ASPECTS OF THE BEHAVIOUR AND ECOLOGY OF GURNEY'S SUGARBIRD *PROMEROPS GURNEYI* VERREAUX, 1871, IN *PROTEA* WOODLAND, SOUTH AFRICA

by

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1. INTRODUCTION

The sugarbirds (Family: Promeropidae), represented by the Cape *Promerops cafer* and Gurney's Sugarbird *P. gurneyi*, are endemic to southern Africa in areas dominated by *Protea* species in their distribution range in the Fynbos biome and along the Drakensberg escarpment (Clancey, 1980; Rutherford & Westfall, 1986). Broekhuysen (1959) was the first to study the biology of a member of the Promeropidae in detail, namely the Cape Sugarbird. His study prompted Skead (1963) to obtain comparative data on Gurney's Sugarbird in the KwaZulu- Natal Drakensberg. After the poineer studies on these two species, several studies were conducted on the Cape Sugarbird, but no further attention was given to Gurney's Sugarbird. A monograph which summarised the biological information of both sugarbird species was published by Skead (1967). Investigations on the pollination role on *Protea* species, nest site selection in *Protea* trees and the energetics of Cape Sugarbirds (satellite fauna in flowers) were the main themes (Burger, Siegfried & Frost, 1976; Mosterd, Siegfried & Louw, 1980; Rebelo, 1987), while little attention was given to Gurney's Sugarbird.

Although the study of Skead (1963) presented the first baseline information on Gurney's Sugarbirds, basic biological data were still needed on aspects such as the birds' movement patterns, their general behaviour and breeding biology. Skead (1963) specifically comments the following regarding their movements; "*It is unwise, at this stage, to infer that a migration is dependent on flowering of proteas or the lack of it, even though evidence is tempting*" and "*The incidence and movements ... in Natal is somewhat obscure*". Furthermore, little mensural data or indications how to distinguish between the sexes were available and aspects of their breeding biology were still unpublished (Maclean, 1985; McLachlan & Liversidge, 1978). The occurrence of the two species in the Amatole Mountains of the Eastern Cape also raised several questions when they were found breeding alongside in the same area, but recently their distribution ranges have contracted (De Swardt, 1997; Skead, 1964 & 1987).

The taxonomical relationships of the sugarbirds are complex, and this family was classified within the Australian honeyeaters based on tongue structure, nest construction and behaviour (Skead, 1967). This classification was based on the findings of Bock (1985) who compared the tongue structures of the genus *Promerops* with those of the Meliphagidae family. His proposal was later rejected after several years as he misidentified the genera *Dedistoma* and *Toxorhamphus* (which he used for comparisons) as Meliphagidae, as these genera are found to be more related to sunbirds (family Melanocharitidae) (Sibley & Ahlquist, 1990). Sibley & Ahlquist (1974) considered the sugarbirds as a specialised starling based on egg-white protein studies, but the egg-white protein analysis was later reanalysed and it was found to be in error as the electrophoretic parameters were similar to the Nectariniidae (Sibley & Ahlquist, 1990). Olsen & Ames (1984), again, proposed a transfer to the thrushes (Turdidae) based on the syrinx of *Promerops* which is considered to be homologous to the "turdine thumb" of the thrushes (Ames, 1975). As a result of these proposals, definite clarification is needed on the current taxonomical position of the *Promerops* genus. Current DNA/DNA hybridization evidence showed that *Promerops* is more related to sunbirds, and were placed in a subfamily of the Nectariniidae, namely the Promeropinae, by Sibley & Ahlquist (1990). In a recent study which compares the feather ultrastructure and skeletal morphology between the Meliphagidae, Nectariniidae and Promeropidae, it was found that feather ultrastructure did not clarify the taxonomical position of *Promerops* and that skeletal morphology suggests that they are neither related to sunbirds nor to the honeyeaters (Farquhar, Lorenz, Rayner & Craig, 1996). Del Hoyo, Elliott & Sargatal (1992) did not follow the classification of Sibley & Ahlquist (1990) and placed them in their own family, as currently followed by Maclean (1993).

An opportunity arose to do a study on Gurney's Sugarbirds in the Lydenburg area, Mpumalanga Province, during the early 1980's. As no projects have been undertaken on this species at that time, a mark-recapture ringing study was initiated during 1986. The main aim was to study the birds' movements which were suspected to occur after the end of the flowering period of *Protea* species in their mountain habitat, as prior to this study, no clarification as to their movements could be found by previous workers (Skead, 1963). This was also the first of a detailed ringing study undertaken on this species (T. B. Oatley, *in litt.*), and the mark-recapture data obtained during this twelve year project represents one of the most detailed investigations ever undertaken on Gurney's Sugarbird. Therefore, the biological data collected on this species during this study, will hopefully assist to put the taxonomical position of the Promeropidae into perspective.

2. STUDY AREA

Gurney's Sugarbird was studied in the Lydenburg area, Mpumalanga Province (formerly eastern Transvaal), from April 1980 until June 1998 and since 1992 in the eastern Free State. The localities of the study sites, climate, vegetation and flowering plant species are described below.

2.1. LYDENBURG, MPUMALANGA

2.1.1. Location of study sites

Gurney's Sugarbirds were studied at various sites in the low-lying suburban areas of Lydenburg, as well as several other sites along the Long Tom Pass to the east of the town (Fig. 1). In the suburban areas the sugarbirds were captured at exotic stands of *Aloe arborescens*, *Protea neriifolia*, *P. repens* and other plant species at various gardens and parks (25°06'S; 30°28'E), the gardens at the Lydenburg Hospital (25°06'S; 30°27'E) and at the Mpumalanga Parks Board Production Unit (hereafter referred to as the Fisheries Institute) (25°07'S; 30°29'E). The study localities along the Long Tom Pass were at several sites in *Protea roupelliae* woodland at the Gustav Klingbiel Nature Reserve (25°05'S; 30°31'E), the farms Nooitgedacht (25°04'S; 30°33'E), Paardeplaats (25°06'S; 30°33'E), Potloodspruit (25°04'S; 30°32'E) and Sterkspruit (25°07'S; 30°31'E). One other study site, the farm Waterval (25°10'S; 30°19'E) not shown in Figure 1, was situated approximately 17 km south west of the Long Tom Pass study area in the Steenkampsberg mountain range.

2.1.2. Climate

Apart from the 1986/87 and 1988/89 seasons, the annual rainfall at the high lying Potato Seed Production Unit on the Long Tom Pass (2 011 m above sea level) were higher than those recorded at the lower-lying Fisheries Institute at Lydenburg (1 432 m above sea level) during the study period (Fig. 2). This is reflected by an annual mean of 858,4 mm on the Long Tom Pass, compared to the 700,3 mm at the Fisheries Institute, which was significantly higher between the period July 1985 to June 1998 ($t_{24} = 2,25$; $p < 0,05$).

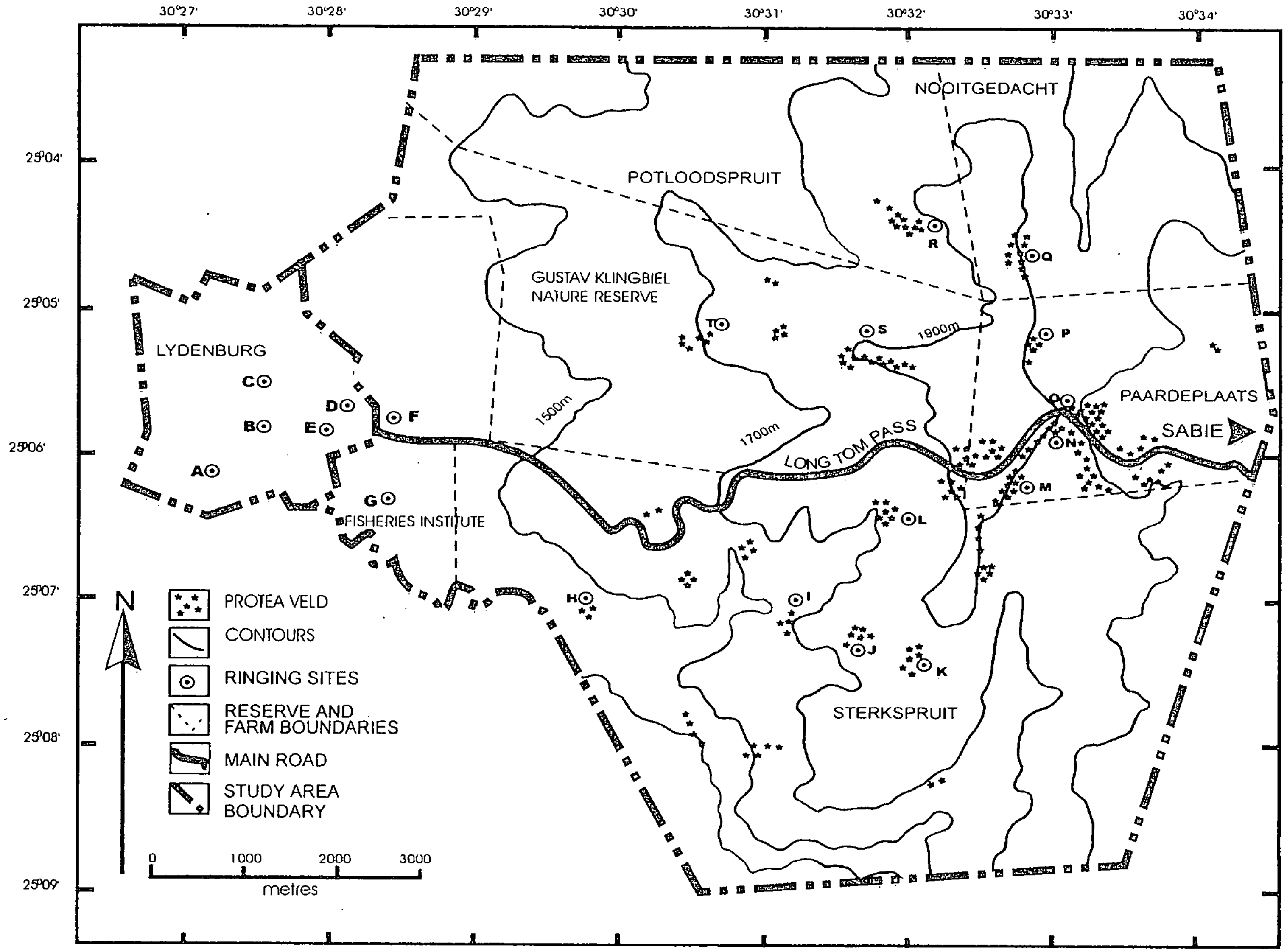


FIGURE 1: Map of the Lydenburg area, Mpumalanga Province, showing the location of the various study sites of Gurney's Sugarbird and the *Protea roupelliae* woodland montane habitat.

