding preferences of the different bird species and the quality and quantity of other nectar sources available. Such influences are difficult to quantify, even subjectively, particularly as many vary markedly over the time a plant species is in flower.

### 3.2.3 Bird-population index

The relative numbers of nectarivorous bird species through the year was established along the transects in the five habitats described in Table 1.1. Each transect was walked 2-6 times every month at a slow but constant speed of about 3 km/h, between 08h00 and 11h00, and generally in fine weather (Emlen 1971; Feinsinger 1976). The species and sex of each bird sighted was recorded, as were details of the bird's first feeding action and incidents of aggression. Relative population density was calculated as the number of birds seen per km walked. In calculating the total relative population every month the figures for each transect were weighted according to the area occupied by each habitat in the study area (see Table 1.1).

### 3.2.4 The birds' feeding preferences

To give an indication of the birds' feeding preferences, the observed frequencies of feeding at particular plant species were compared with the frequencies expected if the birds were showing no preferences. Expected frequencies were determined from the different proportions of the nectar available contributed by each plant species flowering at the time. I used feeding data collected during transect walks, supplemented with random observational data in most months, for the observed frequencies. I had insufficient data, however, for Gurney's Sugarbird and the Lesser Doublecollared Sunbird for some time intervals and preferences at these times have not been established for these

species. The data for consecutive months were pooled; the nectar availability of the different plants lent itself well to a scheme of pairing the months as shown in Table 3.5 (see Results). In this way the major blooming months of most of the main nectar-producers were combined.

Rigorous statistical analysis of the observed/expected feeding-frequency data for the different bird species was not possible because of insufficient degrees of freedom in the resulting  $\chi^2$  contingency tables and many expected frequencies of less than five (Scheffler 1979). I have thus shown the plant species in the order of preference apparent from these data for each bird species over each period. The plants have been subjectively placed in the categories "preferred" (observed > expected), "neutral" (observed  $\approx$  expected) and "avoided" (observed < expected) by inspection of the observed/expected frequencies.

### 3.2.5 Pollen loads carried by the birds

Pollen adhering to the bill and head of each bird caught was sampled with a sticky jelly described by Wooller, Russell & Renfree (1983). A 1x3x3-mm block of this jelly was rubbed in a uniform manner over the bird's head, chin and bill. The jelly contained basic-fuchsin dye to stain the pollen grains. Each sample was melted on a slide under a coverslip for later examination. In many cases separate samples were taken from the top of a birds' head and from its chin and throat in order to

establish the fidelity of the site of pollen deposition on the birds by different plants. In one case (a Gurney's Sugarbird) pollen was also sampled from the bird's back, shoulder, breast and belly.

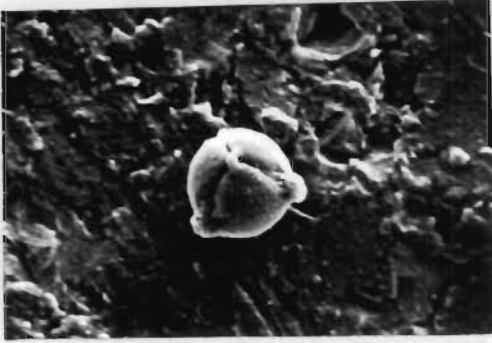
Pollen grains in these samples were identified from a reference collection of pollen from plants in the study area (Fig. 3.1), and counted at 100x magnification in five transects, each the length of the square coverslip. I was unable to distinguish between the pollens of congeneric Protea caffra and P. roupelliae, and Aloe arborescens and A. saponaria under the light microscope and these were recorded as Protea and Aloe respectively. Such sampling should be treated with some circumspection, however, because it only represents surface pollen (Wooller, Russell, Renfree & Towers 1983). Further, such data are only a rough guide to the flowers visited by the birds because different plants produce pollen grains of a different shape, size and stickiness and in different quantities.

### 3.3.6 Foraging at Leonotis leonurus

It was noticed that all four nectarivorous bird species were foraging together in a large patch of L. leonurus, and that Lesser Doublecollared Sunbirds seemed to be more common later in the day. To investigate the possibility of temporal differences in the foraging activity here, the numbers of each bird species seen foraging at the patch was counted every 15 min from 05h00 to 17h00 on one day while I was determining nectar-production rates for this plant.







Halleria lucida (x1000)



Leonotis leonurus (x1000)



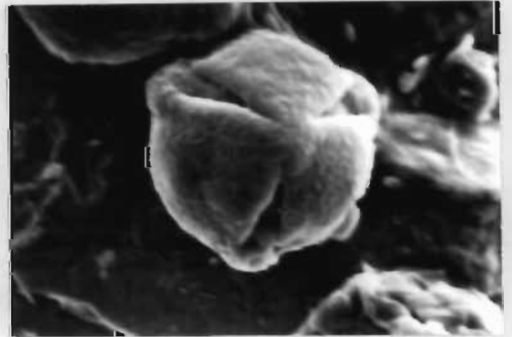
Aloe arborescens (x1000)



Aloe saponaria (x1000)



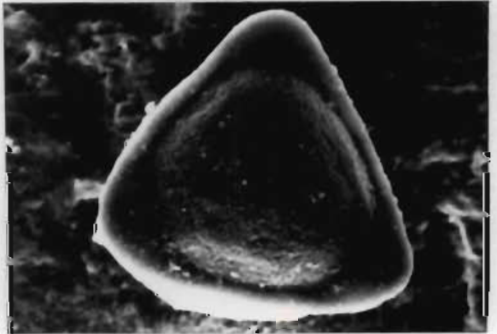
Greyia sutherlandii (x1000)



Phygelius aequalis (x1000)



Protea caffra (x1750)



Protea roupelliae (x1750)

### 3.3 RESULTS

#### 3.3.1 Flowering phenology

There were ornithophilous plants in bloom to some extent all through the year and a succession of flowering peaks occurred (Fig. 3.2).

#### 3.3.2 Plant abundance and total nectar availability

The density of the different ornithophilous plants in the study area varied markedly, as did the nectar-sugar production per plant for each species (Table 3.1). These, together with the index for their tendency for clumping (which was notable for all species to some extent), caused a marked difference in the "potential energy value" of the different plants to the birds (Table 3.1). The proteas and Halleria lucida had very high "potential energy values", Greyia sutherlandii was intermediate, and the other four species were comparatively low in value (Table 3.1).

Total nectar availability fluctuated greatly throughout the study, with peaks in nectar-sugar production in August-September (largely H. lucida and G. sutherlandii nectar) and December-January (P. caffra nectar) (Fig. 3.3). In October-November nectar availability was low: although several species were in flower, only Phygelius aequalis was in heavy bloom and this plant had a low "potential energy value".

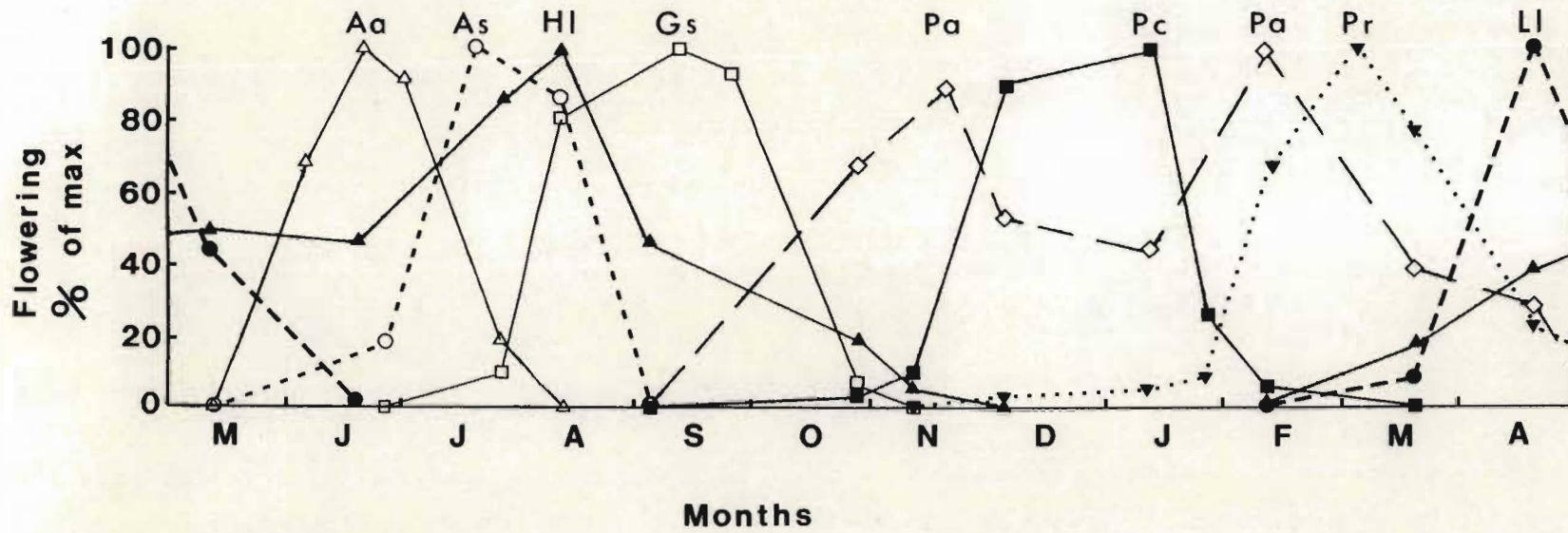


FIGURE 3.2

The flowering phenologies of the eight major ornithophilous plant species.

- |        |                          |        |                            |
|--------|--------------------------|--------|----------------------------|
| ▲ Hl ▲ | <u>Halleria lucida</u>   | ◇ Pa ◇ | <u>Phygelis aequalis</u>   |
| ● Ll ● | <u>Leonotis leonurus</u> | □ Gs □ | <u>Greyia sutherlandii</u> |
| △ Aa △ | <u>Aloe arborescens</u>  | ■ Pc ■ | <u>Protea caffra</u>       |
| ○ As ○ | <u>Aloe saponaria</u>    | ▼ Pr ▼ | <u>Protea roupelliae</u>   |

TABLE 3.1

Nectar-sugar production, density, clumping and the "potential energy value" of the ornithophilous plants (see text).

Plant species	Nectar production (mg/flower/day)	No. of flowers/ inflorescence	No. of inflorescences/ plant	Nectar-sugar production (g/plant/day)	Plant density (no/ha)	"Clumping <sup>1</sup> index"	"Potential <sup>1</sup> energy value"
<u>Halleria lucida</u>	1,6	1	705	1,13	7,3	3	24,7
<u>Leonotis leonurus</u>	1,3	26 <sup>£</sup>	15	0,51	1,1	5	2,8
<u>Aloe arborescens</u>	4,2	17	8	0,57	1,8	5	5,1
<u>Aloe saponaria</u>	1,8	8	2	0,03	1,0	3	0,1
<u>Phygelius aequalis</u>	4,5	13	9	0,53	0,4	3	0,6
<u>Greyia sutherlandii</u>	6,7	42	14	3,90	1,4	3	16,5
<u>Protea caffra</u>	1,6	69 <sup>*</sup>	15	1,66	8,4	4	55,6
<u>Protea roupelliae</u>	2,2	68 <sup>*</sup>	7	1,05	6,7	4	28,1

<sup>1</sup> see text

£ number of flowers per verticillaster

\* number of live flowers

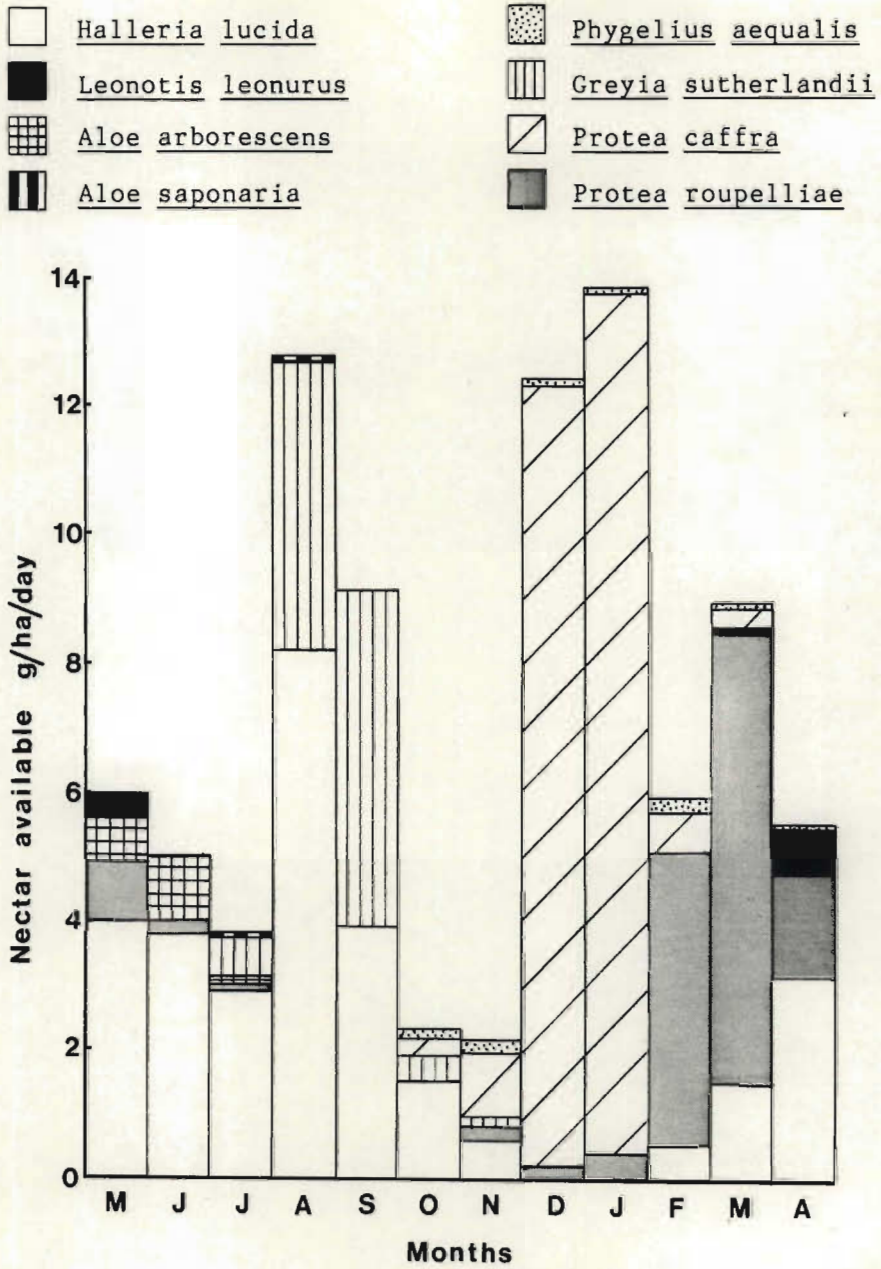


FIGURE 3.3

Nectar-sugar availability in each month for the whole study area, and the contributions of the different ornithophilous plant species to this.