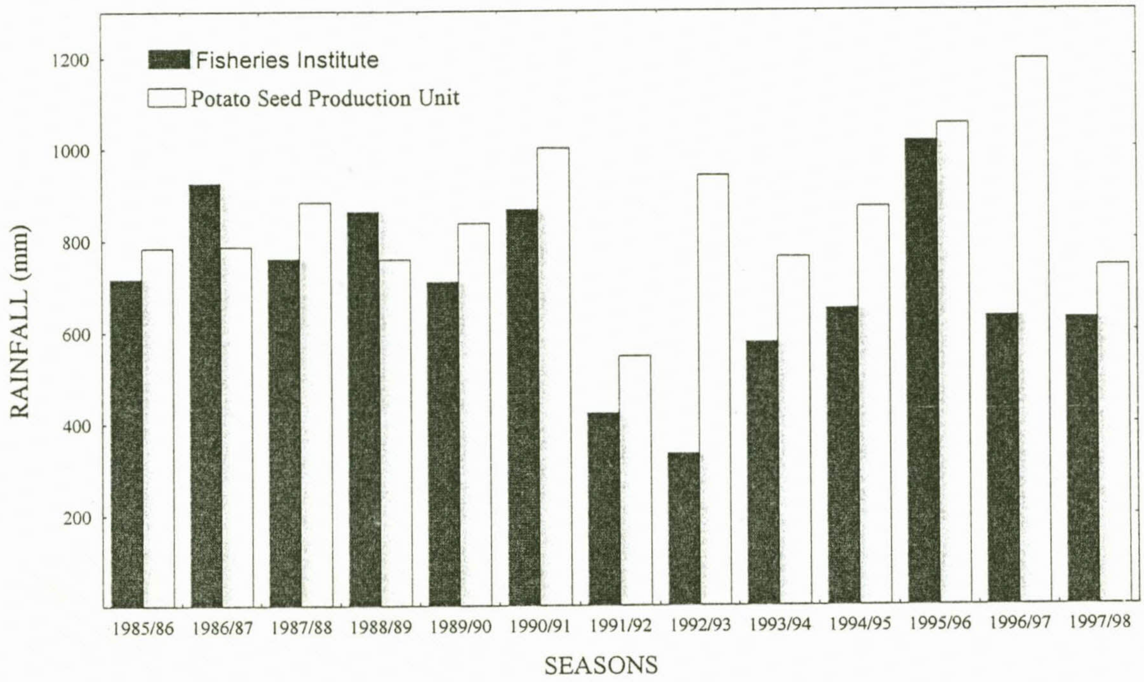


FIGURE 2: Annual rainfall at the Fisheries Institute and Potato Seed Prodution Unit near Lydenburg during the period July 1985 - June 1998.

Climatograms with climatic data of the Fisheries Institute and the Potato Seed Production Unit during the study period are shown in Figures 3 and 4. The rainfall season are from October until March, accompanied with thunder storms and hailstorms. The mean annual temperature at the Fisheries Institute was 28,3°C during the study period, while the absolute maximum and minimum daily temperatures were 37,9°C (September 1994) and -2°C (June 1983), respectively (De Swardt, 1990a). At the higher altitude at the Potato Seed Production Unit, a lower mean temperature of 20,9°C was recorded. Frost occurs regularly during winter in the suburban areas with snow on the higher mountainous areas. During July 1996 heavy snowfalls were recorded on the higher plateau along the Long Tom Pass (T. Bekker, pers. comm.).

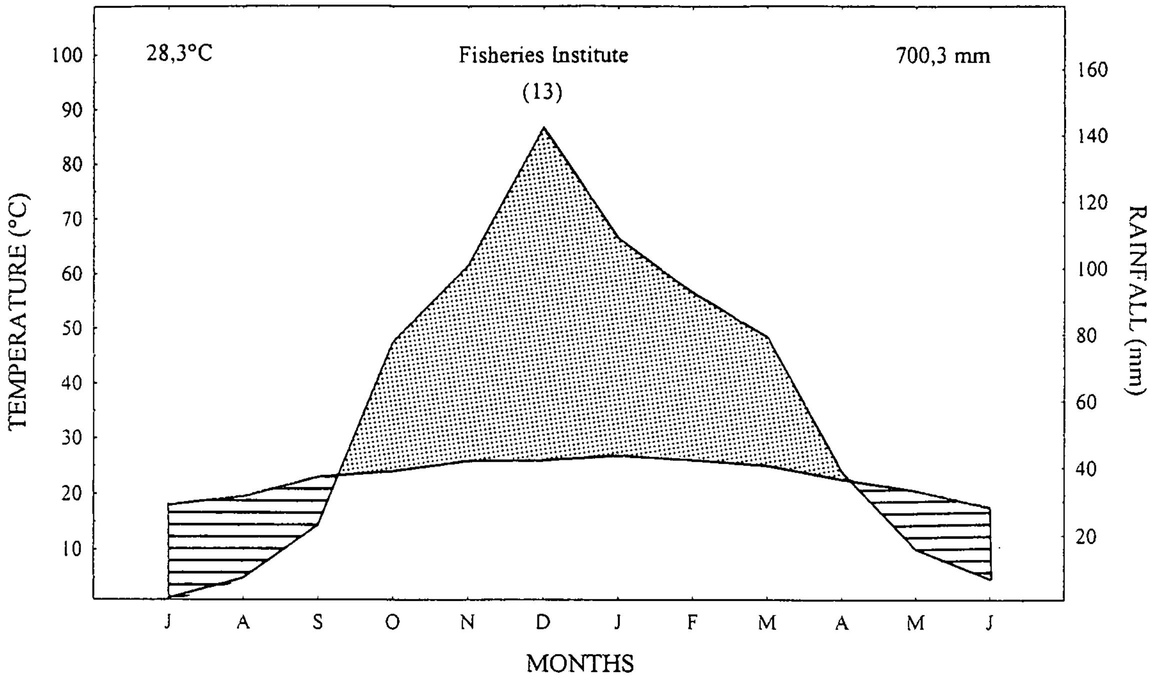


FIGURE 3: Climatogram of the Lydenburg Fisheries Institute during the study period. The numbers at top left and right refer to the mean annual temperature and rainfall respectively, while the number of years of observation is indicated in brackets. The shaded area represents the wet season and the striped area the dry season.

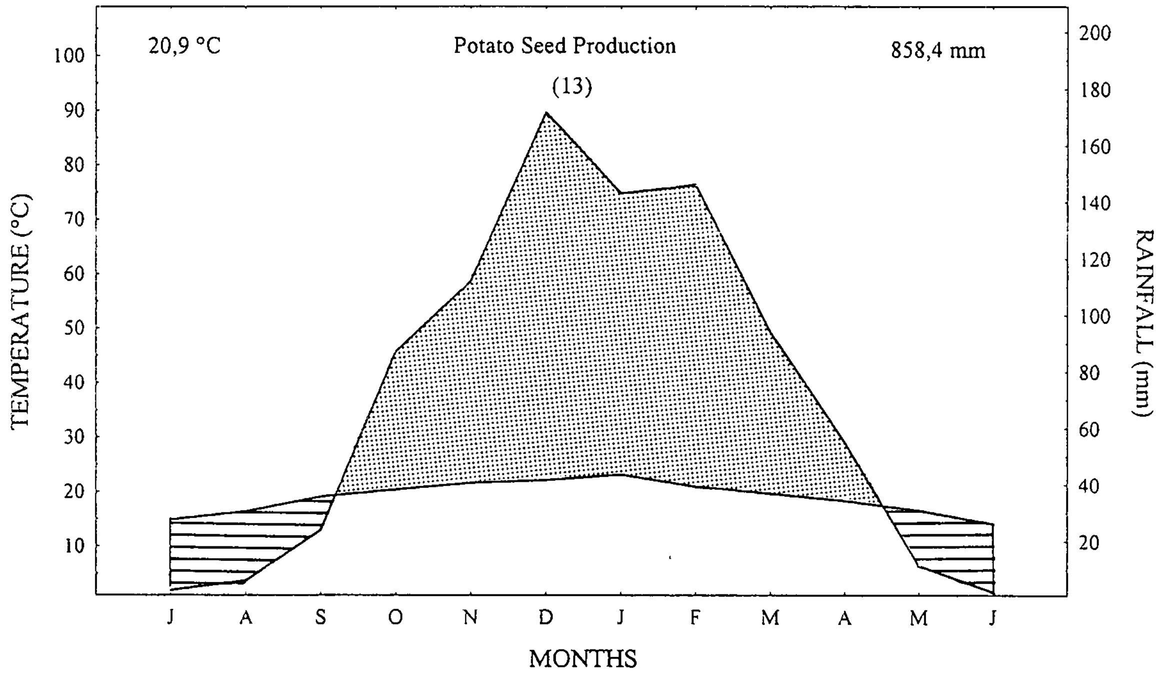


FIGURE 4: Climatogram of the Potato Seed Production Unit along the Long Tom Pass during the study period. The numbers at top left and right refer to the mean annual temperature and rainfall respectively, while the number of years of observation is indicated in brackets. The shaded area represents the wet season and the striped area the dry season.

2.1.3. Vegetation

The Lydenburg study area is situated in the north-eastern Mountain Grassland vegetation type (no. 43) in the grassland biome (Bredenkamp, Granger & van Rooyen, 1996; Rutherford & Westfall, 1986). A detailed description of the vegetation of the Gustav Klingbiel Nature Reserve and Sterkspruit area near Lydenburg is given by De Swardt (1990a). The following habitat types form part of the present study area:

- Grassland: Two grassland areas were recognised of which one mostly occurrs as *Acacia* woodland near watercourses at lower altitudes, while the other can be considered montane grassland at higher altitudes where trees are less common. Grass species such as *Alloteropsis semialata*, *Heteropogon contortus*, *Hyparrhenia hirta*, *Loudetia simplex*, *Themedia triandra* and *Trachypogon spicatus* are abundant at the lower altitudes, while *Harpechloa falx*, *Microchloa caffra* and *Monocybium ceresiiforme* are mostly limited to the higher altitudes. Flowering ephyphites and flowering plants such as *Brunsvigia radulosa, Crocosmia paniculata, Scilla natalensis, Watsonia transvaalensis* and *Dierama* and *Kniphofia* species also commonly occur in the montane grassland areas.

- *Protea* veld: Large stands of *Protea caffra,* with isolated clumps and bands of *P. roupelliae,* occur on montane grassland slopes and plateaus at altitudes above 1 800 m (see Fig. 1 for locations of *P. roupelliae* populations). In most instances the *Protea* veld is limited to rocky mountain slopes or other areas where the substrate is stony.

- Mountain slopes: The tributaries of the Klipgat- and Sterkspruit cut the study area into deep valleys characterised by stony cliffs and scattered trees and shrubs. Trees growing on mountain slopes include *Cussonia paniculata*, *Ekebergia pterophylla* and *Widdringtonia nodifolia,* while smaller woody species such as *Halleria lucida*, *Myrsine africana* and *Pteridium aquilinum* predominate along water courses. Shrubs like *Aloe affinis, A. arborescens*, *Greyia radlkoferi* and *Leucosidea sericea* are important sources of nectar for nectarivorous birds inhabiting the cliffs and mountain slopes.

- Montane forests: Small pockets of forested areas are associated with the ravines cut by the tributaries of mountain streams and are mostly found in shady areas beneath cliffs. Trees which occur in these areas includes *Greyia radlkoferi, Nuxia oppositifolia, Olinia emarginata* and *Syzygium cordatum. Aloe arborescens* and several other flowering plant species are also common in the forest ecotone areas.

2.2. EASTERN FREE STATE

2.2.1. Location of study sites

During 1992 a project on Malachite Sunbirds *Nectarinia famosa* in the Free State Province was initiated and additional data on Gurney's Sugarbird were collected until January 1998 (De Swardt, 1993a & 1995; unpubl. data). The Free State study sites included the Sterkfontein Dam Nature Reserve (28°32'S; 29°01'E) in the Harrismith district and the Golden Gate Highlands and Qwaqwa National Parks in the Clarens and Kestell districts, respectively. Sugarbirds were captured at Wonderhoek (Golden Gate) (28°00'S; 28°00'E) in mixed *Protea caffra/P. roupelliae* woodland and in the Qwaqwa National Park at Honingkloof (28°32'S; 28°44'E), the summit of Qwaqwa Mountain (28°29'S; 28°00'E) and Avondrust (28°28'S; 28°39'E) in *P. roupelliae* woodland (see map in De Swardt & Van Niekerk, 1996).

2.2.2. Climate

Rainfall data (July 1990 - June 1998) were obtained from the Sterkfontein Dam Nature Reserve and Qwaqwa National Park (Fig. 5). The average annual rainfall at Qwaqwa National Park was 817,5 mm and 603,8 mm at the Sterkfontein Dam Nature Reserve. The rainy season occurred mainly during the period November-March, mostly as thunderstorms. In general, winters are cold, with snow occurring regularly at the higher altitudes.

2.2.3. Vegetation

The eastern Free State study localities are situated in the Wet Cold Highveld Grassland vegetation type (no. 41) on the lower slopes of the Drakensberg at altitudes of 1 750 m above sea level (Bredenkamp *et al.*, 1996). These areas are characterised by deep, sheltered gorges with sandstone krantzes at the higher altitudes. The vegetation at Golden Gate Highlands National Park, Qwaqwa National Park and Sterkfontein Dam Nature

Reserve are dominated by montane grassland species such as *Harpochloa falx*, *Hyparrhenia hirta* and *Themeda triandra*. The woody layer consists mainly of *Leucosidea sericea* with extensive stands of *Protea caffra* woodland on the mountain slopes. *P. roupelliae* are confined to isolated clumps on mountainous plateaus and slopes at these localities (see also De Swardt, 1993a; De Swardt & Van Niekerk, 1996), while *P. subvestita* occurs at sheltered places on the Qwaqwa Mountain plateau and at Sterkfontein Dam Nature Reserve.

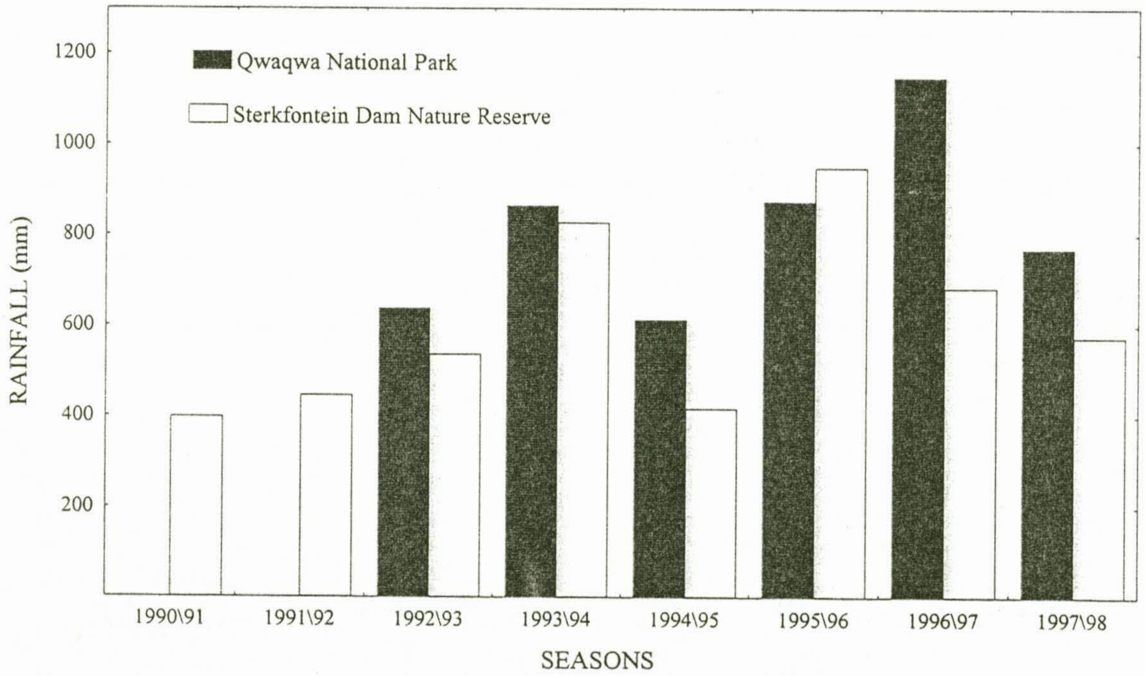


FIGURE 5: Annual rainfall at the Sterkfontein Dam Nature Reserve and Qwaqwa National Park in the eastern Free State during the period July 1991 - June 1998.

2.3 OTHER LOCALITIES

During the study period, additional observations on Gurney's Sugarbirds were carried out at several localities in *Protea roupelliae* woodland in the Eastern Cape Province (former Transkei) during February 1991 and along the escarpment in Mpumalanga Province. An isolated population which occurs in the Waterberg Range at the Marakele National Park (24°27'S; 27°37'E), district Thabazimbi, was also visited during December 1996 to collect comparative data.

3. METHODS

Distributional data of Gurney's Sugarbirds were reviewed and compared using the available information from literature and present distribution ranges of known food plants. Historical records were obtained by gleaning the records from the regional atlasses in Cyrus & Robson (1980), Earlé & Grobler (1987) and Tarboton, Kemp & Kemp (1987), as well as from personal field observations and published sightings (Gouws, 1994; Lawson, 1994). The data on the present distribution ranges of Gurney's Sugarbird and that of *Protea roupelliae* were obtained from the "Atlas of southern African birds" (De Swardt, 1997; Harrison, 1987) and from the "Protea Atlas Project" (Rebelo, 1995; unpubl. data). The distribution pattern of *P. roupelliae* was then compared with the current vegetation types described by Low & Rebelo (1996).

At the study sites Gurney's Sugarbirds were captured with mist nets erected in their flight paths between or in front of *Protea* bushes or *Aloe* clumps with sufficient flowers (De Swardt, 1991a). The sugarbirds were mostly captured at the mountainous localities during summer, but sometimes also during winter, depending on the flowering season of *P. roupelliae*. No capture sessions were carried out in *P. caffra* woodland. In winter, capture sessions were concentrated in the suburban gardens and parks near cultivated flowering species. Twelve metre mist nets were normally used to capture the birds, but at smaller or medium-sized *Aloe* clumps in the suburban areas nine, six or three metre nets were used. De Swardt (1988) designed a copper wire hook device to attach the guy ropes to the net poles, which facilitated the lifting or lowering of the nets. The heights of the nets were then adjusted according to the bird's behaviour and the availability of flowering inflorescences. The hook was later replaced with a modified metal device which was attached to the rope (De Swardt, 1990b) (Fig. 6). A lifting stick was also used to lift the nets to their required heights in mountainous habitats.

FIGURE 6: Non-slip device, which "bites" on the pole when pressed downwards, used to attach guy ropes to net poles when mist netting Gurney's Sugarbirds.

Initially the birds were ringed with 4,3 mm aluminium ring sizes (with an overlap), but later the smaller 3,5 mm ring size, which fits better on the sugarbird's tarsus (T. B. Oatley, *in litt.*), was used. Both males and females were colour-ringed to facilitate individual recognition in the field, especially in the suburban areas during winter. Capture sessions were repeated at the ringing localities to obtain survival and seasonal movement data from recaptures, while special search efforts were conducted to resight colour-ringed individuals. A total of 1 005 hours ($\bar{x}$ = 10,1 hours/day; n = 99) were spent in the field and 5 136 m ($\bar{x}$ = 51,9 m/day; n = 99) of mist nets were used to capture sugarbirds at the Lydenburg study sites. In the eastern Free State, a total of 235 trapping hours ($\bar{x}$ = 7,6 hours/day; n = 31) and 1 761 m ($\bar{x}$ = 56,8 m/day; n = 31) of mist nets were used to trap sugarbirds.

The following standard body measurements, determined with vernier callipers and a wing ruler to the nearest millimetre, were taken from all sugarbirds captured:

- Culmen length – base of the bill (featherline) to bill tip;
- Tail length – base to the tip of the longest tail feather;
- Tarsus length – ankle of the tibia to the third scale of the foot;
- Wing length – shoulder to the longest wing feather, while holding the wing closed.

Two new, additional measurements were used to sex sugarbirds in the hand. These were the total head length (from the tip of the culmen to the back of the bird's head, while holding the bird firmly in the hand), and the width of the bulged sixth primary (P6) (from the rachis to the widest part of the bulged feather). Body mass was determined to the nearest 0,5 g with a Pesola spring balance.

Gurney's Sugarbirds were previously sexed according to a tail and wing length criterion. Although some overlap occurred in the range of measurements of males and females, those of males were mostly longer. Recapture data have, however, shown that sexing by this method is inadequate, mainly in sub-adult individuals (see chapter 5). The application of the total head length and width of the bulged P6 were found to be a more accurate method of sexing individual sugarbirds (De Swardt, 1990c & 1992a). During the breeding season female sugarbirds could also be sexed by the presence of a brood patch. Based on the above mentioned criteria captured sugarbirds were divided in the following age classes: adult male and female, sub-adults and juvenile birds.

Moulting details were determined for all sugarbirds captured (including recaptures). Following Ginn & Melville (1983) the condition of each primary, secondary and tail feather was scored as follows:

- 0 – old, full-grown feather, mostly worn;
- 1 - feather missing or in early pin stage;
- 2 - feather breaking through shaft of pin;
- 3 - feather one or two thirds of its length;
- 4 - feather longer than two thirds of its length;
- 5 – new, full-grown feather.

Body moult was also noted on individual birds. Only the moult scores of the right wing and right section of the tail were analysed, although both sides were recorded.

During the breeding season, intensive searches were made for sugarbird nests in the Lydenburg study area. These were located by searching selected *Protea* bushes or walking through *P. roupelliae* bush clumps. Whenever a sugarbird was flushed from a bush, it was searched for the presence of a nest. Free flying birds seen with nesting material or food were also followed closely. On finding a nest, its contents was recorded, and if possible, monitored. The following nest measurements were taken: height of the nest in the bush, nest cup diameter, depth of the nest and aspect of the nest in the bush. As sugarbirds are prone to desert their nests during the incubation stage, it was important to record the data as quickly as possible, especially during rainy and misty weather conditions. Therefore, egg measurements and mass were only taken from a small sample. When the eggs hatched, measurements of each nestling were taken at regular intervals. Some of the nestlings were later ringed in the nest. In one instance, a time-lapse camera was positioned above the nest in such a way that the behaviour and feeding of the nestlings could be photographed and recorded. Breeding success was calculated as the percentage of the total number of nestlings that fledged successfully from egg clutches from nests recorded during the study period.

Data on the diet of the sugarbirds were obtained from stomach content analyses of specimens shot with a .22/410 rifle, or casualties that died during ringing activities. Fourteen sugarbirds were collected for diet analyses at Paardeplaats (site N) and Sterkspruit (site K) during July 1990, November and December 1992 (De Swardt & Louw, 1994). Insects collected from the sugarbird stomach contents were stored in 70% ethanol, counted and identified to familial level. Direct feeding observations of individuals hawking insects were also recorded. In addition, *Protea* flowers were collected to determine the occurrence of arthropods associated with the flowers. This was compared to the insect fauna recorded in the stomach contents of the sugarbirds. A total of 41 *P. roupelliae* flowers were collected at the Gustav Klingbiel Nature Reserve (site T), Paardeplaats (site O) and Sterkspruit (site K) during the corresponding periods when sugarbirds were collected and again during December 1996 and January 1997. Four flowers, on which sugarbirds were actually seen feeding, were also collected. The *Protea* inflorescences were plucked by hand and sealed in plastic bags. Arthropods associated with the flowers were later removed and preserved in 70% ethanol. Coleoptera beetles were identified using the keys of Holm & Marais (1992), and all insects were deposited in the entomological collection of the National Museum, Bloemfontein.