### 3.3.3 Flowering overlap, pollen loads and site of pollen deposition on the pollinators

The species which showed the most overlap in flowering times are shown in Table 3.2. Those which overlapped tended to have different anther arrangements. There was a distinct difference in the pollen-deposition sites of flowers with ventrally and dorsally placed anthers, but some overlap in strategies occurred where G. sutherlandii and the proteas were involved because they used the whole head of the birds fairly evenly (Tables 3.2, 3.3 and 3.4). The pollen load on the body of the single bird (a Gurney's Sugarbird) from which samples were taken showed that 14% of the total load sampled from various regions of the bird's body was carried elsewhere than on the head (head: 86%, chest: 10%, belly: 2%, shoulder: 2% and back: 0%).

Pollen counts of samples from the birds' heads were very variable (Table 3.4). (Note that these figures indicate only relative loads of surface pollen; examination of feathers removed from the heads of the birds after sampling showed massive numbers of pollen grains still present.) Although the pollen-load data corroborated the feeding-preference results from direct observations quite well, these data should be regarded with some reservation because of the small sample sizes, large variability and, above all, the probable differences in pollen production and deposition by different plant species. The small loads of P. aequalis pollen detected were probably related to the large number of illegitimate visits to this plant, particularly by Greater Doublecollared Sunbirds (see Chapter 2).

TABLE 3.2

Plant species whose flowering overlapped to a considerable extent, the positioning of the anthers in their flowers or inflorescences, and the resultant site of pollen deposition on the birds' heads.

Months	Anther position/pollen deposition site		
	dorsal/forehead & crown	ventral/chin & throat	whorled/whole head
April-May	<u>L. leonurus</u> , <u>H. lucida</u>		<u>P. roupelliae</u>
June-July	<u>H. lucida</u>	<u>A. arborescens</u>	
July-August	<u>H. lucida</u>	<u>A. saponaria</u>	
August-October	<u>H. lucida</u>	<u>A. saponaria</u>	<u>G. sutherlandii</u>
November-January		<u>P. aequalis</u>	<u>P. caffra</u>
February-March		<u>P. aequalis</u>	<u>P. roupelliae</u>

TABLE 3.3

Percentages of the pollen loads from each plant species carried by the birds on their forehead/crown and chin/throat. (Only pollen from the birds' heads was sampled; there may have been some pollen carried elsewhere on the birds - see text.)

Plant species	% pollen on	
	forehead/crown	chin/throat
<u>Halleria lucida</u>	91,0	9,0
<u>Leonotis leonurus</u>	96,1	3,9
<u>Aloe arborescens</u> } <u>Aloe saponaria</u> }	13,5	86,5
<u>Phygelius aequalis</u> *	31,7	68,3
<u>Greyia sutherlandii</u>	52,0	48,0
<u>Protea caffra</u> } <u>Protea roupelliae</u> }	52,8	47,2

\* samples only from Malachite Sunbirds



TABLE 3.4

The numbers of the different pollen grains counted in the samples taken from the heads of nectarivorous and occasional nectar-feeding birds mist-netted during the study. Note that not all species were captured in every month-grouping.

GUR = Gurney's Sugarbird, MAL = Malachite Sunbird, GDC = Greater Doublecollared Sunbird, LDC = Lesser Doublecollared Sunbird, CWE = Cape White-eye, BEB = Blackeyed Bulbul. H. l = H. lucida, L. l = L. leonurus, P. a = P. aequalis, G. s = G. sutherlandii. N = number of samples.

Months	Bird species	N	Mean number of pollen grains from:						
			H. l	L. l	<u>Aloe</u>	P. a	G. a	<u>Protea</u>	Other*
April-May	GUR	4	0	206	0	0	0	95	1
	MAL	8	0	1821	0	0	0	145	0
	GDC	12	22	360	0	0	0	91	0
	LDC	4	9	158	0	0	0	0	0
	CWE	3	11	3	0	0	0	26	4
June-July	GDC <sup>£</sup>	2	51076	0	31	0	0	0	2
August-November	MAL	13	1203	0	0	16	201	25	7
	GDC	5	983	0	39	2	5	30	2
	CWE	7	3	0	0	0	7	6	3
	BEB	3	0	0	2	0	248	0	3
December-January	GUR	2	1	0	0	0	19	666	1
	MAL	4	20	0	0	2	6	419	17
	GDC	7	93	0	2	0	0	1901	0
	LDC	2	21	0	0	0	0	882	1
February-March	GUR	1	4	0	0	0	0	1076	0
	MAL	3	0	0	0	2	0	492	2
	GDC	1	2900	2	0	0	0	87	0

\* Most of these were pollen grains from Cotoneaster sp. and Watsonia sp.

£ Both these birds were females, which were rarely seen to visit A. arborescens. Male Greater Doublecollared Sunbirds commonly fed at A. arborescens and often had faces orange with this plant's pollen.

### 3.3.4 Nectarivorous bird populations

Fluctuations in the nectarivorous bird populations were marked and occurred over the whole study area and within each habitat. These were clearly in response to local changes in nectar availability (Figs 3.4, 3.5 and 3.6). Bird numbers were generally lower in the winter months. Malachite Sunbirds left the study area from May to mid-August and Gurney's Sugarbird was noticeably scarce during the winter (Fig. 3.4). Only Malachite Sunbirds and Greater Doublecollared Sunbirds were seen in the Lower Grassland and Little Berg grassland habitats, and then very rarely (Fig. 3.5). All species were seen often in the Sandstone cliffs and P. caffra savanna habitats, but only the Greater Doublecollared and Lesser Doublecollared Sunbirds were seen in the Forest.

### 3.3.5 Feeding preferences

Some of the bird species did show preferences for the nectars of some plants at different times (Table 3.5). However, all of the bird species were seen feeding on the nectars of all the plant species, even if only rarely; there were only two exceptions to this: Lesser Doublecollared Sunbirds were not seen to visit P. aequalis and Gurney's Sugarbirds were not observed to visit A. saponaria. Malachite Sunbirds were not seen to feed at A. arborescens but they were absent from the study area while it was in flower.

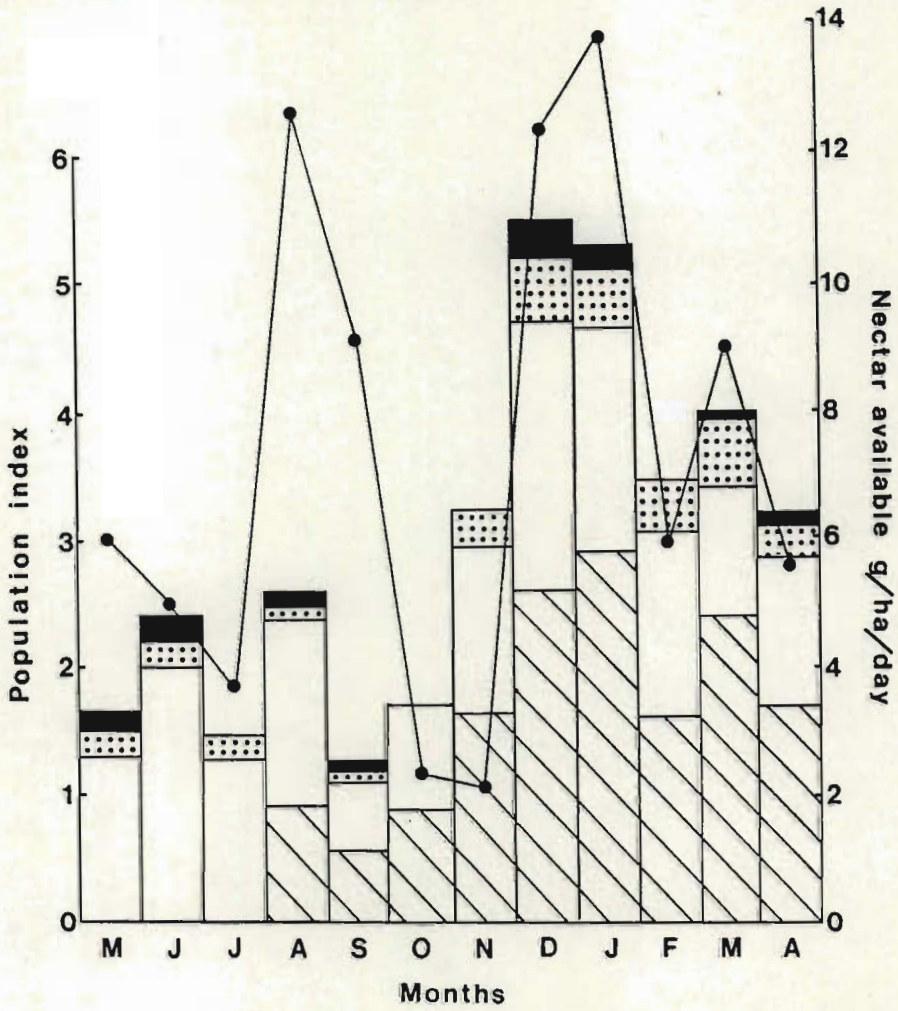
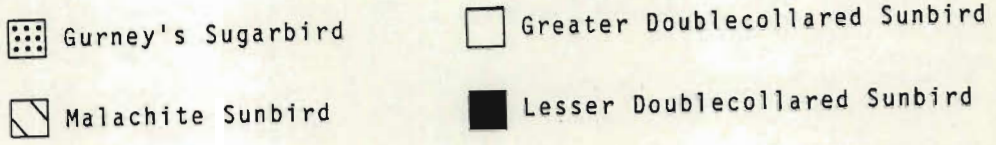
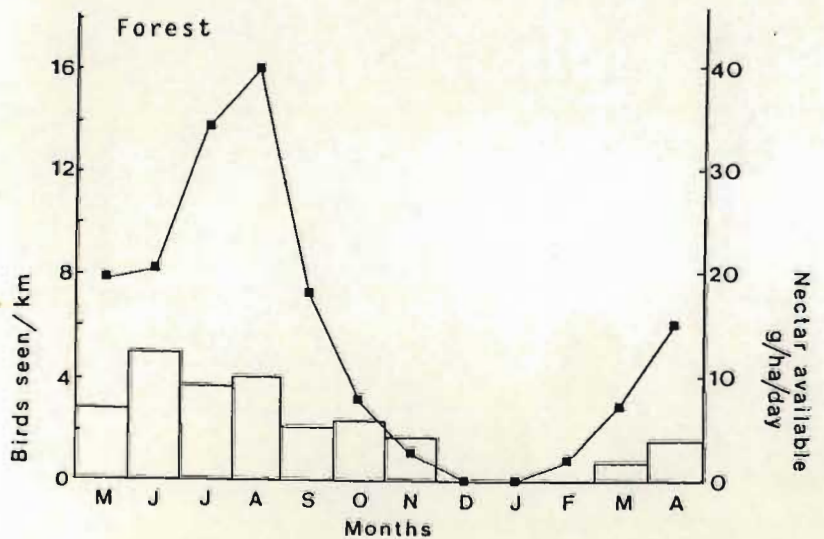
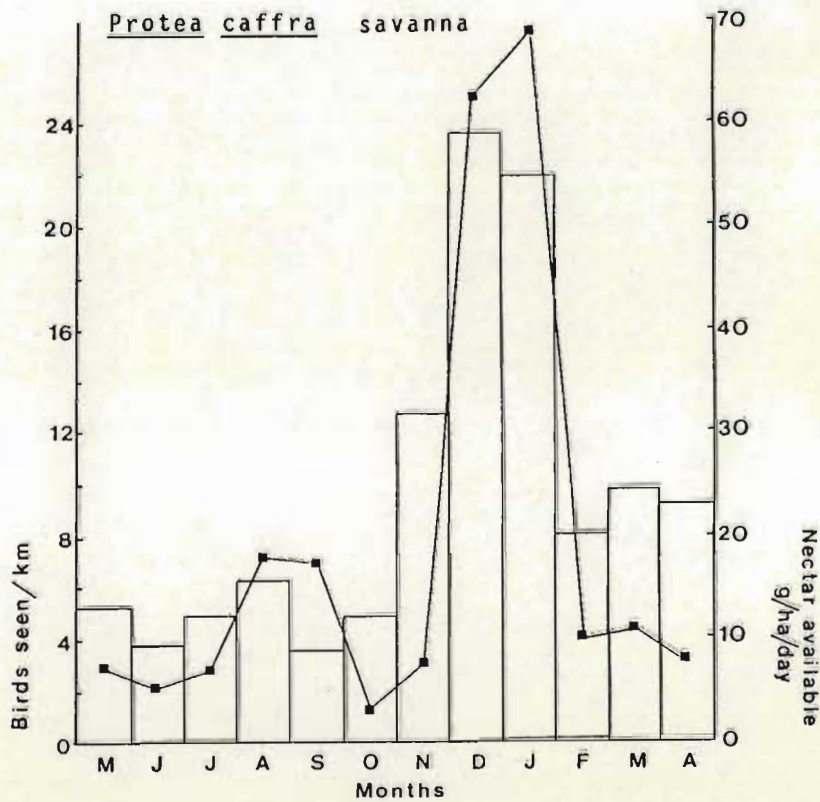
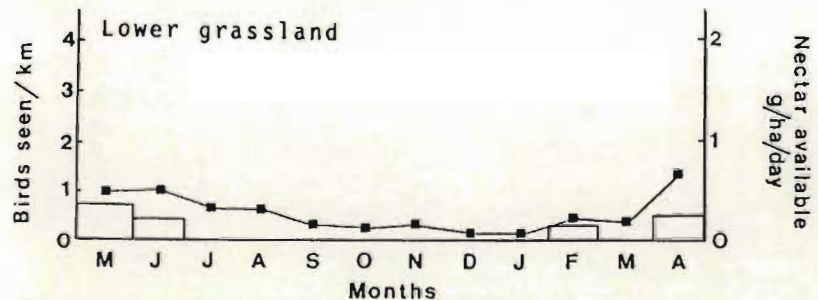
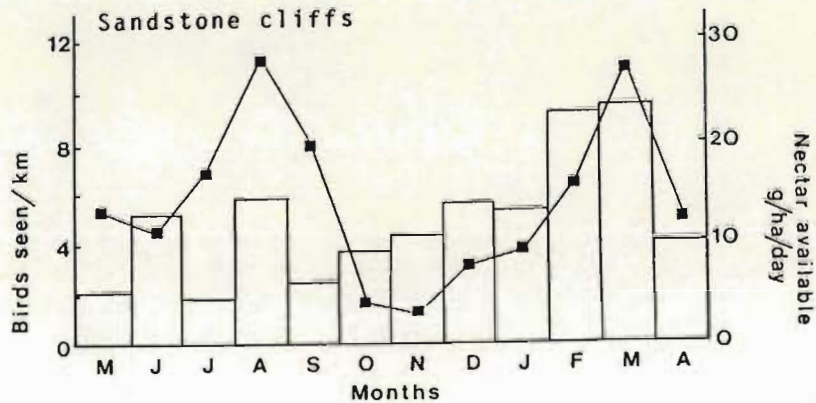
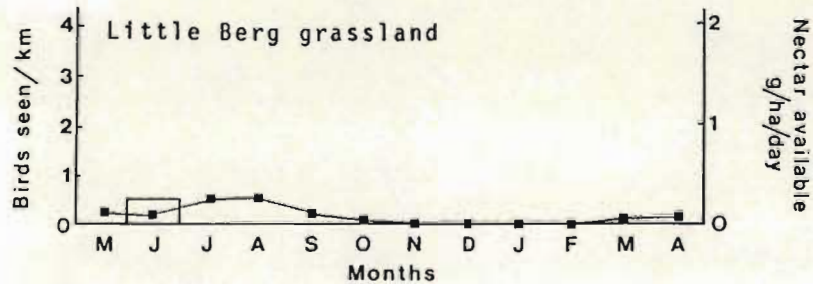