As sugarbirds showed a preference for *Protea roupelliae* woodland clumps to any other vegetation type (such as *P. caffra* woodland), capturing sessions were carried out exclusively in this vegetation type. Other bird species associated with grassy hillsides or rocky areas were also captured and ringed in the *P. roupelliae* clumps. As the sugarbirds were observed to leave the mountainous areas during winter, the flowering phenology of *P. roupelliae* was determined (De Swardt, 1989 & 1991a). At Paardeplaats (sites N & O), the flowers of 15 randomly selected *Protea* bushes were counted monthly during the period December 1986-June 1988. This was repeated with a larger sample of 25 bushes during the period November 1989-August 1990. For each individual tree a mean value was determined. Following Zietsman, Van Wyk & Botha (1989) the overall average for each observation date was used to indicate flower availability.

The different *Protea* clumps at the Lydenburg study area were plotted on an aerial photograph (scale 1:5000) and a Digital Planometer used to calculate the *Protea* veld surface areas from the photographs. Mean population sizes of Gurney's Sugarbird and Malachite Sunbird per site were estimated by the formule $X=N/Y$, where N is the number of individuals trapped at each site and Y the number of trapping days (De Swardt, 1993b). Densities were then calculated from X/Z, where Z is the area of the clump in hectares. Regression analyses were performed on the *Protea* clump-sizes and number of birds captured at each study locality. Population density figures obtained were derived from the number of unringed sugarbirds mistnetted and later retrapped at the ringing sites. Free-flying sugarbirds observed were excluded from the analysis. Seasonal density figures of sugarbirds were determined at two frequently visited ringing localities (sites N & O) where capturing sessions occurred during regular intervals throughout the study period. Site fidelity of sugarbirds was ascertained when individuals were later recaptured at the same *Protea* clumps where they were originally ringed.

Sugarbird survival is based on individually recognised birds older than a year recaptured during the course of the study. Prior to survival modelling, the validity of the general Jolly-Seber model was first checked using the goodness-of-fit tests provided by program RELEASE (Burnham, Anderson, White, Brownie & Pollock, 1987; Lebreton, Burnham, Clobert & Anderson, 1992). In the case of the male sugarbird data there was no evidence that the assumptions of the Jolly-Seber model were violated (tests 2.Ct, 2.Cm, 3.Sr and 3 of program RELEASE were all non-significant; $p > 0,1$), and the Jolly-Seber model therefore provided a suitable starting point for the survival analysis.

The female data were too sparse to support the goodness-of-fit tests. The mark-recapture data were analysed through application of multinomial probability models parameterised in terms of apparent survival rates and recapture/resighting probabilities (Lebreton *et al.*, 1992). Initially, both survival and recapture/resighting (hereafter referred to as recapture) rates were modelled as differing between years and between the sexes (equivalent to applying the Jolly-Seber model to each sex separately). Attempts were then made to simplify recapture rates with survival using a combination of likelihood ratio tests (LRTs) and Akaike's Information Criterion or AIC (Lebreton *et al.*, 1992). The latter is a simple means of identifying the most parsimonious model describing a given dataset while avoiding numerous statistical tests. All models were fitted using software SURGE4 (Clobert, Lebreton & Allaine, 1987; Pradel, Clobert & Lebreton, 1990). The annual survival rate of Gurney's Sugarbird obtained from the SURGE model was used to calculate expectation for further life by the formula LE = (2-m)/m, where m is annual mortality rate (Rowan, 1964).

All statistical analyses were conducted on Statistica version 5.0 (Stasoft Inc.). Student's t-tests were used on the biometric data for comparison between different measurements while regression analyses were performed between sex and age classes of the birds (Zar, 1984). Comparisons were made between culmen and total head lengths, wing and tail lengths, and between the width of the bulged P6 and wing length in males. Reduced major axis regression analysis were done to determine differences of regression lines between culmen/total head length and wing/tail lengths in adult and sub-adult sugarbirds (Sokal & Rholf, 1981). Coefficients of variation (CV's) and F-ratio tests were use to compare differences in the variability of traits with different mean values (Sokal & Rholf, 1981). Spearman rank correlations were used to describe relationships of morphological traits. Sugarbird biometric data collected outside the Lydenburg study area (Free State study sites and site U on the farm Waterval) were excluded from these analysis. Tail and wing lengths in moult or heavily abraded were also excluded from the analysis. ANOVA tests were used to test the relationships of sugarbird influxes to suburban areas seasonal rainfall during wet and dry seasons. The mean seasonal rainfall figures of the weather stations at the Fisheries Institute and Potato Seed Production Unit along the Long Tom Pass were compared with a student's t-test, while regression analyses were performed on the number of available flowers and monthly rainfall at the Long Tom Pass. A Chi-square test was used to test the significance of the distances and number of birds of the two movement routes between the mountainous and suburban areas (Zar, 1984). Probability values (p) of less than 0,05 were considered as significant.

4. DISTRIBUTION

4.1. INTRODUCTION

Gurney's Sugarbird is endemic to southern Africa with an eastern distribution range along the Drakensberg escarpment (Clancey, 1980). Two isolated populations occur in the Soutpansberg and Waterberg mountain ranges, while the race *Promerops gurneyi ardens* occurs in the eastern highlands of Zimbabwe and adjacent Mozambique (De Swardt, 1997; Maclean, 1993). The aim of this section is to review the literature on the historical and current distribution of Gurney's Sugarbirds and to compare it with the known distribution of their main food plants and the vegetation in which these plant species occur (Low & Rebelo, 1996; Rutherford & Westfall, 1986). Studies on nectarivore populations were mostly carried out in the Fynbos biome (Broekhuysen, 1966; Richardson & Fraser, 1992; Siegfried, 1983) and elsewhere (Dowsett-Lemaire, 1989) where attempts were made to investigate the manner in which species richness, density and biomass varied in relation to vegetation type (Prys-Jones & Clark, undated). This study investigates nectarivore populations in vegetation similar to fynbos, namely the high altitude grasslands of the Drakensberg escarpment where *Protea roupelliae* is abundant (see De Swardt, 1992a), and factors which affect sugarbird densities (and other nectarivores) therein.

4.2. RESULTS

4.2.1. Distribution

Gurney's Sugarbirds are mainly confined to the Drakensberg escarpment, with isolated populations in the Soutpansberg and Waterberg mountain ranges, and the *ardens* subspecies in the eastern highlands of Zimbabwe and adjacent Mozambique (De Swardt, 1997; Fig. 7). The population in the Waterberg mountain range occurs at an altitude of 1 800 m above sea level, in *Protea roupelliae* woodland, in the Waterberg Moist Mountain Bushveld vegetation type (no. 12) at Marakele National Park, Thabazimbi district (Low & Rebelo, 1996). This conservation area was visited during December 1996 when 4 - 6 pairs were observed on the plateau and Peacock (pers. comm.) recently observed three individuals on 5 September 1998 in the same area. The Soutpansberg population is at the same elevation in the Soutpansberg Arid Mountain Bushveld (no. 11). Both vegetation types were previously known as the Northeastern Mountain Sourveld originally described by Acocks (1988). The distribution pattern of Gurney's Sugarbird coincides with that of *P. roupelliae* in the grassland biome (see Fig. 7). The following grassland vegetation types are important, determining sugarbird and *Protea* species distribution ranges: Wet Cold Highveld Grassland (no. 41), Moist Upland Grassland (no. 42), Northeastern Mountain Grassland (no. 43), Alti Mountain Grassland (no. 46) and Short Mistbelt Grassland (no. 47) (Low & Rebelo, 1996).

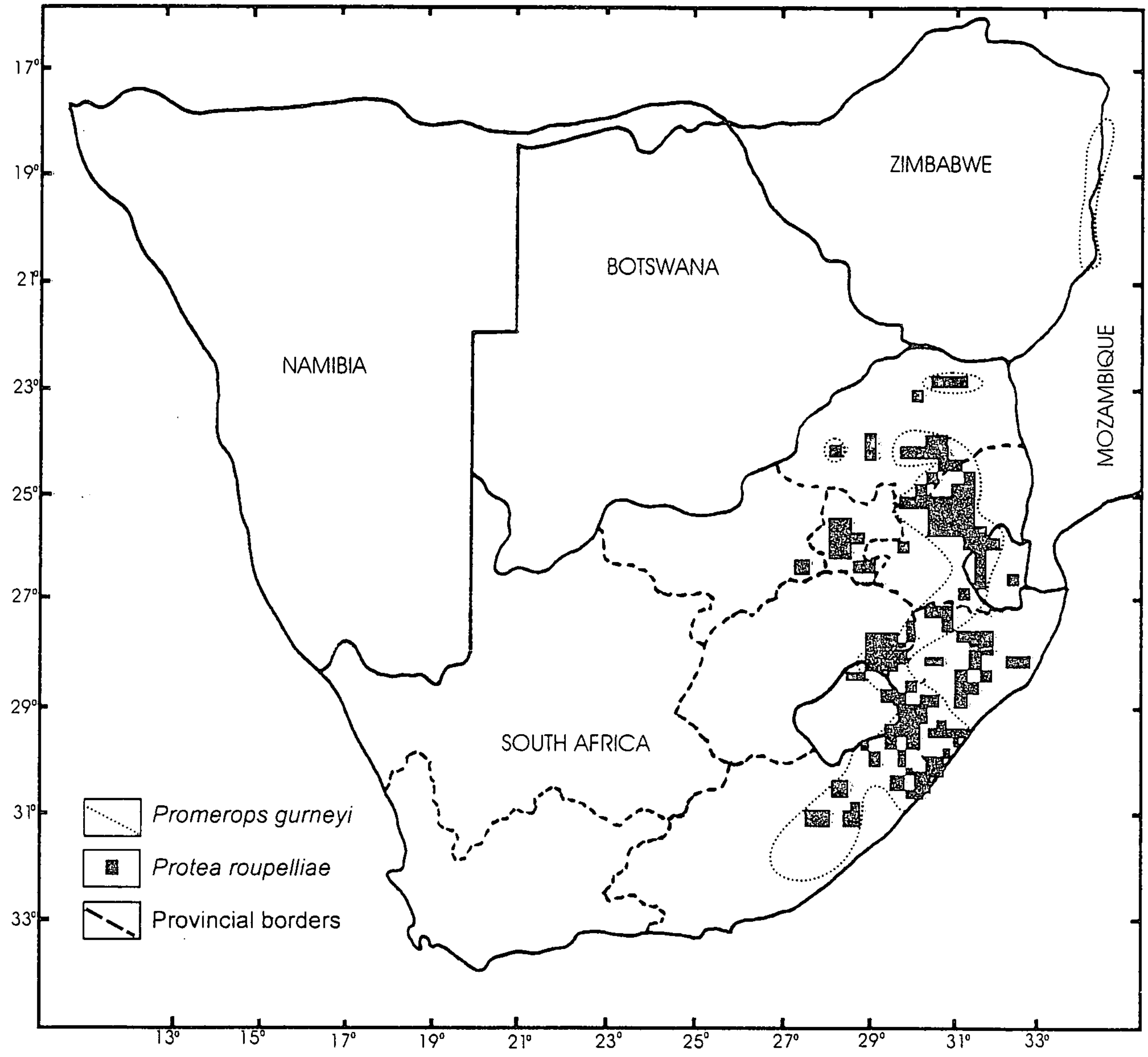


FIGURE 7: Distribution of Gurney's Sugarbird and *Protea roupelliae* in southern Africa. Distribution data after De Swardt (1997) and Rebelo (1995).

4.2.2. Nectarivores captured in *Protea roupelliae* woodland

During the study period, 1 106 nectarivore specimens were captured in bush clumps of *P. roupelliae* at Lydenburg (Mpumalanga Province), Sterkfontein Dam Nature Reserve and Qwaqwa National Park (Free State Province) (Table 1). The higher number of Malachite Sunbirds (45,0%) than Gurney's Sugarbirds (43,3%) captured, is attributed to the scarcity of sugarbirds in the eastern Free State localities, which were not as abundant as at the Mpumalanga study sites. Gurney's Sugarbird was found to be associated only with *Protea* clumps in the study areas, while the Malachite Sunbird is an opportunist, actively flying along the mountain sides and streams and foraging on a wide range of plant species, amongst others *Gladiolus* and *Kniphofia* species. Gurney's Sugarbird was less frequently observed in other vegetation types in the study areas such as *P. caffra* woodland, forest verges or grasslands associated with cliffs. Although sugarbirds were observed visiting *P. caffra* and *Greyia radlkoferi* inflorescences at a forest kloof adjacent to a *Protea* clump, they always returned to *P. roupelliae* clumps (De Swardt & Louw, 1994). During the winters of 1996 and 1997 sugarbirds were recorded and captured in *Protea* clumps at Paardeplaats (site N) during the early morning, and found later during the day in the valley foraging on *Aloe arborescens* inflorescences on the krantzes and near small forest patches.

TABLE 1: Nectarivores captured in *Protea roupelliae* woodland in the Mpumalanga and Free State study sites during the period December 1986 - June 1998 (1 240 trapping hours; 6 897 net metres).

Species	Number captured	% Occurrence	Preferred vegetation-type
Nectarinia famosa	497	45,0	*P. roupelliae* woodland
Promerops gurneyi	479	43,3	*P. roupelliae* woodland
Nectarinia afra	82	7,4	*P. roupelliae* woodland
Nectarinia amethystina	48	4,3	*P. roupelliae* woodland
Total	1106	100,0	

4.2.3. Factors affecting densities in *Protea roupelliae* woodland

4.2.3.1. Clump size

The mean *Protea* clump size was 1,5 ha (range: 0,75-3,15 ha; n = 10) (Table 2). A significant correlation exists between *Protea* clump size and the mean number of birds per site for Gurney's Sugarbirds ($r = 0,276$; $p < 0,05$; df = 8) and Malachite Sunbirds ($r = 0,044$; $p < 0,05$; df = 7) (Fig. 8). Bird densities varied considerably and were often higher at some of the smaller *Protea* clumps. Factors such as rainfall, flowering periods and fire probably influenced these values. Mean densities of 4,3 Gurney's Sugarbirds and 3,9 Malachite Sunbirds per hectare were recorded at the selected study sites in the Lydenburg area (Table 2).

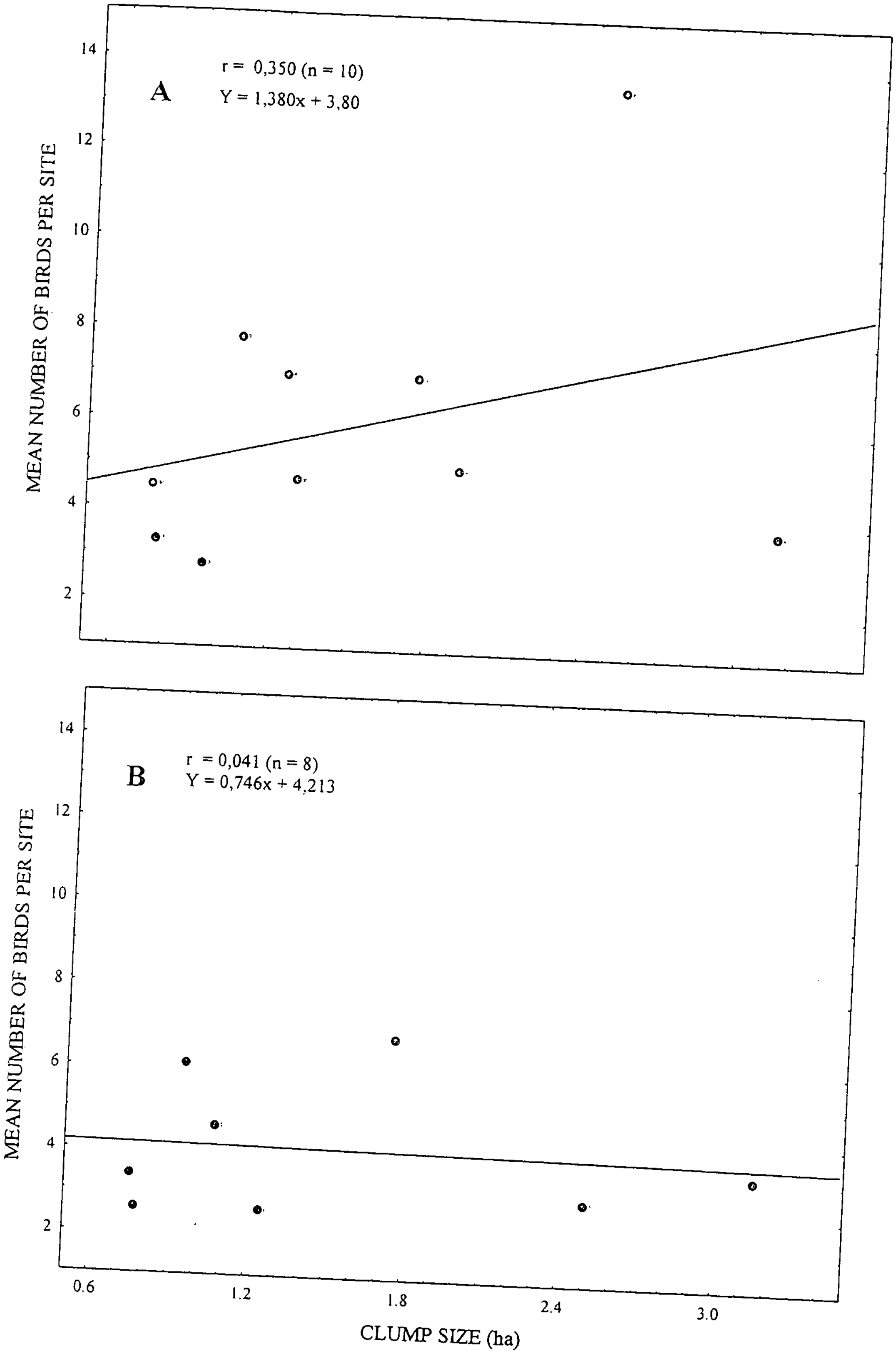


FIGURE 8: Relationship between mean numbers of Gurney's Sugarbirds (A) and Malachite Sunbirds (B) per site and *Protea roupelliae* clump size at the study sites at Lydenburg during the period December 1986 - January 1997.

TABLE 2: Population densities of Gurney's Sugarbirds and Malachite Sunbirds in the Lydenburg area during the period December 1986 - January 1997. (a), average of 10,2 net hrs/day (988 hrs) and 51,5 net m/day (4 998m) (n=97); (b), average of 9,7 net hrs/day (562 hrs) and 49,1 net m/day (2 847m) (n=58).

Study localities	No. of trap days	Number captured	Mean at site	Surface area (ha)	Birds per hectare
Gurney's Sugarbird (a)					
Paardeplaats (N)	24	108	4,5	0,75	6,0
Paardeplaats (O)	33	93	2,8	0,95	2,9
Gustav Klingbiel (S)	10	70	7,0	1,75	4,0
Sterkspruit (L)	8	63	7,8	1,07	7,3
Sterkspruit (I)	6	23	3,8	3,15	1,2
Sterkspruit (J)	3	15	5,0	1,92	2,6
Sterkspruit (K)	3	10	3,3	0,77	4,3
Nooitgedacht (Q)	4	28	7,0	1,25	5,6
Potloodspruit (R)	2	27	13,5	2,50	5,4
Waterval (U)	4	19	4,7	1,30	3,6
Total/mean	97	456	5,9	1,54	4,3
Malachite Sunbird (b)					
Paardeplaats (N)	11	37	3,4	0,75	4,5
Paardeplaats (O)	16	97	6,1	0,95	6,4
Gustav Klingbiel (S)	12	82	6,8	1,75	3,9
Sterkspruit (L)	7	32	4,6	1,07	4,3
Sterkspruit (I)	3	11	3,7	3,15	1,2
Sterkspruit (K)	5	13	2,6	0,77	3,8
Nooitgedacht (Q)	2	16	8,0	1,25	6,4
Potloodspruit (R)	2	6	3,0	2,50	1,2
Total/mean	58	294	4,8	1,52	3,9

Seasonal densities of sugarbirds at Paardeplaats (sites N & O) were monthly analysed as relativly large numbers of sugarbirds were captured at these sites. Sugarbird densities were higher during winter (June/July), spring (September/October) and early summer (Fig. 9). Sub-adult sugarbirds concentrated at *Protea* clumps with available inflorescences during the winter, and high numbers of juveniles were captured at these localities during the November - December breeding season.

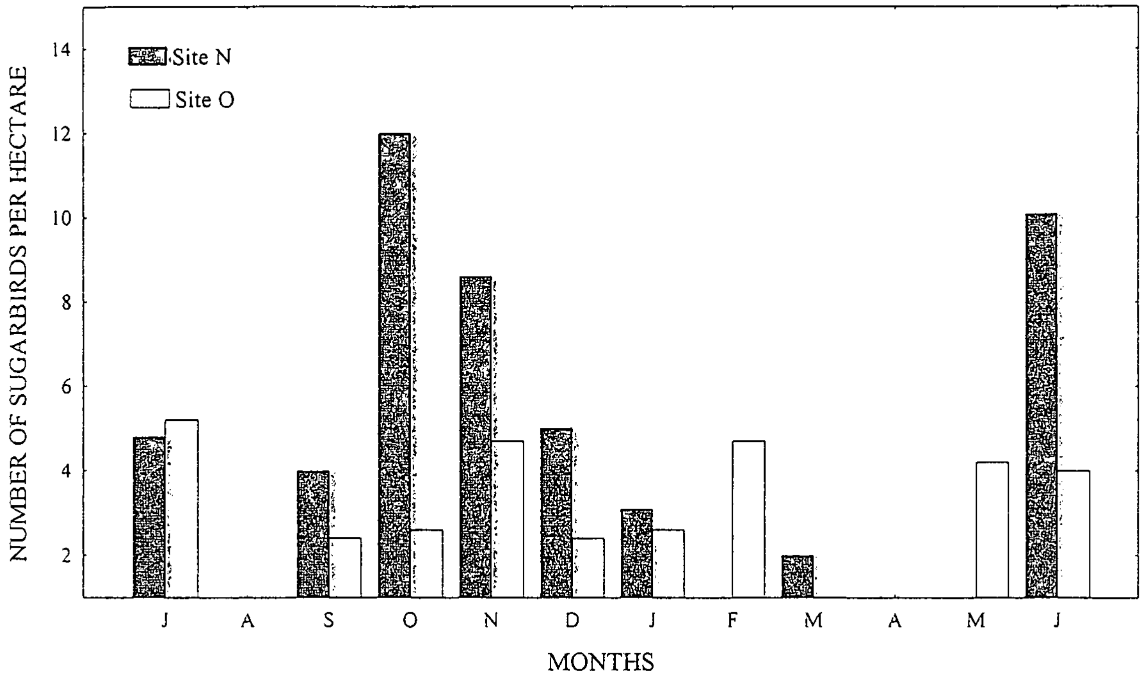


FIGURE 9: Seasonal densities of Gurney's Sugarbirds at Paardeplaats (sites N & O), Lydenburg, during the period December 1986 - January 1997.