FIGURE 3.4

Monthly nectarivorous bird populations (histogram) and nectar-sugar availability (●—●) for the whole study area.





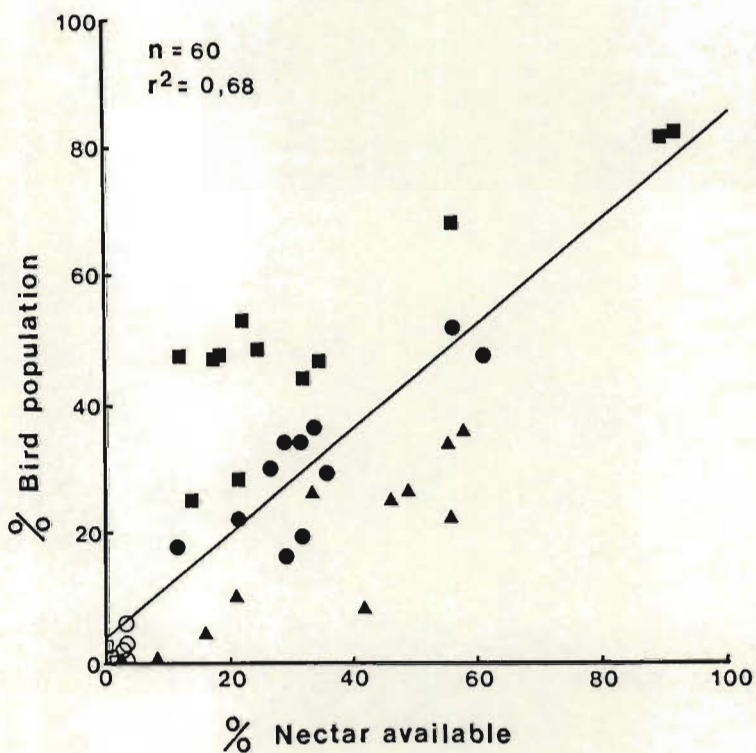


FIGURE 3.6

The correlation between nectar availability and bird numbers recorded along each of the five transects every month. Percentages (of the total in the study area for each month) were plotted to reduce as far as possible variations which occurred because of other factors (e.g. season).

○ Lower grassland

● Sandstone cliffs

■ *Protea caffra* savanna

□ Little Berg grassland

▲ Forest

TABLE 3.5

Nectar-feeding preferences (observed versus expected) of the nectarivorous birds for two-monthly periods. GUR = Gurney's Sugarbird, MAL = Malachite Sunbird, GDC = Greater Doublecollared Sunbird, LDC = Lesser Doublecollared Sunbird; H.l = H. lucida, L.l = L. leonurus, A.a = A. arborescens, A.s = A. saponaria, P.a = P. aequalis, G.s = G. sutherlandii, P.c = P. caffra, P.r = P. roupelliae; N = number of feeding observations.

Months	Bird species	N	Preferred (observed > expected)	Neutral (observed ≈ expected)	Avoided (observed < expected)
April-May	GUR	23	L.l, P.r	A.a	H.l, P.a
	MAL	60	L.l, P.r	P.a	H.l
	GDC	36	L.l, A.a	H.l, P.a	P.r
	LDC	18	L.l,	H.l, A.a	P.a, P.r
June-July	GUR	26	P.r, A.a	G.s	H.l, A.s, L.l
	MAL	-	-	-	-
	GDC	92	A.a, A.s, L.l	H.l	G.s, P.r
	LDC	19	L.l, G.s	H.l, A.a, As	P.r
August-September	GUR	-	-	-	-
	MAL	64	-	H.l, G.s	A.s
	GDC	79	A.s, H.l	-	G.s
	LDC	-	-	-	-
October-November	GUR	32	P.c, P.r	H.l, G.s	P.a
	MAL	85	P.c	H.l, G.s	P.r, P.a
	GDC	90	P.c	P.a	H.l, G.s, P.r
	LDC	-	-	-	-
December-January	GUR	52	P.r	P.c	P.a
	MAL	87	-	P.c, P.r	P.a
	GDC	82	-	P.c	P.a, P.r
	LDC	38	-	P.c	P.a, P.r
February-March	GUR	33	-	P.r, L.l	H.l, P.c, P.a
	MAL	84	-	P.r, L.l	H.l, P.c, P.a
	GDC	30	H.l, P.c, L.l	P.a	P.r
	LDC	-	-	-	-

### 3.3.6 Incidence of aggression

Although the overall occurrence of interspecific aggression seemed to be low, except in the large stands of flowering P. caffra, the dominance hierarchy was: Gurney's Sugarbird > Malachite Sunbird > Greater Doublecollared Sunbird > Lesser Doublecollared Sunbird (Table 3.6). This was in order of size of the bird species, which is a common trend in nectarivorous bird interactions (Lyon 1976; McFarland 1985). Most of the aggression observed was, however, intraspecific (83% of observations during transect counts) and much of this was directed by male birds at the females.

### 3.3.7 Foraging at Leonotis leonurus

There was a tendency for Gurney's Sugarbirds and Malachite Sunbirds to be more common earlier in the day at the L. leonurus patch studied, and for the Greater Doublecollared and Lesser Doublecollared Sunbirds to forage in greater numbers later in the day (Fig. 3.7). This distinction was, however, far from strict and it was quite common to see all four species feeding together.



TABLE 3.6

Aggressive encounters between nectarivorous birds seen during transect walks and random observations during other walks. (Species abbreviations as in Table 3.5)

		Species attacked			
		GUR	MAL	GDC	LDC
Species attacking	GUR	11	4	4	0
	MAL	1	123	14	2
	GDC	0	1	69	5
	LDC	0	0	0	1

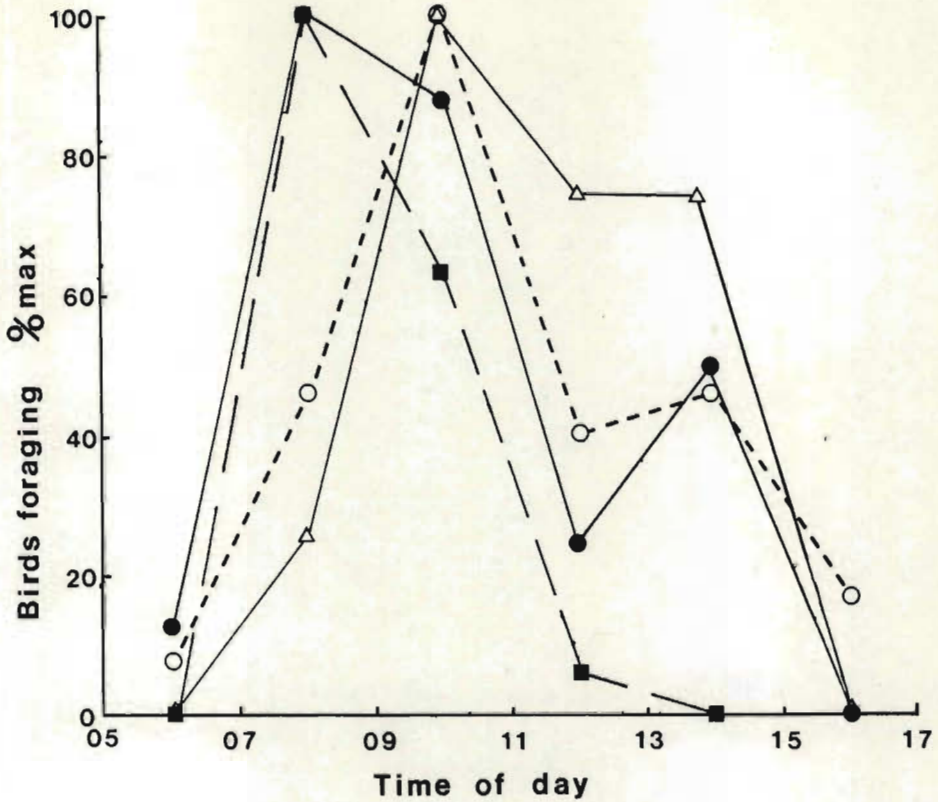


FIGURE 3.7

Foraging activity of nectarivorous birds (as a percentage of the maximum for each species) for 2-h intervals at a large patch of L. leonurus during a day in April.

■—■ Gurney's Sugarbird

○--○ Greater Doublecollared Sunbird

●—● Malachite Sunbird

△—△ Lesser Doublecollared Sunbird

### 3.4 DISCUSSION

#### 3.4.1 How do the ornithophilous plants share the available pollinators?

The succession of flowering peaks of ornithophilous plants in this study (Fig. 3.2) appeared to be the main way in which the plants "shared" the available avian pollinators in the community, so reducing competition for pollination by flowering at different times. Such partitioning has been reported in many studies of plant-pollinator interactions (e.g. Stiles 1975, 1977, 1978a, 1978b, 1980; Carpenter 1976a; Waser 1976; Feinsinger 1978; Ford 1979; Opler 1983; Pyke 1983; Rebelo et al. 1984; Ford & Paton 1985).

Partitioning of this sort is particularly clear where there are relatively few plant species in the community sharing the same pollinators and if the individual pollinator species are not narrowly specialized to feed on one or two particular plant nectars. It is thus more evident in temperate communities than in species-rich tropical ones (Grant & Grant 1964; Carpenter 1976a, 1976b; Waser 1978) and certainly this observation is supported by the present study in the Drakensberg. Grant & Grant (1964), Heinrich (1975) and Stiles (1975, 1978b) suggested that such partitioning was particularly apparent in closely related sympatric plant species; my study supported this suggestion in respect of the two Aloe species and the two Protea species. Although each of these congeneric pairs flowered in the same

seasons and often occurred sympatrically (probably because they require similar ecological conditions (Kochmer & Handel 1986)), their flowering peaks were staggered (Fig 3.2). This was less clear in the Aloe example, probably because there was less nectar available to the birds at this time and they tended to make good use of all nectar resources available. Rathcke (1983) proposed a model in which, as nectar availability increases, so competition for pollinators increases and the mechanisms to avoid such competition become more evident. Although the Drakensberg birds became more numerous in summer, there was more nectar available, and competition for pollination between common and highly nectariferous plants like the two Protea species would be more intense and cause a more distinct divergence, in this case, of flowering times.