4.2.3.2. Flower availability

A significant correlation was found between the number of open flowers present and the monthly rainfall at the Potato Seed Production Unit on the Long Tom Pass during the study period ($r = 0,697$; $p < 0,05$; $df = 10$) (Fig. 10). The peak flowering period of *Protea roupelliae* also coincides with the months with the highest rainfall (De Swardt, 1991a; see Chapter 8). In July 1990, 27 sugarbirds were captured at Nooitgedacht (site Q) where flowers were in abundance, while flowering inflorescences were less abundant elsewhere.

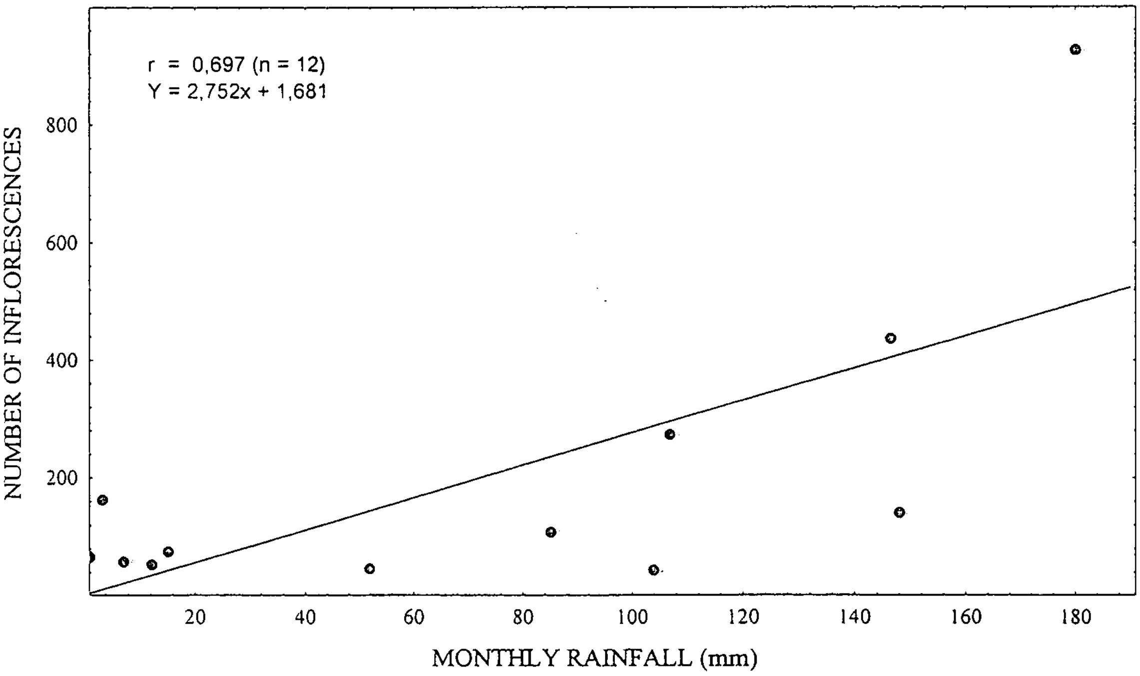


FIGURE 10: Relationship between the number of *Protea roupelliae* inflorescences present at Paardeplaats (sites N & O), Lydenburg, and the monthly rainfall at the Long Tom Pass weather station during the 1986/87 - 1989/90 seasons.

4.2.3.3. Fire

Most of the *Protea* clumps were burnt on several occasions during the study period. The fire histories and the occurrences of the following known fires are described below:

The first fire occurred at Nooitgedacht (site Q) during late July 1990 after a large number of sugarbirds were captured earlier that month when the flowers were abundant. Subsequent to the fire only a few sugarbird pairs were present at this site, but an individual (ring no. 4-64984) was recaptured higher up in the valley at an unburnt *Protea* clump at Paardeplaats (site P) on 25 November 1992. This individual was recaptured only a kilometre from its original ringing site. A second fire, which severely burnt the *Protea roupelliae* community at Sterkspruit (site L), swept through the grasslands along the Long Tom Pass during October 1991. The *Protea* clump experienced a crown burn and the trees were totally destroyed by the fire. Before the fire, a mean of 7,6 sugarbirds (range: 2 - 23; SD = 8,1; n = 8) were captured per day, while during December 1991 (after the fire), only one pair was present and for only a short time. As a result of the fire, some of the sugarbirds ringed at site L were recaptured away from their original ringing sites. Three individuals ringed at the latter site were recaptured at the Fisheries Institute (site G) some time after the fire occurred (see Table 16). Likewise, a bird (ring no: 4-38949) recaptured three times at site L before the fire was recaptured for the fourth time at the Fisheries Institute. The birds probably dispersed to the surrounding *Protea* clumps in the area before they moved to the suburban areas of Lydenburg during the winter.

A third accidental fire occurred in August 1996 when the whole area of the Gustav Klingbiel Nature Reserve (including site S) was burnt. The *Protea* trees at the study site on the plateau experienced total crown burn (95% of the trees), with no flowers or sugarbirds observed in December 1996 when the site was visited for the first time after the fire. A smaller *Protea* clump (site T) lower down the plateau in the Reserve was visited on 27 January 1997 to obtain recapture data of sugarbirds ringed at the burned study site (S). Apart from an individual suspected to be one of the birds captured during January 1996 or earlier and which had probably dispersed from the burnt site, no other sugarbirds were observed at this or the burnt site. These examples suggest that sugarbirds will vacate the immediate vicinity if *Protea* clumps are destroyed by fire and move to adjacent *Protea* clumps. It is also more likely that sugarbirds from such burnt sites move to the suburban areas during the winter months.

4.2.3.4. Site fidelity

Forty-one individuals (7,4%), encompassing 30 males, seven females and four unsexed sugarbirds, were recaptured at *Protea roupelliae* clumps where they were originally ringed. Strong fidelity to these sites was observed mostly in males, suggesting that they return or stay in their territories throughout the year. Of the 63 male sugarbirds ringed at the Paardeplaats localities (sites N & O), 14 (23,8%) were recaptured. Most of these recaptures were during the winter months (June/July), but also during the summer breeding season.

4.2.3.5. Localised movements

Movements between *Protea* clumps were observed in fifteen individual sugarbirds (ten males, four females and a sub-adult) during the study period. Localised movements were mostly the result of fires in *Protea* veld or natal dispersal of sub-adults which were later recaptured as adult birds (see Chapter 8 for examples).

4.3.DISCUSSION

4.3.1. Distribution

De Swardt (1992a) found that Gurney's Sugarbird is closely associated with *Protea* woodland and that its distribution range closely follows the distribution pattern of *Protea roupelliae* along the Drakensberg escarpment. The range of Gurney's Sugarbird extends southwards to the *P. subvestita* populations in the Amatole Mountain range of the Eastern Cape (De Swardt, 1997), where the latter species is locally distributed along the Drakensberg to the Lesotho - Free State border (Rebelo, 1995). *Protea subvestita* is less resistant to severe fires than other *Protea* species and large areas have been eradicated by too frequent fires during the 1960's in attempts to eradicate dense stands of *Cliffortia* spp. (Rebelo, 1995; Skead 1987). Historically, both Gurney's and Cape Sugarbirds occurred in *P. subvestita* communities in the Amatole Mountain range and were also found breeding alongside (Skead, 1964). Presently, Gurney's Sugarbirds are localised in this area and the distribution ranges of these two sugarbird species no longer overlap, mainly as a result of the uncontrolled fires which destroyed their habitat (Fraser, 1997; Skead, 1987). Although Gurney's Sugarbirds were observed to be relatively common in their distribution range, they mostly occur at inaccessible places in the higher mountainous areas. They could, therefore, be more common in mountainous areas than is indicated by the present Bird Atlas data (see De Swardt, 1997).

The distribution of Gurney's Sugarbirds extends further northwards along the Drakensberg escarpment, following the vegetation types of the Grassland Biome (Low & Rebelo, 1996). They occur, marginally, in the eastern Free State and are common, but localised, at the Golden Gate Highlands National Park, Qwaqwa National Park and at the Sterkfontein Dam Nature Reserve along the Lesotho and KwaZulu-Natal border (De Swardt 1993a; De Swardt & Van Niekerk 1996). Hypothetically they also occur in Lesotho, mostly along the eastern border adjacent to KwaZulu-Natal (Bonde, 1993). The two isolated populations of Gurney's Sugarbird in the Soutpansberg and Waterberg mountain ranges occur in islands of *Protea roupelliae* woodland at altitudes above 1 800 m in the Savanna Biome (De Swardt, 1997). The vegetation in these areas was previously known as the North-eastern Mountain Sourveld veld type, but is currently separated into the Soutpansberg Arid and Waterberg Moist Mountain Busveld vegetation types (Acocks, 1988; Low & Rebelo, 1996). The status of the sugarbird population at Kransberg in the Waterberg has been reviewed by Craib (1981) when 18-25 pairs were observed in *P. roupelliae* woodland during 1979. Craib (1981) also searched for nests, but no breeding activities were observed. During December 1996 and September 1998, the same area was visited (now the Marakele National Park) and only a small population was present. Since Craib (1981) concluded that no breeding occurred in the Waterberg, no further searches for nests were made in subsequent years. It is, however, possible that repeated fires over the years and low seasonal rainfall (dry years) could have influenced the breeding success of this sugarbird population. In an attempt to shed more light on the questions posed by Craib (1981), and for comparative purposes with the present study, an investigation of the biology of this isolated sugarbird population is urgently required.

The race *Promerops gurneyi ardens* occurs in the eastern highlands of Zimbabwe and adjacent Mozambique where it mainly inhabits *Protea-Brachystegia-Phillipia* scrub veld (Friedman, 1952; Irwin, 1981). *Protea roupelliae* does not occur here, but *P. angoliensis*, *P. caffra*, *P. dracomontana*, *P. gaugedi* and *P. petiolaris* commonly occur in the eastern parts of Zimbabwe (Beard, 1963; Beasly, 1995; Rebelo, 1995). The Chimanimani Mountains are most important for the conservation of Gurney's Sugarbirds and the birds were mostly recorded at altitudes above 1 200 m (Beasly, 1995; Jackson, 1973). Considerable seasonal movements also occur in relation with flowering plant species and birds are known to move to the lower altitudes (Manson, 1985). Little is, however, known about the sugarbirds' breeding requirements in Zimbabwe and Mozambique and how they differ from the nominate race (Steyn, 1973).

4.3.2. Nectarivores captured in *Protea roupelliae* woodland

The relatively high occurrence of nectarivores and other species captured in *Protea roupelliae* woodland at the Free State and Lydenburg study localities (Table 1), notably Gurney's Sugarbirds and Malachite Sunbirds, implies that this woodland habitat type only supports low densities of non-nectarivore species which are only temporary residents or just passing through (De Swardt, 1993b). The latter species utilised a certain niche in the *Protea* veld such as the rocky mountain slopes, montane grassland and adjacent forest areas and kloofs. Examples of other species captured were mostly birds that are common in the montainous areas of Lydenburg and the escarpment (De Swardt, 1990a; Maclean, 1993). Of all the bird species captured in *P. roupelliae* woodland, Gurney's Sugarbird is the only one almost exclusively associated with this vegetation and was only observed as a temporary visitor in other habitat types (De Swardt, 1992a). The sugarbirds mostly foraged on the nectar of this *Protea* species, used the trees as nest sites or foraged on beetles associated with *Protea* inflorescences (De Swardt & Bothma, 1992; De Swardt & Louw, 1994).