Thompson (1978), Pleasants (1980; 1983) and Poole & Rathcke (1979) have criticized casual inspection of a succession of flowering peaks arranged from earliest to latest and interpreted as attributable to a response to competition for pollinators. Poole & Rathcke (1979) used data that Stiles (1977) had interpreted in this manner and showed that the temporal arrangement in flowering and overlaps in flowering were not significant when compared with a model based on a null hypothesis of random flowering patterns. Similar analyses (e.g. Thompson 1978; Pleasants 1980; Kochmer & Handel 1986) have, however, shown some communities to have successions in flowering peaks and flowering overlaps significantly different from a null hypothesis. Stiles (1979) has defended his interpretation (Stiles

1977) with the argument that Poole & Rathcke's model shows that statistics are "a two-edged sword" and in this instance were biologically unreal in ignoring, for example, the seasonality of the plants in his study. Gilpin & Diamond (1984) have also attacked the indiscriminate use of null hypotheses in community ecology. Whether, and to what extent, the observed successions of flowering are a result of competition between plants for pollinators is difficult to elucidate and remains indecisive (see papers in Strong et al. (1984); Diamond & Case (1986)). In any event the observed pattern would certainly reduce potential competition between plant species for pollination.

Some insight may be gained by comparing the flowering seasons of the same plant species in different communities. For example, Robertson (1924) noticed that introduced plant species tended to have longer flowering seasons than native species. A study of the flowering phenology of many of the species in this study which occur in other quite diverse communities (e.g. H. lucida, L. leonurus, A. arborescens) could be enlightening. For example, L. leonurus flowers later and for longer (June to September) on the Natal Coast (Frost & Frost 1980). It would be interesting to investigate reasons for this difference, including a study of the flowering phenology of the other ornithophilous plants in the area.

Often, however, there is some degree of overlap in flowering times, and in the present study several combinations of plant species showed considerable simultaneous flowering (Table 3.2). Positioning of the anthers (and stigma) in such a way as to

segregate pollen-transport sites on the pollinator is a simple but presumably effective way of avoiding competition through interspecific pollen transfer among such plants (Stiles 1975; Brown & Kodric-Brown 1979).

By classifying the sites of pollen deposition on the birds as (a) forehead and crown, (b) chin and throat, and (c) whole head, according to the arrangement of anthers and pollinator approach (Fig. 2.1, Table 3.2), it was clear that the plants which overlapped in flowering used different pollen-deposition sites. The separation of strategies is obvious for plants which use either the forehead/crown or the chin/throat sites (see pollen distributions Table 3.3), but the general scattering of the pollens of the proteas and G. sutherlandii would seem a less effective means of partitioning. This is surely better, however, than having identical, narrowly-defined transport sites to those of other plants in flower at the time. In the plants which scatter pollen over the whole head, pollen is probably also distributed in considerable quantities on the lower parts of the visiting birds' bodies when they perch on or lean over the upward-facing flowers in the inflorescences. Although I have data collected from only one Gurney's Sugarbird, they support this supposition (p 89). So there appear to be three strategies to share pollen-transport sites on birds in this study: high-fidelity forehead/crown deposition, high-fidelity chin/throat deposition, and a generalized "shotgun" strategy.

Such partitioning would reduce "competition through interspecific pollen transfer" (Waser 1983b) among the plants;

"competition through pollinator preference" would still occur and this will be discussed shortly. The only exception to this trend was the H. lucida and L. leonurus combination (Table 3.2): both deposited their pollen on the top of the birds' heads and they had a similar nectary-anther distance. There was thus no appreciable difference in pollen-transport sites and birds carried significant amounts of both pollens on their heads (Table 3.4). One would expect there to be some sort of divergence in the site of pollen deposition on the pollinators in this example, particularly from the point of view of L. leonurus, because it flowered only while H. lucida was in bloom.

It appears in this case that there is "competition through pollinator preference": all the nectarivorous birds in this study, particularly Malachite Sunbirds which were the most abundant at this time, showed a marked preference for L. leonurus (see later discussion). This preference was borne out by the greater abundance of L. leonurus pollen on all the birds' heads (Table 3.4). It seems from these data that H. lucida is at a competitive disadvantage, both through "pollinator preference" and probably, as a result, "interspecific pollen transfer".

An interesting factor here is the small size of the pollen grains of H. lucida (Fig. 3.1), which may confer some advantage in reducing "competition through interspecific pollen transfer" (Brown & Kodric-Brown 1979). This might be particularly important in the case of H. lucida because it flowers for most of the year. Size and shape of pollen grains and the influence this has on

clogging not only stigmatic surfaces, but also pollen-transport sites on the pollinators, have received almost no attention from researchers.

Another method by which plants can apportion pollinator resources is by temporal partitioning, i.e. by producing nectar at different times (Schoener 1974; Feinsinger 1976). All the plants in this study produced nectar diurnally, as expected for ornithophilous plants (see Chapter 2), and in all cases nectar production was matinal (Fig. 2.2). There was thus no clear diurnal partitioning by the plants (although the birds may have had their own scheme of this sort - see below). The reason for this could be that the strategy would circumvent "competition through pollinator preference", but would still render the plants open to "interspecific pollen transfer" to a large extent.

By looking at the prevalence of the different methods adopted by plants to reduce competition for pollinators in this system, it is possible to infer a hierarchy of their effectiveness and simplicity. Divergence in flowering time was the most important, and this simple ploy, although obviously governed by climatic and edaphic factors, might be expected to be most effective in avoiding both sorts of competition. Divergence in the site of pollen deposition on the pollinator seems to be next in the hierarchy and reduces "competition through interspecific pollen transfer". Then come the pollinator preferences (discussed in the next section), which would reduce both sorts of competition, depending on the degree of commitment to specialization and its accompanying risks and benefits for both plant and pollinator



(see Chapter 2). And lastly, temporal divergence in diurnal nectar production, which did not occur in the plants of this study, and has rarely been reported in studies of ornithophilous plant communities; it seems to be the last resort, and one useful only in averting "competition through pollinator preference". I believe this hierarchy is displayed in other communities, although it is probably obscured in more species-rich tropical communities in which competition is likely to be more intense (Diamond 1978) and plants explore every avenue of divergence and every combination of divergence strategies. (e.g. see studies by Baldwin (1953), Colwell (1973), Snow & Snow (1980); Opler (1983) and Kodric-Brown et al. (1984)).

The lack of diurnal temporal segregation in this study, and the order of the strategies described in the hierarchy above, suggest that "competition through interspecific pollen transfer" is probably the more important form, as Feinsinger (1978) and Waser (1978) have hypothesized.

#### 3.4.2 How do the birds share the available nectar resources?

Many studies have shown strong and sometimes obligatory feeding preferences among coexisting nectarivorous birds through coevolution with particular plant species, or groups of plant species. These involve divergent specialization among both plants and birds to partition the available resources (pollinators and nectar respectively), probably catalyzed by competition (e.g. Colwell 1973; Feinsinger 1976, 1978; Brown et al. 1978; Snow &

Snow 1980; Feinsinger & Swarm 1982; Pimm & Pimm 1982; Kodric-Brown et al. 1984; Feinsinger et al. 1985; and references therein). Such partitioning entails morphological and physiological adaptations of both birds and plants, and behavioural ones in the birds (see Chapter 2 and the introduction to this chapter).

The birds in my study did show some resource partitioning, the importance and implications of which I shall discuss, but, with few exceptions, all the bird species fed at all the main plant species at some time. Close single plant-bird associations such as have been found in tropical studies, particularly of hummingbirds, were not seen; the birds seemed to retain a ready plasticity in their feeding, with a few clear preferences superimposed on this opportunistic foundation. Siegfried & Rebelo (1986) came to a similar conclusion about the birds in their study of ornithophilous Erica species in the Cape.

In considering the feeding preferences of the bird species in my study (Table 3.5), it was difficult to establish a clear order of the preferences of each bird species for the nectars of the ornithophilous plants in the community. This was because preferences changed as the combinations of plants in flower and their flowering intensity changed, and as the abundance of the different bird species fluctuated over the annual cycle.

However, three major points of interest emerged from consideration of the feeding preferences observed during the study:

- (a) The smaller bird species (Greater Doublecollared Sunbirds and Lesser Doublecollared Sunbirds) used plant species which produced smaller, scattered nectar resources (exemplified by A. saponaria) far more than than did the larger birds (Gurney's Sugarbirds and Malachite Sunbirds).
- (b) Malachite Sunbirds and Gurney's Sugarbirds showed a distinct preference for Protea nectar, particularly that of P. roupelliae. Greater Doublecollared Sunbirds and Lesser Doublecollared Sunbirds relished the nectar of P. caffra, but rarely visited P. roupelliae.
- (c) The nectar of L. leonurus was strongly preferred by all four nectarivorous bird species, despite larger amounts of nectar being available from H. lucida and P. roupelliae at the same time.

These points will serve as a basis for discussion of feeding preferences and organization of the avian nectarivore guild and of the structure of the ornithophilous plant community.

- (a) Observation: smaller bird species used and sometimes preferred scattered nectar sources; larger birds ignored them.

This was particularly clear for A. saponaria, and to a lesser extent in P. aequalis and A. arborescens (Table 3.5), which were preferred by the Greater Doublecollared Sunbirds and (with the exception of P. aequalis) Lesser Doublecollared Sunbirds. Many

studies have reported avian nectarivores which forage at low-density and scattered nectar sources (e.g. Feinsinger 1976, 1978; Wolf et al. 1976; Snow & Snow 1980; Pimm & Pimm 1982; Wooller 1982; Collins 1983c; Dobkin 1984; Paton & Carpenter 1984). The birds which adopt this strategy are generally smaller, subordinate species which are excluded from high-density nectar sources by larger and aggressively dominant species. They thus use nectar resources which are probably inadequate to sustain the larger dominant species and which are certainly unprofitable to defend (Wolf & Hainsworth 1971; Covich 1974; Lyon 1976; Boyden 1978; Ford 1979; Pimm & Pimm 1982).

But aggression, and particularly territorial defence, was not common in this study and patterns of this were not clear at any of the resource densities. The smaller species fed on the other richer nectar sources at the same time as using A. saponaria nectar. It thus seems that the smaller birds were using dispersed nectar sources because they could afford to (they have lower foraging costs and total energy requirements), and not necessarily because of exclusion from other more profitable sources by larger birds. The use of the scattered nectar resources by the smaller birds would diminish nectar demand (and therefore exploitation competition) at the other plants favoured by the larger birds.

Greater Doublecollared Sunbirds and Lesser Doublecollared Sunbirds seemed to compete directly for the nectar of A. saponaria and A. arborescens. However, there may have been

temporal partitioning at A. arborescens where these plants were clumped (see later discussion), and Lesser Doublecollared Sunbirds were unable to extract all the nectar from A. arborescens and probably A. saponaria because of the long corollas of these flowers (Chapter 2). The limited amount of nectar removal by Lesser Doublecollared Sunbirds at these plants, although obviously enough to sustain the smaller birds in their foraging, together with their generally low abundance, probably accounted for insufficient nectar resource depletion to warrant aggressive exclusion of the Lesser Doublecollared Sunbirds by the Greater Doublecollared Sunbirds. Only two aggressive encounters between these species was recorded at A. saponaria.

(b) Observation: Malachite Sunbirds and Gurney's Sugarbirds avidly sought Protea nectar, particularly that of P. roupelliae. Greater Doublecollared Sunbirds and Lesser Doublecollared Sunbirds took the nectar of P. caffra but rarely that of P. roupelliae.

This was not always clear in the data analysis of expected versus observed feeding, with both plants generally occurring in the "observed  $\approx$  expected" column (Table 3.5). This, however, stems from the situation at the time that these plants were flowering: almost all the nectar available in the study area during their peak blooms was Protea nectar. So even if the birds fed only at proteas at these times (particularly in the case of P. caffra), the preference would not be reflected because the number of "observed" feeding visits would be close to the number "expected". If, however, a species was avoiding one of these

plants and favouring others, this would show up well (as it has done in the case of Greater and Lesser Doublecollared Sunbirds' avoidance of P. roupelliae).

The undoubted popularity of Protea nectar (noted also by Skead 1963; Skead 1967; Craib 1977) is not surprising because of the density of the flowers, both in the inflorescence and relating to the density and clumping of the plants which gave them the highest "potential energy values" (Table 3.1). This was particularly so for P. caffra. A probable testimony to the great preference of all the bird species for feeding at this plant was that no other ornithophilous plant species flowered to a significant extent at the same time (Fig. 3.2). P. aequalis peaked either side of the P. caffra peak, and H. lucida, which seemed to flower nearly all year to a large extent, declined in bloom to zero over this period in apparent submission to this plant's attractive superiority.

It is difficult to ascribe importance to factors which could contribute to the popularity of P. caffra apart from the superabundance and high density of its nectar-sugar (despite rather a low nectar concentration). A second reason would be that its nectar seems easily accessible to all the nectarivorous bird species (Chapter 2). A third reason could be the large arthropod fauna which these inflorescences attract, which may in turn attract the birds (Chapter 4).

The same can be said of P. roupelliae and its appeal to Malachite Sunbirds and Gurney's Sugarbirds, although on a

slightly smaller scale despite a larger nectar-sugar production per inflorescence (Table 3.1). The consistent preference of these birds for visiting this plant, even when its flower density was low, and over P. caffra at times, may be related to the avoidance by the Greater and Lesser Doublecollared Sunbirds of feeding at these flowers. This is presumably because the smaller birds cannot feed efficiently at the P. roupelliae inflorescences because of the deep-seated nectar and long effective corolla (Chapter 2). The smaller birds may, however, also have been excluded through aggression (see Wooller 1982), though there was little evidence of this. Another possibility in explaining the popularity of P.roupelliae with the larger bird species is the provision of rewards other than nectar which may be particularly attractive or accessible to them (see Chapter 4). It is interesting that H. lucida resumed flowering as P. caffra declined and P. roupelliae increased in flowering intensity, thus making use of (and supporting) the Greater and Lesser Doublecollared Sunbirds.

(c) Observation: L. leonurus was strongly preferred by all the nectarivorous bird species.

It is difficult to see why the nectar of L. leonurus was so highly sought after: the plant had one of the lowest "potential energy values" (Table 3.1). H. lucida, P. roupelliae and A. arborescens were in flower at the same time and produced larger and apparently more worthwhile rewards. Why were the birds

showing such a preference for L. leonurus over these plants which at other times they sought avidly?

This may relate to the very orderly arrangement of the flowers on the spikes in neat, compact whorls. The flowers were set at an angle ideal for the rapid insertion of the birds' bills, probably leading to efficient foraging by all four species (see Chapter 2 and the studies of Gill & Wolf (1977, 1979), Gill (1978) and Frost & Frost (1980) which have looked at sunbird foraging at Leonotis species elsewhere).

It is unlikely to be a result of flower morphology or the high nectar quality of L. leonurus because these aspects are very similar to those of the simultaneously-flowering H. lucida, although they would be contributing factors. It is possible that the pollen of L. leonurus is eaten and is of some critical nutritional value at this time (see Chapter 4). I can offer no definite answer to this question, but leaving the reasons for the plant's desirability as a matter for conjecture and future investigation, the equally puzzling question remains as to how, or indeed, if, the bird species partition this resource.

I did not detect any clear spatial partitioning, as has been described for some hummingbirds feeding at high-density nectar sources (Colwell et al. 1974; Feinsinger 1976), although unfortunately I made no quantitative assessment of this possibility.

There was some evidence of temporal partitioning (Fig. 3.7), the larger species (Gurney's Sugarbird and Malachite Sunbird)



feeding in greater numbers earlier, and the smaller species later in the day. The picture was complicated in L. leonurus because it had two daily peaks in nectar production, but some trend remains evident, although the temporal separation it suggests was by no means strict.

Other studies of sunbirds and of hummingbirds and honeyeaters have shown similar partitioning of dense, highly profitable nectar sources (Wolf 1975; Gill & Wolf 1975a, 1975b; Frost & Frost 1980; Craig & Douglas 1984; McFarland 1985). All of these have indicated that the observed temporal staggering was maintained by aggression between the birds, the larger dominant species excluding the subordinate species until such time as defence of the resources becomes unprofitable (as nectar replenishment rates diminish); the aggressors then abandon the clump, giving access to smaller subordinate species which are able to use the remaining resources profitably .

In the present study, however, there was one striking feature at variance with this explanation: there seemed to be very little interspecific aggression at L. leonurus. Almost all aggression observed was intraspecific, and, although the larger species were dominant when interspecific aggression did occur, it was common to see two or three, or even all four species feeding contentedly together in the patch, occasionally even at the same plant. Interspecific encounters usually occurred when a subordinate species ventured too close to a dominant species, and involved behaviour called "displacement" (McFarland 1985) in

which the dominant supplanted but did not pursue the subordinate.

A similar lack of overt interspecific aggression was observed throughout much of the study, particularly during periods of low nectar availability. Feeding preferences and resultant partitioning of nectar resources were rarely distinct, often resulting in a large overlap in diet. At A. arborescens, all possible combinations of Gurney's Sugarbird, Greater Doublecollared Sunbird and Lesser Doublecollared Sunbird were seen feeding at the same clump at the same time, with apparent indifference to the activities of the other birds.

I propose three theories to explain these observations, all of which may be playing a role at some time to some degree: (a) "economical aggression", (b) clump size and (c) mixed-species foraging flocks.

(a) "Economical aggression"

All other studies have shown the importance of aggression in achieving much of the partitioning of nectar resources among nectarivorous birds. But aggressive interaction is energetically expensive for the aggressor. Studies of feeding territoriality in sunbirds have shown that it accounts for about 40% of the energy expenditure of the territorial birds while they are maintaining a territory, and 6-13% of their total daily energy expenditure (Gill & Wolf 1975a, 1975b, 1979; Wolf 1975; Frost & Frost 1980). Continued attempts to impinge on a dominant bird's territory must

also be energetically costly for an intruder, although this aspect has received little attention. If a subordinate species were to accept that it is likely to be supplanted or chased by a dominant species and learn when and to what extent such aggression was likely, it could alter its foraging behaviour and times accordingly. This would reduce the energy expenditure not only of the subordinate bird, but the aggressor as well, and in so doing, reduce the total energy requirements of the whole avian nectarivore guild and lessen demand for nectar resources.

Many authors have suggested that maintenance of territoriality in nectarivorous birds may be achieved at relatively low cost by display and vocalization, rather than direct aggression (e.g. Cody 1974; Wolf 1978; Frost & Frost 1980). Frost & Frost (1980) described how Olive Sunbirds N. olivacea actively defended L. leonurus patches until nectar was depleted to a level at which this was no longer profitable, and then adopted shorter chases and more vocalizations and displays to defend a clump. Greater Doublecollared Sunbirds were extremely vocal at A. arborescens clumps in the present study, even during feeding bouts. Although both Gurney's Sugarbirds and Lesser Doublecollared Sunbirds were seen feeding with the Greater Doublecollared Sunbirds at times, Lesser Doublecollared Sunbirds and other Greater Doublecollared Sunbirds did not attempt to feed until after peak nectar production (09h00 - 11h00). Although I could not be sure, it seemed always to be the same male Greater Doublecollared Sunbird which returned to the clump to feed, and a few aggressive

encounters were observed between male Greater Doublecollared Sunbirds at A. arborescens.

The existence of some temporal partitioning at L. leonurus, but with little overt interspecific aggression accompanying it, supports the idea of "economical aggression" to some extent. Gurney's Sugarbird and Malachite Sunbirds were certainly the most vocal and active during the morning at the L. leonurus patch which I observed. However, this theory is partially contradicted by the fact that, despite the general tendency for the smaller species to be more common later in the day, all four species were often seen foraging close to one another.

## (2) Clump size

The L. leonurus patch in these observations may have been so large as to preclude its effective defence. At its peak, the patch consisted of 584 flowering spikes in an area of about 700 m<sup>2</sup>. Such an explanation seems unlikely, however, despite this large size, for two reasons. Firstly, in Frost & Frost's (1980) study, a L. leonurus clump of 328 spikes was defended by an Olive Sunbird on the Natal coast (although no indication was given as to the area this covered, and the bird was hard pressed to maintain the territory). Secondly, defence of portions of large high-density nectar sources by nectarivorous birds has been reported (Stiles & Wolf 1970; Colwell et al. 1974; Primack & Howe 1975; Feinsinger 1976).

### (3) Mixed-species foraging flocks

Mixed-species foraging is a common phenomenon in birds and there have been several theories advanced by zoologists to explain it. Diamond (1981) outlined five theories; three of them are worth considering here. One is the "Gang Theory" in which it is advanced that flocking may allow members to overpower the dominant territorial birds by force of numbers. In my study, for example, Greater Doublecollared and Lesser Doublecollared Sunbirds might forage together at the patch in the interests of obtaining nectar which the dominant birds (Malachite Sunbirds or Gurney's Sugarbirds) would defend against only one or a few subordinates. This has been observed in honeyeaters (Paton 1980) and in hummingbirds at patches where intruder pressure is high (Gill 1978). An extension of this idea, which would fit the situation at L. leonurus better, is that there are simply too many nectarivorous birds of any description foraging at the clump to make territoriality a worthwhile proposition; rather the birds put their heads down and feed as efficiently as they can.

This brings me onto the second theory, the "Convoy Theory", in which it is suggested that mixed-species flocking increases the likelihood of predator detection, and decreases the likelihood of an individual being eaten. This in turn may lead to an increase in feeding efficiency resulting from a reduced need for individual vigilance (Barnard & Stephens 1983). It is difficult to say how important predation is in sunbird and sugarbird populations. It is not considered a major factor in hummingbirds: their main predators are birds (particularly raptors), and they

may often be caught by raptorial insects and in spider webs! (Miller & Gass 1985). The birds in my study were twice seen to take cover in dense bushes when raptors flew over. However, Berner & Grubb (1985) have shown that food availability is more likely to be important than predation in influencing the formation of mixed-species foraging groups.

The third theory is the "Feeding Efficiency Theory". Mixed-species foraging flocks have similar (or in my study at the L. leonurus patch seemingly identical) diets (Morse 1970; Diamond 1981). There is an inverse relationship between food density and flocking with an increase in the tendency to flock with a decrease in food availability, particularly if diets overlap because of decreased food variety (Cody 1974). Many reasons for this have been proposed (Pulliam 1973; Diamond 1981; Barnard & Stephens 1983; Berner & Grubb 1985), but the most likely is the idea that the birds keep track of where food has already been collected by foraging in a flock, and in this way avoid wasting time foraging in areas recently visited by others.

This hypothesis seems particularly feasible if nectar is the scattered resource sought because food variety is low, and, although easily located, flowers may be empty. It can be applied only in a very broad way in the L. leonurus patch however, because, although L. leonurus was highly sought after and occurred at low overall density in the study area, it was at high density where it grew because of the plant's tendency to clump. So perhaps the best way to make use of it is for all species to

start foraging at the same time, and as nectar resources are depleted and the rate of replenishment diminishes, so the larger species fall out. This would account partially for the observed temporal partitioning at L. leonurus in that the larger species' foraging intensity decreases through the day sooner than that of the smaller ones. The birds do not, however, all start with equal intensity, possibly as a product of "economical aggression". Mixed-species flocks certainly did not keep track of exploitation by travelling about together visiting successive patches of L. leonurus. Probably such behaviour is advantageous only when food is scarce, and is scattered randomly or difficult to detect (Cody 1974; Diamond 1981).

Most interspecific aggression occurred at high nectar-density in the large stands of P. caffra in which Gurney's Sugarbirds, Malachite Sunbirds and Greater Doublecollared Sunbirds seemed at times to be defending feeding territories from those birds they could dominate. These appeared to be shifting territories, particularly in the less dominant species which were often supplanted by larger ones, but unfortunately none of the birds observed were ringed and individuals' movements were hard to monitor. Again, despite the considerable aggressive activity, there was much inconsistency. For example, Malachite and Greater Doublecollared Sunbirds could be found feeding near to each other; the Malachite Sunbird might chase the Greater Doublecollared Sunbird for quite a distance, but then both of them would return to resume feeding where they left off.

Some of what I have already discussed about the behaviour at the L. leonurus patch may have applied at the proteas also, despite the great abundance of nectar. Possibly the high nectar density facilitated small territories (Collins 1983b) with an assiduously defended core (particularly in the morning) and a peripheral buffer zone defended less tenaciously, as has been found in some hummingbirds (Paton & Carpenter 1984). This would explain the inconsistencies in the aggression observed. Or maybe the superabundance of the nectar made strict feeding territoriality unnecessary (Siegfried & Rebelo 1986). Unfortunately I did not make studies of possible temporal variations in the occurrence of aggression, or temporal and spatial differences in foraging of the different bird species at P. caffra.

It is impossible at this stage to say if, and to what extent, the ideas discussed here apply to the nectarivorous bird community in this study. More detailed investigation of temporal partitioning, aggressive interaction (overt and "economical") and the possibility of spatial partitioning is required. It would be interesting and probably illuminating to compare the results of such investigations at different-sized clumps and flower densities, particularly of L. leonurus.

#### 3.4.3 Nectar availability and fluctuations in nectarivorous bird populations

Despite the succession of flowering peaks over the annual cycle (Fig. 3.2), the availability of nectar, or rather nectar-



sugar, varied markedly (Fig. 3.3). Large variation has been shown in many other studies, and nectarivorous birds have been found to be remarkably vagile in tracking nectar resources, both on a local scale (e.g. Coe 1961, 1967; Skead 1967; Pettet 1977; Greig-smith 1980; Feinsinger & Swarm 1982; Ford 1983; Collins et al. 1984; Rebelo et al. 1984; Feinsinger et al. 1985), and over long distances (Wolf et al. 1976; DesGranges 1978; Feinsinger 1980; Feinsinger et al. 1985). In these studies and in mine (Figs 3.4, 3.5 and 3.6) there was a general tendency for local population levels of nectarivorous birds to correlate with nectar availability, with large fluctuations in both. In the present study the correlation was not as strong as has been reported in some other studies (see Gass & Montgomerie 1981), suggesting that other factors (e.g. competition, feeding preferences, habitat preferences, climate) were influencing the distribution of the birds as well. For example, only Greater Doublecollared Sunbirds and Lesser Doublecollared Sunbirds were seen in the Forest habitat. H. lucida nectar was available there in considerable quantities for most of the year, and the habitat may have acted as a retreat for the smaller species if interference and exploitation competition with the larger species was high. This was a clear example of partitioning of nectar resources through habitat selection (Wolf 1970; Linhart 1973; Feinsinger et al. 1982).