In a similar study on resource partition of sunbird populations in Kenya, Gill & Wolf (1978) designed a model for nectarivore species where two species of different sizes may co-exist if the smaller is a mobile exploiter of scattered flowers while the larger is a sedentary territorial exploiter of locally dense flowers. During the present study, Malachite Sunbirds were observed to exploit the same nectar resources as the sugarbirds, but their association was not limited by the presence of *P. roupelliae*. Malachite Sunbirds are opportunistic in their feeding behaviour and they exploit a wide range of plant species (Unpubl. data). A situation similar to that in Kenya is, therefore, suggested for the co-existence of the two nectarivore species in *P. roupelliae* woodland at the Lydenburg and eastern Free State study areas. Male Cape Sugarbirds were observed to displace feeding Orangebreasted Sunbirds *Nectarinia violacea* at *Leucospermum conocarpodendron* inflorescences (Wooller, 1982). Likewise, male Gurney's Sugarbirds were observed acting aggressively on several occasions, defending nectar resources from Malachite Sunbirds and other species. The sunbirds were usually displaced following aggressive alarm calls by the sugarbirds when they met on the same inflorescence of a *Protea* bush. Male Malachite Sunbirds were also frequently observed being chased by territorial sugarbirds during the day. Greater Double-collared Sunbirds *N. afra* and Black Sunbirds *N. amethystina* were also chased by the sugarbirds, but less frequently. Owing to their smaller sizes they probably do not pose such a threat to the sugarbirds (pers. obs.). The nest sites of sunbirds are mostly situated in small bushes in the overhanging vegetation on the banks of streams and gullies, whereas sugarbirds nest exclusively in *Protea* bushes (Maclean, 1993).

4.3.3. Factors affecting densities in *Protea roupelliae* woodland

Gurney's Sugarbird densities recorded at some of the smaller *Protea roupelliae* clumps in the Lydenburg study area suggest that the size of the clumps is an important factor determining bird numbers. More sugarbirds were captured at clumps where the bushes were more densily arranged, such as sites K, L & O. These sites have escaped fires for the past five years or more and formed thickets with smaller inter-bush distances. At larger sites, *e.g.* N, M & R, lower bird densities were encountered mainly as a result of recent fires in the area. At the latter sites *Protea* trees occur in long stretches of woodland with greater inter-bush distances. Craib (1977) recorded three or more pairs of sugarbirds per *P. roupelliae* clump (2,025 ha) in the Machadodorp district, Mpumalanga Province, and suggested that one breeding pair would be confined to a smaller *Protea* clump (*ca.* 0,5-1 ha). Sugarbird densities in *Protea* woodland can be expected to vary considerably during the year as a result of fire and the flowering season of proteas. During this study at Paardeplaats (site N & O), sugarbird densities were low during the breeding season and high when the young fledged from their nests. Sub-adults also concentrated at food sources during the winter months. Tarboton *et al.* (1987) mentioned high bird densities of 20 sugarbirds per hectare in *Protea* veld with sufficient flowers available. Lower densities of sugarbirds can be expected at large stands of *P. roupelliae* woodland which have recently been burnt (large portion of flowers destroyed resulting in fewer flowers available for the birds to feed on). This is probably one of the main factors which affect sugarbird densities (De Swardt, 1993b). In Mountain Fynbos, Fraser (1989) found that bird densities decreased during the six week period following the occurrence of fire. Birds usually escape from the area immediately and will only return when conditions resemble the status prior to the fire (Kruger & Bigalke, 1984). The same response was observed at Sterkspruit (site L) near Lydenburg where the sugarbirds vacated the area after a fire during October 1991. The area was totally burnt, and it is unlikely that sugarbirds will re-colonise the site in the near future (pers. obs.; see Chapter 9). Three of the sugarbirds originally ringed at this site were recaptured in the suburban areas of Lydenburg during the winter.

The importance of *Protea roupelliae* woodland to Gurney's Sugarbirds is reflected by their fidelity to certain sites. Site fidelity is probably related to the quality of their territories which depends on the availability of food, shelter and nest sites (De Swardt, 1992a). As trapping of sugarbirds was repeated at most of the sites in Lydenburg, valuable site fidelity data for these birds were obtained. Most of the recaptures were made during the period November - March, while only few were recaptured during the non-breeding season, suggesting that they are territorial during the breeding season (De Swardt & Bothma, 1992; De Swardt, 1992a). Sugarbirds disperse after the breeding season, into the valleys and cliffs where they forage between stands of *Aloe arborescens* and available *Protea* flowers which are scattered during the winter months (De Swardt, 1989). The association of bird species with a particular habitat is regarded as an important factor in bird community ecology. In a study in Arizona, United States of America, Mills, Dunning & Bates (1991) found a significant correlation between total breeding bird density and total vegetation volume. The model proposed by Mills *et al.* (1991) can also be applied to predict changes in Gurney's Sugarbird populations in *Protea roupelliae* woodland which resulted from disturbances such as habitat destruction (mainly afforestation) and fire. The management and conservation of the habitat with which the birds are associated is, therefore, important (Allan, Harrison, Van Wilgen & Thompson, 1997; De Swardt, 1992a). Harrison, Allan & Van Hensbergen (1994) considered Gurney's Sugarbird as a primary indicator species in scrub habitats in their Drakensberg range, and these guidelines are important in environment planning and consultancy.

5. BIOMETRICS AND MOULT

5.1. INTRODUCTION

Biometric data on Gurney's Sugarbirds are scanty. Maclean (1985) listed measurements from only four males and two females with a large overlap in tail length and small ranges in their other body measurements. Except for eleven specimens in the collection of the Transvaal Museum, Gauteng Province, which were examined during 1986, no other sources of biometric data could be found for comparisons with this study. De Swardt (1990c & 1992a) reported biometric data and sexing methods for Gurney's Sugarbird, as later published in Maclean (1993). The current sugarbird biometric database has been expanded and re-analysed and the unsexed individuals were divided into sub-adult and juvenile birds. Skead (1967) reviewed the occurrence and function of the bulged sixth primary (P6) in the sugarbird family when it was first noticed in the Cape Sugarbird, but unknown in Gurney's Sugarbird. De Swardt (1990c & 1992a) first recorded the presence of this bulged primary feather in Gurney's Sugarbird, and used it as a guide to sex this species in the hand. Bill morphology, body mass and wing lengths are reviewed here as adaptations for effective foraging in nectarivore species (Paton & Collins, 1989; Rebelo, 1987).

Studies of inter– and intra-population variations in ornament and body size are important sources of information relating to models of sexual selection (Alatalo, Höglund & Lundberg, 1988; Barnard, 1991; Craig, 1989). Unfortunately, too little is known about actual variation in traits that might be important in natural or sexual selection. In particular, field studies of variation in birds have the potential to contribute much to the verification or rejection of sexual selection theories, and are superior to museum studies (Barnard, 1991). Field studies are biologically more meaningful for this purpose than museum studies, as data are collected from natural, self-defined rather than arbitrarily-defined populations, and measurement errors due to variable preservation of specimens are avoided (Barnard, 1991). The morphological variation of ornament and body size, and the functions of exaggerated tail lengths in mating systems, were studied in several species including the Longtailed Widow *Euplectes progne*, Jackson's Widow *E. jacksoni*, African whydahs (*Vidua* spp.) and the Scarlet-tufted Malachite Sunbird *Nectarinia johnstoni* (Andersson, 1982; Barnard, 1995; Evans & Thomas, 1992). In this chapter I analysed data on phenotypic variation in body size, mass and ornamental length in a marked population of Gurney's Sugarbirds at the study localities around Lydenburg, Mpumalanga Province. Sugarbird males are significantly larger than females in body size, mass and length of the ornamental tail, which is long, flexible and strongly graduated (see De Swardt, 1992a). The males also defend their *Protea* clump territories from other males and are monogamous during the breeding season (De Swardt & Bothma, 1992). These sugarbird ornamental data were compared with patterns of previously studied African passerine species which have different mating systems and degrees of sexual dimorphsm.

No moult studies on Gurney's Sugarbirds were previously available and Craig (1983) did not include the sugarbird family in his review on moult in southern African passerine species. The data presented here are the results of the first detailed moult study on a member of the endemic Promeropidae family in southern Africa. No data are available on the moult of Cape Sugarbirds (Craig, 1983). The moult sequence of Gurney's Sugarbird was, however, compared with other related taxa such as starlings (Sturnidae), sunbirds (Nectariniidae) and honeyeaters (Meliphagidae) (Craig, 1996; Ford, 1980; Hanmer, 1981; Paton, 1982a & b).

5.2. RESULTS

5.2.1. Biometrics

Sugarbird biometric data obtained from 227 males (41,4%), 188 females (34,3%), 90 sub-adults (16,4%) and 43 juveniles (7,8%) are given in Tables 3 & 4.

TABLE 3: Biometrics of adult male and female Gurney's Sugarbirds.

	Males				Females			
Parameters	N	Mean	±SD	Range	N	Mean	±SD	Range
Body mass (g)	227	38,0	3,0	30,0- 46,7	188	31,7	3,0	23,0- 46,0
Bulging of P6 (mm)	138	13,7	0,9	11,1- 16,1	17	10,8	0,7	9,7- 12,0
Culmen length (mm)	227	28,9	1,0	25,9- 31,9	188	27,5	0,9	25,0- 29,8
Tail length (mm)	175	152,1	14,4	122,0-187,0	188	106,7	10,4	83,0-135,0
Tarsus length (mm)	224	21,7	0,9	19,0- 23,8	178	20,6	1,1	17,0- 23,7
Total head length (mm)	199	54,5	1,1	50,5- 56,9	155	51,8	1,0	47,5- 53,5
Wing length (mm)	227	93,8	3,4	86,0-103,0	188	85,4	2,8	79,0- 96,0

TABLE 4: Biometrics of sub-adult and juvenile Gurney's Sugarbirds.

	Sub-adults				Juveniles			
Parameters	N	Mean	±SD	Range	N	Mean	±SD	Range
Body mass (g)	90	34,5	3,6	24,0- 44,0	41	28,5	3,9	20,0- 38,0
Culmen length (mm)	90	28,3	1,0	25,8- 30,6	43	26,3	1,7	18,1- 29,4
Tail length (mm)	87	113,3	11,1	88,0-137,0	43	95,8	14,0	40,0-115,0
Tarsus length (mm)	85	21,1	0,9	17,7- 23,1	43	20,6	1,1	17,4- 22,9
Total head length (mm)	80	53,2	1,4	50,0- 56,7	36	50,6	2,3	41,1- 54,1
Wing length (mm)	90	88,5	3,6	79,0- 96,0	43	85,7	4,8	71,0- 97,0

5.2.1.1. Culmen length

The mean culmen length of males was significantly longer than that of females ($t_{413} = 14{,}15$; $p < 0{,}05$). Sub-adult and juvenile culmen lengths were shorter than those of adult birds, but the ranges were similar. The mean culmen length of females and juveniles differed significantly ($t_{229} = 6{,}16$; $p < 0{,}05$), while those of adult male and sub-adult sugarbirds did not ($F_{89,226} = 1{,}03$; $p > 0{,}05$).