Looking at total nectar availability and bird populations monthly (Figs 3.3 and 3.4), three points of interest emerge.

Firstly, in August and September the bird population did not increase in proportion to the sudden surge in nectar production, as would seem possible considering the increase in bird numbers in December and January in response to a similar increase in nectar abundance. This may be because the nectar of the August-September peak (that of H. lucida and G. sutherlandii) was not as eagerly sought as the P.caffra nectar constituting the second peak. It may also be due to low "reserves" of nectarivorous birds, particularly Malachite Sunbirds, in the Drakensberg area at this time, or to a low arthropod abundance (see Chapter 4).

Secondly, the return of at least some of the Malachite Sunbirds to the study area coincided with the nectar-production peak in August and September. And thirdly, the nectarivorous bird population started to increase markedly in November, when nectar production was at its lowest.

Other studies have shown that the arrival of migrant nectarivorous birds coincides with an increase in abundance of nectar in the community (Wolf et al. 1976; Desgranges 1978; DesGranges & Grant 1980; Feinsinger 1980, Wooller 1982), as occurred in this study. In the hummingbird communities, migrant species are generally subordinate generalists and the residents dominant and territorial; the migrants are therefore accommodated in the community because of large nectar supplies and a plasticity in the migrants' feeding. In contrast to this, in my study, the residents (mostly Greater Doublecollared Sunbirds) were not dominant and did not defend feeding territories against the migrant Malachite Sunbirds; and Gurney's Sugarbirds which

were capable of defending feeding territories against Malachite Sunbirds did not appear to do so.

DesGranges & Grant (1980) postulated seven ways in which hummingbirds could be accommodated into a resident nectarivorous bird community:

(a) if migrants were dominant

This was probably a factor in my study because the Malachite Sunbirds were dominant over all except Gurney's Sugarbirds, but the importance of this is difficult to gauge; it did not, however, appear to play a large role because little interspecific aggression was noted.

(b) if migrants were territorial

This is related to the first proposition. Again here, despite the possible dominance of the Malachite Sunbirds, there was little evidence of interspecific territoriality.

(c) if migrants showed greater feeding plasticity, or

(d) if migrants used resources neglected by residents

It is possible that these suggestions apply in my study. Malachite Sunbirds tended to feed opportunistically on H. lucida and G. sutherlandii nectar, while Greater Doublecollared Sunbirds showed a marked preference for H. lucida nectar at the time of the Malachite Sunbirds' arrival (Table 3.5). The reasons for this preference may be that the Greater Doublecollared Sunbirds are smaller and have proportionally higher energy demands and prefer the more concentrated nectar. The larger Malachite Sunbirds can

make good use of both nectars, and can cope with the larger volumes of nectar (for equivalent energy gain) obtainable from G. sutherlandii, and benefit from its larger overall nectar-sugar production despite the low nectar concentration (see Chapter 2). It is interesting that DesGranges & Grant (1980) found a similar pattern in that the migrant hummingbirds in their study used the nectar from more generalized cup-shaped flowers (like G. sutherlandii) while residents (which were dominant in their study) used the nectar of specialized tubular flowers (like H. lucida).

(e) if migrants were better "fugitive species"

Being migrants, such birds are likely to be better colonists of new nectar sources, responding quickly to changes in nectar availability in local habitats. Wolf et al. (1976) found this to be the case in their study of a hummingbird community. It did not seem to hold, though, in the present study: Greater Doublecollared Sunbirds, and not the Malachite Sunbirds, were generally the first to exploit plant species just as they were coming into flower (e.g. H. lucida and P. caffra). This was probably because the smaller birds could better use the smaller, scattered resources which even the major nectar-producing plants constituted in their initial (and final) stages of flowering.

(f) if resources were not limiting

This may well have been the case at the time that the Malachite Sunbirds arrived. As mentioned, the nectarivorous bird

population was low at this time, despite the surge in nectar production by H. lucida and G. sutherlandii.

(g) if migrants formed mixed-species flocks with residents

I have discussed the possibility of mixed-species flocks in connexion with L. leonurus. There was, however, only a little evidence of mixed-species foraging in August-September at H. lucida when Greater Doublecollared Sunbirds and Malachite Sunbirds were occasionally seen feeding in the same tree or bush. More commonly the Malachite Sunbirds formed small flocks among themselves (particularly the males) and fed together, despite considerable animosity between members of the group; such behaviour has also been noted by Skead (1967) for this species. Possibly here the birds were keeping track of which nectar sources had already been visited, as discussed earlier for mixed-species flocks. Mixed-species flocking was more prevalent in October and November when nectar levels were very low; small flocks of Malachite and Greater Doublecollared Sunbirds fed on the very small (but concentrated) volumes of nectar of the exotic Cotoneaster sp. (Rosaceae) bushes near the Research Station.

As DesGranges & Grant (1980) point out "there is considerable room for overlap between these different hypotheses and several may act in concert in any particular situation." This seems true in the present study, although the important ones here appear to be different from those emphasized in the hummingbird communities studied (DesGranges 1978; DesGranges & Grant 1980; Feinsinger 1980).

#### 3.4.4 Why do Malachite Sunbirds migrate in winter?

The most obvious feature of the fluctuations in the bird populations was the migration of Malachite Sunbirds from the study community at the beginning of May and their return in August. This trend has been noted by Skead (1967), Cyrus & Robson (1980) and Brown & Barnes (1984); the birds appear to move to the warmer lowlands of Natal. It has been suggested that Gurney's Sugarbirds make a similar but partial migration (Skead 1963; Skead 1967). My study supports this observation: Gurney's Sugarbirds were seen much less frequently from May to October than between November and April (Fig. 3.3), but I have no evidence as to where the birds go.

The departure of the Malachite Sunbirds was clear, and it did not appear to be in response to lower nectar levels per se; it may have been because of the dwindling of L. leonurus and P. roupelliae nectar supplies, of which the birds were fond. But A. arborescens flowered at this time and into June and Malachite Sunbirds relish the nectar of this plant (Skead 1967). The birds may, however, travel to lowland areas for that reason: the prolific flowering of the aloes there in winter. I have discussed how all the birds favoured L. leonurus nectar and how they seemed to compete for it. Malachite Sunbirds are highly mobile (Skead 1967), and they may follow L. leonurus flowering peaks to lowland areas where this plant flowers somewhat later (personal observation; Frost & Frost 1980). Another possibility influencing

the departure of the Malachite Sunbirds may be the availability of arthropod-food which was markedly low from May to August (see Chapter 4). Gurney's Sugarbirds seemed to leave at about the same time, probably for similar reasons, probably making particular use of Protea nectar in the lowland areas (Skead 1963). The two larger species of nectarivorous birds are likely to be better equipped morphologically and physiologically to undertake migrations of this kind than the smaller doublecollared sunbirds (Tucker 1971; Hainsworth & Wolf 1972b; Brown et al. 1978).

It is possible, however, that the Malachite Sunbirds and some Gurney's Sugarbirds migrate because of the low winter temperatures which set in in May (Fig. 1.3).

Many hummingbirds (Lasiewski 1963; Hainsworth & Wolf 1970, 1972a; Carpenter 1976b; Hainsworth et al. 1977; Schuchmann et al. 1983), a honeyeater (Collins & Briffa 1983a, 1983b) and some sunbirds (Cheke 1971b) have been shown to undergo large drops in body temperature and enter torpor during periods of cold and, in the case of hummingbirds, food scarcity. Energy conservation through torpor can be considerable. For example, Wolf & Hainsworth (1972) showed an 80% reduction in metabolic rate in a torpid hummingbird at an ambient temperature of 6°C.

Larger birds are better able to withstand low temperatures and food scarcity because they have lower metabolic rates, slower heat losses and a relatively large capacity for energy storage (Lasiewski 1963; Lasiewski & Dawson 1967; Brown et al. 1978). It

may be for these reasons that larger sunbirds underwent less extreme drops in body temperature in Cheke's (1971b) study; but this may also indicate that smaller birds would have evolved more efficient torpor.

Brown et al. (1978) have pointed out that smaller birds would be able to enter and recover from torpor far more rapidly than larger birds because of their more rapid heat losses and gains (higher thermal conductance) and could thus take advantage of the energy-saving afforded by torpor and respond to changes in their environment more quickly. Brown et al. (1978) further point out that, although physiologists measure metabolic rates per g body weight, the ecological unit is the individual and, as they show, smaller hummingbirds suffer smaller overall energy losses and require less total energy to function than larger ones.

There may well be, then, a difference in the capacity of the bird species in this study to enter torpor and thus to conserve energy when the ambient temperatures are low. It seems likely that the smaller Greater Doublecollared and Lesser Doublecollared Sunbirds would be better at this. In further support of this idea is the observation that Malachite Sunbirds have been recorded in the study area in all months except July in years previous to this study (Cyrus & Robson 1980), and in July the minimum temperatures are considerably lower than in the other winter months. The return of the Malachite Sunbirds at the time when nectar resources suddenly increased but temperatures were still quite low also supports this idea to some extent: the larger birds could then find enough food to weather the cold. The



thermoregulatory abilities of the birds of this study would be extremely interesting to investigate and the results would be useful in interpreting much of the ecology of the community.

But even ignoring the possibility of different thermoregulatory abilities and strategies, Malachite Sunbirds and Gurney's Sugarbirds require larger amounts of energy than smaller birds, and this is more pronounced at low temperatures. From May to July (the coldest months) nectar availability was low and scattered, and the larger birds probably could not obtain enough food to survive because their energy demands were much greater than at other times as a result of the low temperatures (Collins 1983a). Presumably, however, the Gurney's Sugarbirds which remained at this time could find enough food, but only in reduced numbers.

Malachite Sunbirds have an additional energetic burden in the form of a moult into eclipse plumage in the early winter. Not only would this be an energy drain, it may also increase heat losses because of poorer feather cover and hence lowered insulation. All these factors, together with the probability of larger nectar and arthropod supplies in the lowlands, would combine to encourage the Malachite Sunbirds to migrate.

#### 3.4.5 Some concluding remarks

Aggression has featured prominently in this discussion and in those of many similar studies. But in contrast to most other studies the patterns of aggression and its role in structuring

the nectarivorous bird community of this study were not clear; I have been able to say little definite about aggression because of a failure to detect any consistency in it. Some other authors have noted and been puzzled by this too (Skead 1967; Cheke 1971a), while others have found definite trends and shown how it is important in food allotment between species and individuals in sunbird communities (e.g. Gill 1978; Frost & Frost 1980, 1981; Wooller 1982; Collins 1983b, 1983c). A detailed study of intraspecific and interspecific agonistic behaviour and territoriality in the Drakensberg community, with its mosaic of variation in bird species abundance and nectar availability in varying forms, may give some insight into this complex subject. The lack of consistency may relate to a lack of predictability in amount and timing of nectar production, and emphasizes the need for long-term study of this and other aspects dealt with in this chapter (Lyon 1976; Pimm 1978; Holmes et al. 1986; Wiens 1986; Powers 1987).

Many authors have pointed out that nectar and nectarivory provide an almost ideal field of interaction for attempting to demonstrate and explain resource partitioning (Feinsinger 1976; Brown et al. 1978; Wiens 1983). Nectar is a narrowly defined resource and its energetic and nutritional values are relatively easy to measure. Its abundance in a community is comparatively simple to determine and it is used by a well defined guild of consumers which, in the case of birds, are quite easy to observe. There has been a tendency for studies of competition to concentrate on species-rich communities where it is assumed that

competition is likely to be most evident and intense (Diamond 1978; Diamond & Case 1986). Many of these have been of nectarivory, particularly in birds (e.g. Colwell 1973; Colwell et al. 1974; Feinsinger 1976, 1978; Feinsinger et al. 1985). But the complexity of these communities makes such studies and their interpretation complicated and unwieldy, and, as noted earlier in discussion of divergence among plants to share pollinators, underlying trends may thus be obscured.

A more thorough and quantitative investigation of the plant community and the avian nectarivore guild of this study would seem a better proposition (see the studies and suggestions made by Feinsinger (1976), Montgomerie & Gass (1981), Waser (1983b) and Holmes et al. (1986)). The comparative simplicity of the community in the Drakensberg, by virtue of the small number of plant and bird species involved, would lend it well to an investigation rising to the challenge set by Wiens (1983) to definitively link community structure with competition.

## CHAPTER 4

THE IMPORTANCE OF ARTHROPODS IN THE DIETS  
OF THE NECTARIVOROUS BIRDS

## 4.1 INTRODUCTION

In considering the feeding ecology of the nectarivorous birds in the preceding chapters I have concentrated on nectarivory. At the outset of the study I emphasized investigation of bird-plant, bird-bird and plant-plant interactions because these aspects most intrigued me and promised to be interesting to study. That nectar was the most important energy source for the birds seemed likely from brief field observations of the species concerned and from the literature (e.g. Skead 1967; Ford & Paton 1976; Pettet 1977; Mostert et al. 1980). From the literature, however, it was clear also that all nectarivorous bird groups depend upon arthropod-food for many essential components of their diets, most notably protein. Indeed, while nectar may provide the bulk of the bird's carbohydrate and water requirements, arthropod-food probably fulfils most of the rest of their nutritional needs (Ford & Paton 1976; Mostert et al. 1980; Montgomerie & Gass 1981; Baker & Baker 1986).

Although it has never been shown that nectarivorous birds feed predominantly on arthropods (largely, of course, because they then would fall into the occasional nectar-feeding category), this may occur seasonally in some species while breeding or when

nectar is scarce (Wolf 1970; Montgomerie & Redsell 1980; Pyke 1980; Ford & Paton 1985).

I wanted to investigate the importance of arthropods in the diets of the nectarivorous birds of this study for three reasons:

- (a) To determine if nectar was, as I assumed, a more important source of energy to the birds than arthropods.
- (b) To determine the extent and variation of arthropod-feeding by the different bird species seasonally in order to consider properly what has already been discussed in preceding chapters: fluctuations in bird populations, feeding preferences and interactions at flowers, and so on.
- (c) To determine the relative importance of arthropods and nectar in the diets of sunbirds (Nectariniidae) and sugarbirds (Promeropidae).

It is difficult to find a common unit by which to measure the relative values of nectar- and arthropod-food to the birds. Both provide energy and water, but arthropods are probably more important as a source of other nutritional requirements not present in sufficient quantities in nectar (Baker & Baker 1980, 1986). It is thus probably best to use the foraging efforts of the birds as an index to the relative importance of these dietary components. Another way, which also uses the birds as an indicator, is to investigate how variation in the availability of

the different food resources affects the abundance of the birds (Pyke 1983).

I also examined the birds' diets for other food items.

## 4.2 METHODS

### 4.2.1 Arthropod availability

Arthropods were sampled using a 25-cm diameter sweep-net. Three 100-sweep samples were taken from the vegetation along the transects in the Sandstone-cliffs, Protea savanna and Forest habitats in every month except August. The numbers of arthropods in the samples were taken as an index of arthropod availability each month (Janzen 1973a, 1973b). Arthropod biomass was not used because a few large insects in some samples caused immense bias in the results. Many of the arthropods taken by the birds were flying insects; I did not sample these separately (e.g. see Pyke 1983, 1985), but assumed that vegetation sweep-samples broadly reflect fluctuations in the abundances of all types of arthropods (Janzen 1973a, 1973b; Collins & Briffa 1982).

### 4.2.2 Bird foraging behaviour

During the population-transect walks (Chapter 3) and other random walks the first foraging action of each nectarivorous bird seen was recorded as either nectar-feeding or arthropod-feeding. The percentage of feeding actions given to arthropod-feeding by

the different bird species in each month was taken to represent the foraging effort the birds devoted to this food. Data were combined for successive months as was done for the nectar-feeding data of this sort (see Chapter 3).

#### 4.2.3 Faecal samples

Each nectarivorous bird mist-netted during the study was put in a brown-paper bag till it defaecated. This faecal sample was scraped from the paper and placed on a slide, teased apart with needles and mounted in the same way as described for pollen samples (p 81) (Collins & Briffa 1982).

The abundance of arthropod fragments in each sample was scored in five transects of the slide under the medium power of a microscope. In a few cases fragments were identified to order (Calver & Wooller 1982; Ralph et al. 1985), but this was rarely possible because the arthropod remains were heavily macerated. Pollen grains in the faecal samples were counted or their numbers estimated as described for the pollen samples (p 82). Absolute numbers of fragments and grains in each sample were determined by multiplying in proportion to the area of the slide examined in the counts. Other items in the faecal samples were identified and counted where possible.

## 4.3 RESULTS

### 4.3.1 Arthropod availability

Arthropods were most abundant in summer, followed by a sharp fall in numbers from April to June coinciding with a drop in temperatures and rainfall (Figs 4.1 and 1.2). In mid-winter (June-July) arthropod availability was about a third that of summer.

### 4.3.2 Bird foraging behaviour

An overall average of 8,7% of the birds' foraging actions were in search of arthropods. The seasonal variation of this is depicted in Fig. 4.1 (average for all species) and Fig. 4.2 (for the different species). Arthropod-foraging was higher from June to November than over the rest of the year, with a peak at 16% of foraging actions in October-November followed by a sharp drop to 3,1% in December-January. The averages for the different species for the year were: Gurney's Sugarbird 7,4%, Malachite Sunbird 8,5%, Greater Doublecollared Sunbird 7,9% and Lesser Doublecollared Sunbird 10,8%. Lesser Doublecollared Sunbirds tended to feed slightly more on arthropods than the other species, particularly when nectar supplies were low in June-July (Figs 4.2 and 3.3). (This was possibly also the case when nectar was scarce in October-November, but I have only eight feeding records for the Lesser Doublecollared Sunbird over this period; of these, however, four were on arthropods.)



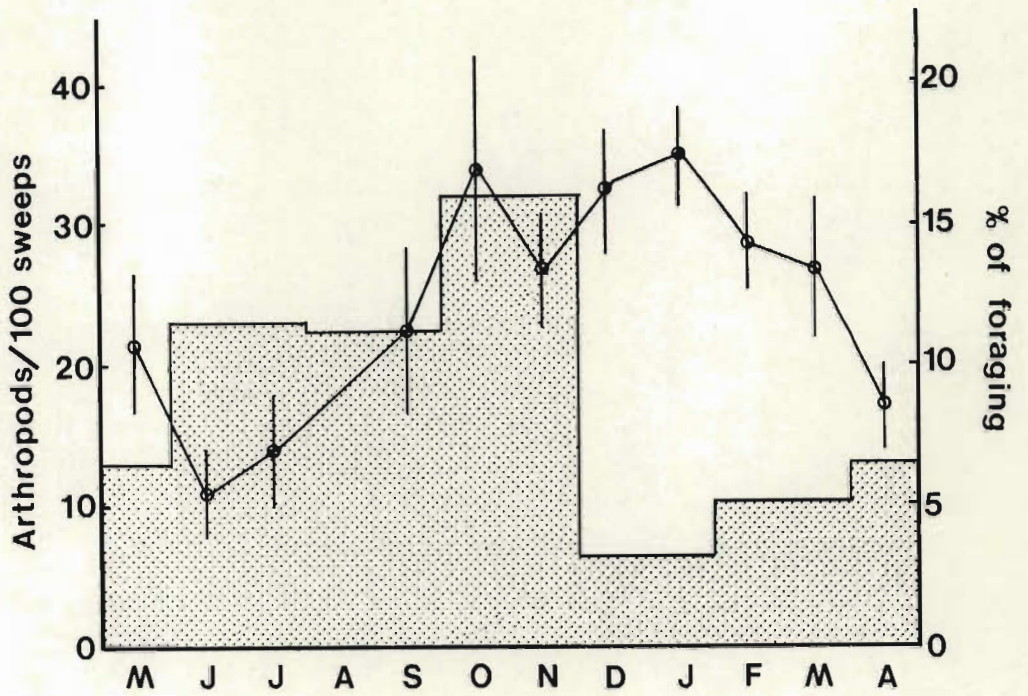


FIGURE 4.1

Monthly arthropod availability (curve; vertical bars represent  $\pm$ S.E.) and the mean percentage of foraging devoted to arthropod-feeding by the nectarivorous birds for two-monthly periods (histogram).

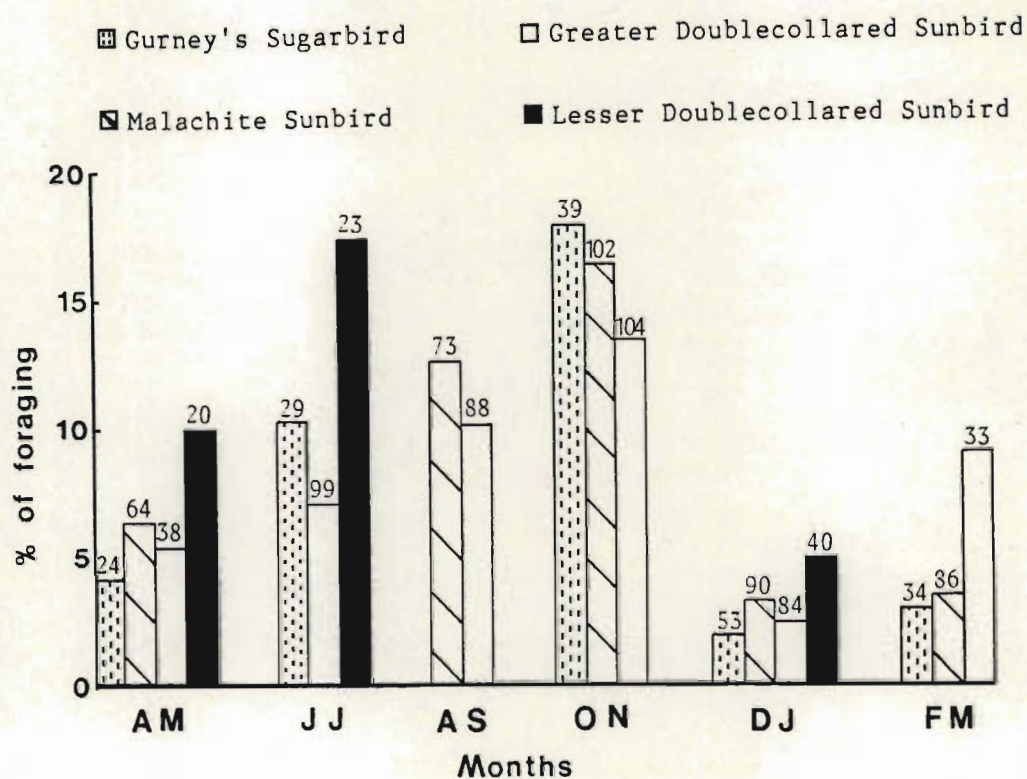


FIGURE 4.2

The percentages of foraging devoted to arthropod-feeding by the different nectarivorous bird species over the year. Numbers over the bars indicate the total number of feeding actions (*i.e.* on nectar and arthropods) recorded. Bars were plotted only if the total number of records for that species over that period was 20 or more; hence some species are absent from some of the two-monthly plots.

### 4.3.3 Faecal samples

Arthropod remains were detected in 92,2% of all the faecal samples. The fragments were small and heavily macerated and thus difficult to identify. Five orders of insects were identified (figures in parentheses indicate the number of samples in which the orders were detected): Diptera (4), Lepidoptera (3), Hymenoptera (3), Coleoptera (3) and Mantodea (1). There tended to be more arthropod fragments in the faeces in the summer months December-March (Table 4.1), despite rather a low incidence of arthropod-foraging recorded for this period (Figs 4.1 and 4.2).

Pollen grains were often very numerous in the faecal samples, particularly those of Leonotis leonurus, Halleria lucida, Greyia sutherlandii and the proteas, depending on the time of the year (Table 4.1 and Fig. 4.3). This component of the samples was very variable, however. Gurney's Sugarbird seemed to ingest particularly large amounts of protea pollen.

Also occurring in many of the samples (69%), often in high numbers, were small hairs from the inside of the perianth of the protea florets (Table 4.1 and Fig. 4.3). Gurney's Sugarbirds and Malachite Sunbirds in particular seemed to ingest these in large numbers when the proteas were flowering.

TABLE 4.1

The mean numbers of arthropod fragments, pollen grains and protea-floret perianth hairs found in the faecal samples collected during the study. Not all species were captured in each period and some are thus absent from some of the month-groupings.

N = Number of samples. GUR = Gurney's Sugarbird; MAL = Malachite Sunbird; GDC = Greater Doublecollared Sunbird; LDC = Lesser Doublecollared Sunbird; CWE = Cape White-eye. L.l = L. leonurus; H.l = H. lucida; G.s = G. sutherlandii.

+ = <100; ++ = <1000; +++ = <10 000; ++++ = >10 000.

Months	Species	N	no. of arthropod fragments	no. of pollen grains from				no. of protea-perianth hairs
				L.l	Protea	H.l	G.s	
April- July	GUR	4	48	++	++++			1 210
	MAL	8	208	+++	++			232
	GDC	13	94	++	+	++		130
	LDC	4	210	+++	+			26
	CWE	3	95	+	+			19
August- November	MAL	13	185		+++	+++	+++	121
	GDC	5	323		+	++	++	20
	CWE	7	138		+	+	+	6
December- March	GUR	3	119		++++			3 050
	MAL	6	257		+++	+		1 620
	GDC	8	222	+	++	++		980
	LDC	2	107		++	+		460

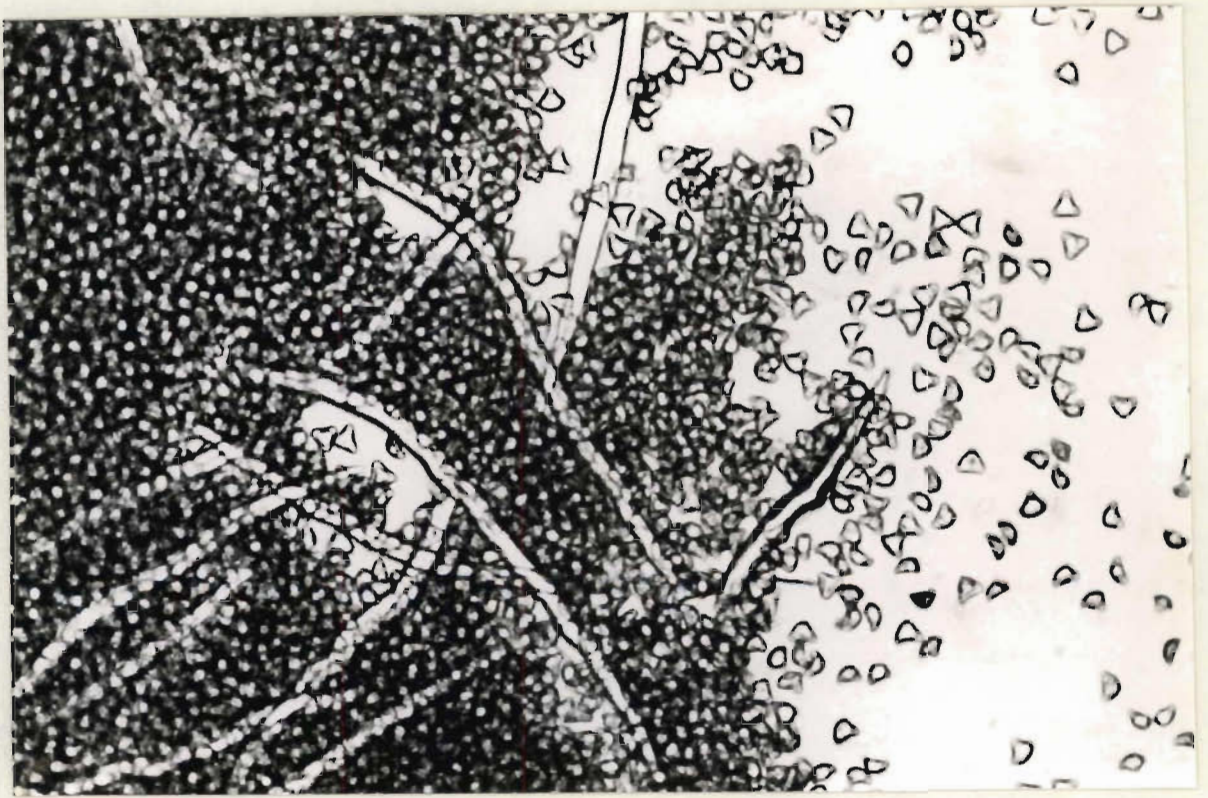


FIGURE 4.3

Part of a faecal sample from a Gurney's Sugarbird showing the vast numbers of, in this case, protea pollen grains, and the protea-floret perianth hairs found in many of the faeces examined. (Magnification x400).

#### 4.4 DISCUSSION

##### 4.4.1 The value of arthropods to nectarivorous birds

I have found no quantitative assessment of the importance of arthropod-food to sunbirds and sugarbirds, but arthropods are considered to be important in their diets (Skead 1967; Pettet 1977; Mostert et al. 1980). As mentioned, the best way in which to gauge the value of arthropods to nectarivorous birds is to monitor the foraging effort they devote to this food. In this study, an average of 8,7% (seasonal range, all species 2-18%) of the birds' feeding actions were in search of arthropods.

In general, these figures are similar to those found for hummingbirds and honeyeaters, although the data for these groups are very variable. Hummingbirds have been reported to increase their arthropod-foraging when breeding (Wolf & Wolf 1971; Waser 1976; Montgomerie & Redsell 1980) and when nectar is scarce (Wolf 1970). Generally hummingbirds spend less than 10% of their time feeding on arthropods, but in one instance they have been reported to feed exclusively on these while breeding (Montgomerie & Redsell 1980). Honeyeaters devote 4-40% and occasionally up to 80% of their foraging efforts to catching arthropods, depending on the honeyeater genus, and, like hummingbirds, take more arthropod-food during breeding and at times of nectar shortage (Ford & Paton 1976; Pyke 1980; Collins & Briffa 1982; Paton 1982).

Ford & Paton (1976) tried to assess the value of arthropods in the diet of the New Holland Honeyeater Phylidonyris novaehollandiae, but this they did only in terms of energy. Using direct observations and crude energy values and budgets, they estimated that the birds were barely able to balance their arthropod-foraging (hawking) energy expenditure with the food thus obtained; nectar-foraging, on the other hand, furnished an energy intake at a rate of up to ten times that at which it was expended. Ford & Paton (1976) suggested that intake of nectar may supplement energy expenditure on arthropod-feeding.

There are, though, three points to bear in mind with regard to Ford & Paton's (1976) study. Firstly, less energetic forms of arthropod-foraging such as foliage gleaning (39% of arthropod-feeding actions of the birds in my study) would probably ensure a positive energy budget for arthropod-feeding. Secondly, many bird species, even some nectarivorous ones at times (Montgomerie & Redsell 1980), feed solely on insects successfully; it thus seems probable that the birds in Ford & Paton's (1976) study had no need to balance their arthropod-foraging energy budget critically because of the abundant energy available from nectar. Thirdly, and most importantly, the value of arthropods to nectarivorous birds is rarely in terms of energy; arthropods are more likely to be of specific nutritional value. Thus, despite the possibility of an energy deficit in foraging for arthropods, they are essential in the diet and must be obtained by the birds.

The rather low incidences of arthropod-feeding in my study and in many of the other studies mentioned above is misleading. It is

clear that, although effort spent on arthropod-foraging may be low in comparison with that for nectar, the birds cannot exist for any length of time without this added component of their diet; they rely almost exclusively on arthropods for all aspects of their nutrition other than their carbohydrate and water requirements (Baker & Baker 1980, 1986; Mostert et al. 1980; Paton 1980, 1981; Gass & Montgomerie 1981). Arthropod remains were found in over 92% of the faecal samples in this study, and Collins & Briffa (1982) and Collins et al. (1984) found arthropod fragments in nearly all the honeyeater faeces which they examined.

Arthropods, rather than nectar, might even be the limiting food at times, accounting for the frequent lack of close correspondence between nectar availability and nectarivorous-bird abundance. While arthropods seemed to play some role in this regard in the present study (see Chapter 3), no studies which have monitored all three variables have shown any consistent correlation between nectarivorous bird numbers and arthropod availability (Fig. 4.1; Collins & Briffa 1982; Pyke 1983; Collins et al. 1984; Ford & Paton 1985).

Amino-acid concentrations are low in bird-nectars, probably because nectarivorous birds are able to feed on arthropods to fulfil their protein requirements (Chapter 2; Baker & Baker 1986), but it is interesting to speculate on reasons for the presence of amino acids in ornithophilous-flower nectars at all. The amino acids may be a relic of a possible earlier



entomophilous condition (see Chapter 2). In some cases amino acids in the nectars may result from pollen falling into the nectar (Baker & Baker 1986). It is even conceivable that some plants are attempting to supplement the protein needs of the birds that pollinate them in a bid to obtain "pollinator preference" (see Chapter 3).

The birds' need for arthropod-food is emphasized by the increase in this foraging activity leading into the breeding season (May-November; breeding season September-February (Skead 1963; Skead 1967; Brown & Barnes 1984)), despite low insect availability over the first few months of this period (Fig. 4.1). In the winter months (May-August), however, increased foraging for arthropods could be largely because they are scarce at this time, though no less important in the birds' diets; foraging time may therefore be increased in order to gather enough arthropod food. Further, the high availability of arthropods and increased incidence of arthropod-foraging by the birds in October-November coincides with an extreme drop in nectar supplies (Fig. 3.3); the birds may merely be feeding more on arthropods because of the dearth of nectar at this time (e.g. see Wolf 1970; Pettet 1977; Pyke 1980; Montgomerie & Gass 1981). The Lesser Doublecollared Sunbirds in particular appeared to feed more frequently on arthropods when nectar supplies were low, possibly because of competition with the larger species for nectar (see Chapter 3).

Undoubtedly, though, the birds do require larger numbers of invertebrates in their diets before and during breeding to satisfy the high demands of both the parents and chicks for

nutrients not available in sufficient quantities in nectar (e.g. proteins, fats, minerals) (Broekhuysen 1959; Skead 1967; Waser 1976; Wolf & Wolf 1976; Hainsworth 1977; Montgomerie & Redsell 1980; Paton 1982, 1985). It is probably a combination of the onset of breeding, high arthropod availability and the low nectar supplies which induces the increased arthropod-feeding from August to November.

Oddly, in this connexion, arthropod-feeding records for the birds are relatively few over much of the breeding season (December-February) (Fig. 4.1). It is improbable that this is attributable to the high availability of nectar at this time because, although large supplies of nectar would be required, large numbers of arthropods would also be needed. I suspect the reason for this anomaly to be that many of the foraging actions recorded as nectar-feeding visits to the protea inflorescences which were extremely abundant at this time may in fact have been to feed on the arthropods which abounded in the protea heads, particularly those of P. caffra. The frequently enormous arthropod faunas hosted by the inflorescences of proteaceous plants have been noted by several authors (Horn 1962; Gess 1968; Mostert et al. 1980; Coetzee & Giliomee 1985), and Mostert et al. (1980) found in the stomachs of Cape Sugarbirds Promerops cafer large numbers of arthropods from the proteas visited by the birds.

It is interesting to note that the nectarivorous birds of this study commonly obtained arthropods attracted to many

entomophilous as well as ornithophilous flowers. For example, all the nectarivorous bird species were strongly attracted to Leucosidea sericea plants in search of the numerous insects which the nectar of this plant attracted.

During most of the breeding period in the Drakensberg, nectar supplies were high, but this was not the case early on (October-November). The birds may, however, initiate breeding as soon as possible in anticipation of the nectar-resource increases which will be more important in rearing the chicks than in egg formation (Skutch 1950; Perrins 1970; Wolf & Wolf 1976).

#### 4.4.2 Other items in the birds' diets

Pollen grains, particularly those of H. lucida, L. leonurus and the proteas, were found in nearly all the faecal samples collected, and a few samples appeared to consist of little else. On three occasions I observed nectarivorous birds "nibbling" at the anthers of flowers: Gurney's Sugarbird at Aloe arborescens and Malachite Sunbirds at L. leonurus (twice).

Is it possible that pollen is an important item in the diet? Pollen is a rich food source, particularly in amino acids (Faegri & van der Pijl 1979; Simpson & Neff 1983). Paton (1981), however, investigated the importance of pollen in the diets of New Holland Honeyeaters and concluded that they derived negligible nutrient from it, despite the large numbers of grains the birds appear to ingest (Recher 1977; Paton 1981). Paton (1981) based this assertion on the assumption that, because the

protoplast contents of the grains were still visible under the microscope, the pollen had not been digested. He further stated that even if fully digested, the quantity ingested would provide only 20% of the birds' protein requirements and 0,2% of their energy needs.

Digestion of the pollen exine requires digestive specialization which only the collembolan insects have thus far been shown to possess (Simpson & Neff 1983). Some insects grind or puncture the exine to extract the contents. Simpson & Neff (1983) state, however, that "in general, pollen-feeding requires little or no modification of the gut", with the nutrient obtained through the exine and pores by osmosis, osmotic shock and possible encouragement of pollen-tube growth (Howell 1974).

Churchill & Christensen (1970) showed that the Purplecrowned lorikeet Glossopsitta porphyrocephala once considered to be nectarivorous, was relying on pollen as its staple food: the birds' digestive tracts were choked with it and nectar was rarely available during the study. March & Sadleir (1972) reported that much of the diet of the Bandtailed Pigeon Columba fasciata consisted of hemlock pollen at certain times of the year. Bleitz (1970) kept some species of hummingbirds in captivity successfully for the first time by adding pollens to the birds' artificial nectar supplies. Oatley & Skead (1972) have suggested that occasional nectar-feeding birds may derive some specific nutritional benefit from the apparently accidental ingestion of pollen while nectar-feeding. Howell (1974) claimed that pollen

was an essential source of some amino acids in the diets of some nectar-feeding bats. It is possible, then, that pollens may supply or supplement essential nutrients in which a nectarivorous bird's other foods are deficient.

I cannot be sure that any of the birds of this study deliberately ate pollen and, without a knowledge of faecal passage rates, I cannot ascertain how much was consumed. While much of it may be taken inadvertently during nectar-feeding, it is possible that pollen could be an important nutrient source. This may be particularly so for certain bird species at certain times or under certain conditions, but the scanty data which I have collected show no obvious trends to support these possibilities. This aspect of the birds' diets requires further investigation.

Also present in 69% of the faecal samples were small hairs from the inside of the perianth of the florets of P. caffra and P. roupelliae (Table 4.1). These were quite numerous in some samples, particularly the faeces of Gurney's Sugarbird (Fig. 4.3). Cheke (1971a) found similar hairs from P. kilimandscharica in the stomachs of the sunbirds he studied; some of the stomachs contained little else. He concluded that the hairs formed an important part of the birds' diets.

I cannot say whether the birds of my study were ingesting the hairs on purpose, for the same reasons that I cannot be sure of purposeful and useful ingestion of pollen grains. The hairs may play a part in the nutrition of sunbirds and sugarbirds and, along with nectar, in attracting the birds to pollinate the

proteas. This may explain the almost invariable need for the presence of protea species for the occurrence of sugarbirds (Skead 1967); Gurney's Sugarbird faeces contained especially large numbers of the hairs. An investigation into the nutritional value of the hairs is required.

#### 4.4.3 Concluding remarks

An undoubted value of arthropods (and possibly also pollen and the protea-floret perianth hairs) in the birds' diets implicit in the above discussion and distinct from any specific nutritive worth is their contribution to a broad-based diet, despite specialization and seeming emphasis in nectar-feeding in nectarivorous birds. When nectar supplies are low the birds can, and appear to, maintain themselves by increased arthropod-feeding. They could probably feed exclusively on arthropods if the need arose. This, together with the common mobility, transience and nectar-feeding plasticity of many nectarivorous birds (see Chapter 3), may account for the success of the various nectarivorous-bird groups.

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