5.2.1.2. Total head length

The mean total head length of male sugarbirds was significantly longer than that of females ($t_{352} = 23{,}80$; $p < 0{,}05$). Since the range of the total head measurement, in sub-adult sugarbirds, varied from 50,0 to 56,7 mm, almost identical to that of adult males, most of them were assumed to be males. However, the mean total head length of sub-adult birds was significantly shorter than that of adult males ($t_{277} = 8{,}15$; $p < 0{,}05$), but longer than that of the adult females ($t_{233} = 8{,}81$; $p < 0{,}05$). A significant correlation was found between the culmen and total head lengths of males ($r = 0{,}663$; $p < 0{,}05$; df = 202) and females ($r = 0{,}450$; $p < 0{,}05$; df = 157), respectively (Fig. 11). The regression coefficients between adult male and unsexed sub-adult culmen/total head lengths do not differ significantly ($t_{265} = 0{,}681$; $p > 0{,}05$), but have the same regression line elevations ($t_{226} = 13{,}50$; $p < 0{,}05$). The reduced major axis regression shows no significant difference between the regression lines of adult male ($Y = 0{,}900x + 20{,}125$) and sub-adult sugarbirds ($Y = 0{,}823x + 15{,}542$).

5.2.1.3. Tarsus length

The mean tarsus length of the males was significantly longer than that of the females ($t_{400} = 10{,}22$; $p < 0{,}05$), but did not differ between males and sub-adults ($t_{307} = 4{,}83$; $p > 0{,}05$; df = 310) or between females and juvenile sugarbirds ($t_{219} = 0{,}06$; $p > 0{,}01$; df = 219).

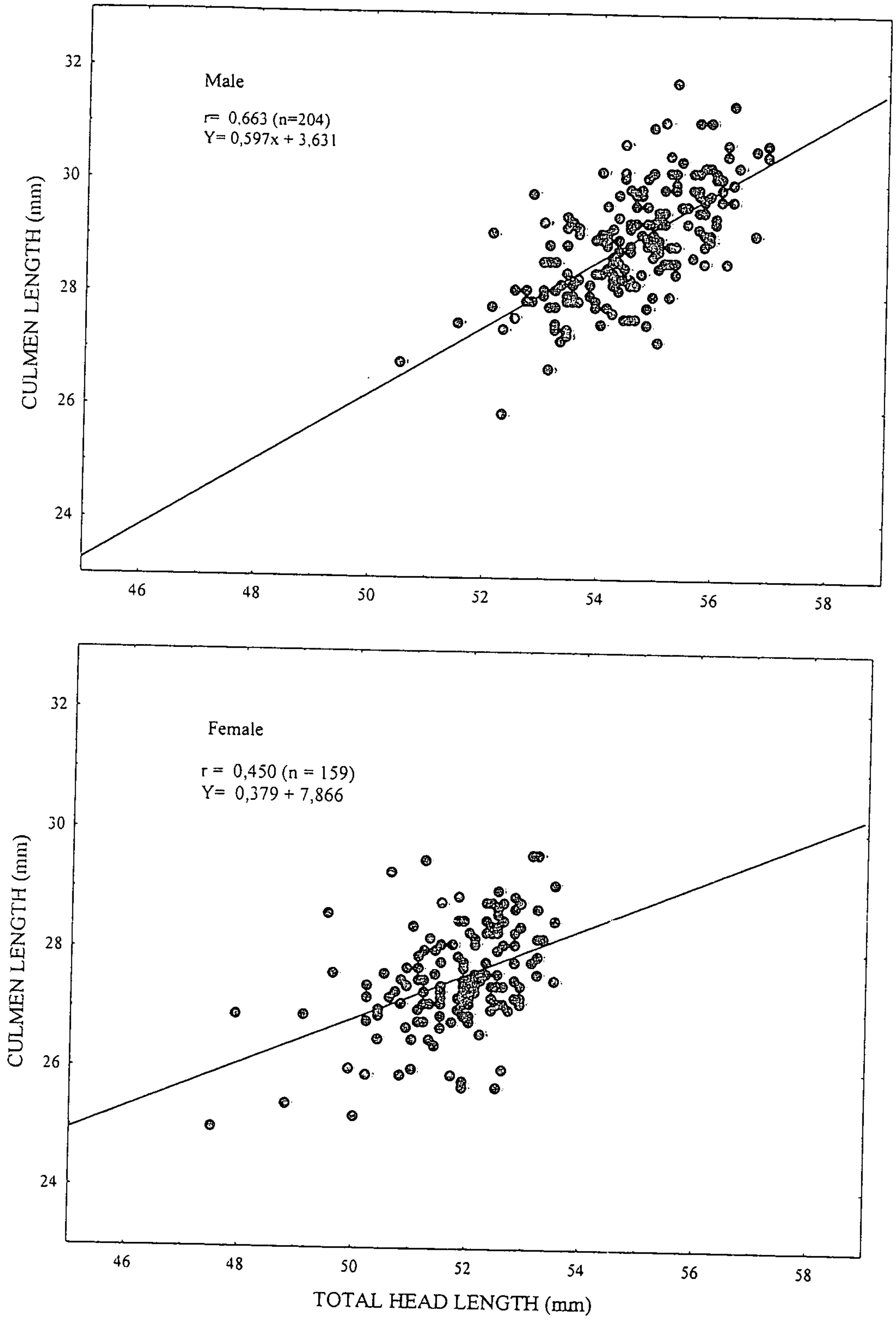


FIGURE 11: Relationship between culmen and total head lengths in adult Gurney's Sugarbirds at the Mpumalanga and Free State study sites during the period December 1986 - June 1998.

5.2.1.4. Wing length

Mean wing length of adult males was significantly longer than that of adult females (t_{413} = 27,14; $p < 0,05$). Although the range in both sexes was more or less the same, male wing lengths were usually above 90 mm (Fig. 12).

5.2.1.5. Tail length

Tail length of adult males and females differed significantly (t_{361} = 34,61; $p < 0,05$). Mean male tail length was 30% longer than that of females. Sugarbirds with tail lengths exceeding 140 mm were regarded as males as they also showed bulged P6 (Fig. 13). The mean tail length of unsexed sub-adults was longer than those of adult females (see Tables 3 & 4).

The wing and tail lengths of adult males ($r = 0,628$; $p < 0,05$; df = 179) and females ($r = 0,524$; $p < 0,05$; df = 183) was significantly correlated (Fig. 14). The regression coefficients between adult male and unsexed sub-adult wing and tail lengths do not differ significantly (t_{250} = 1,0; $p > 0,05$), but have not the same regression line elevations (t_{251} = 1,61; $p < 0,05$). These were also significant with the reduced major axis regression between adult males ($Y = 0,202x + 64,048$) and sub-adult sugarbirds ($Y = 0,326x + 51,598$).

5.2.1 6. Bulging of primary six (P6)

The presence of the bulged P6 was recorded in more than half of all males captured (60,8%), but only occasionally in females (9,0%). The maximum width of the P6 in males ranged between 11,1 and 16,1 mm ($\bar{x}$ = 13,7 mm; SD = 1,1; n = 138). Whenever present, the P6 in females was bulged only slightly or not at all ($\bar{x}$ = 10,8 mm; SD = 0,7; n = 17). A significant correlation existed between the width of the P6 and wing length in males ($r = 0,467$; $p < 0,05$; df = 136) (Fig. 15). Amongst males, individuals with a tail length exceeding 160 mm have a wing length of more than 95 mm and a wide bulge of 14 mm or more. A male (ring no. 4-38911) recaptured after 28 months on 18 June 1989 in the suburban areas of Lydenburg (site B) had, for instance, a tail length of 172 mm, wing length of 100 mm and a P6 of 14,9 mm.

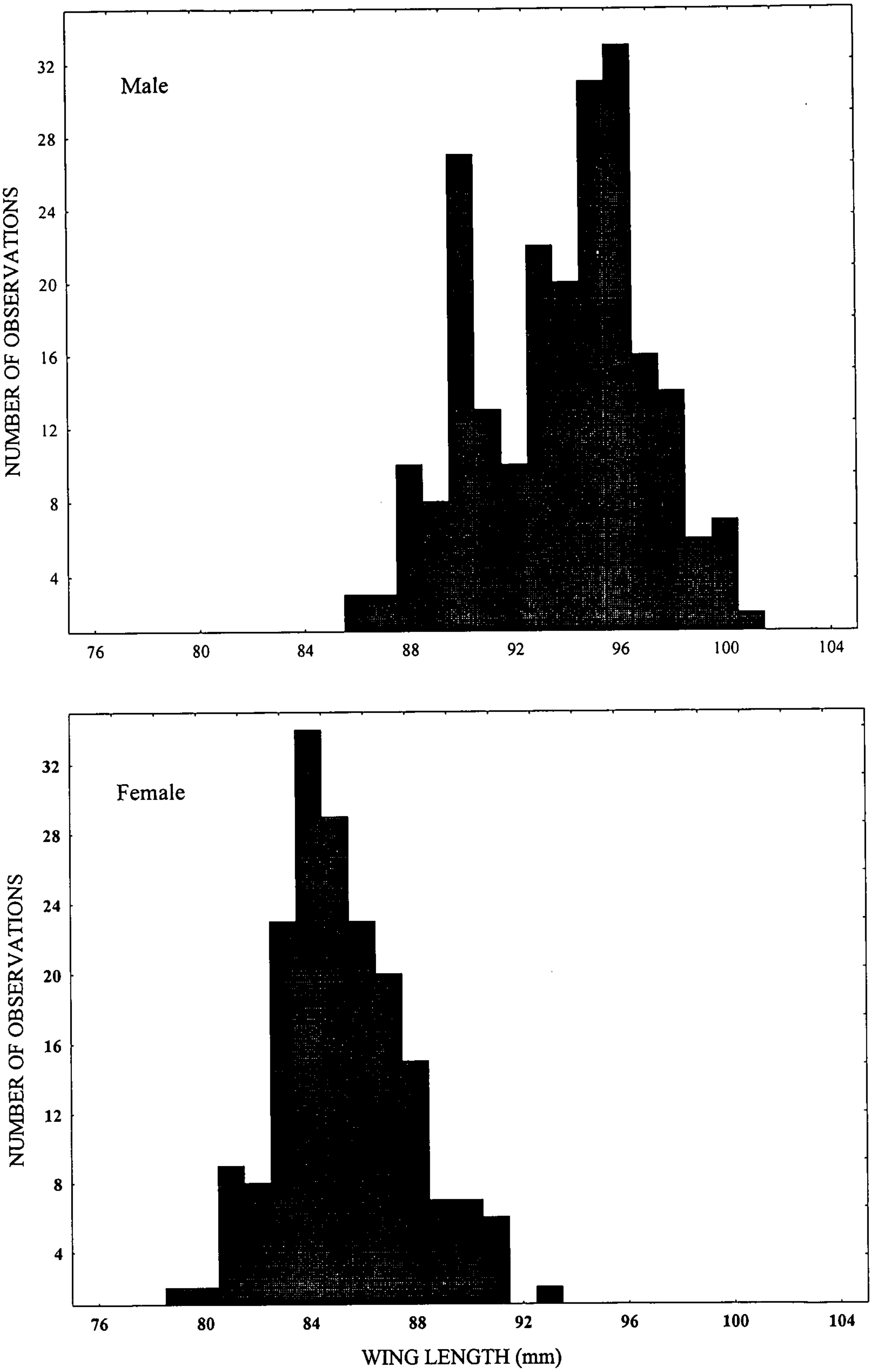


FIGURE 12: Histogram of wing lengths of adult Gurney's Sugarbirds at the Mpumalanga and Free State study sites during the period December 1986 – June 1998.

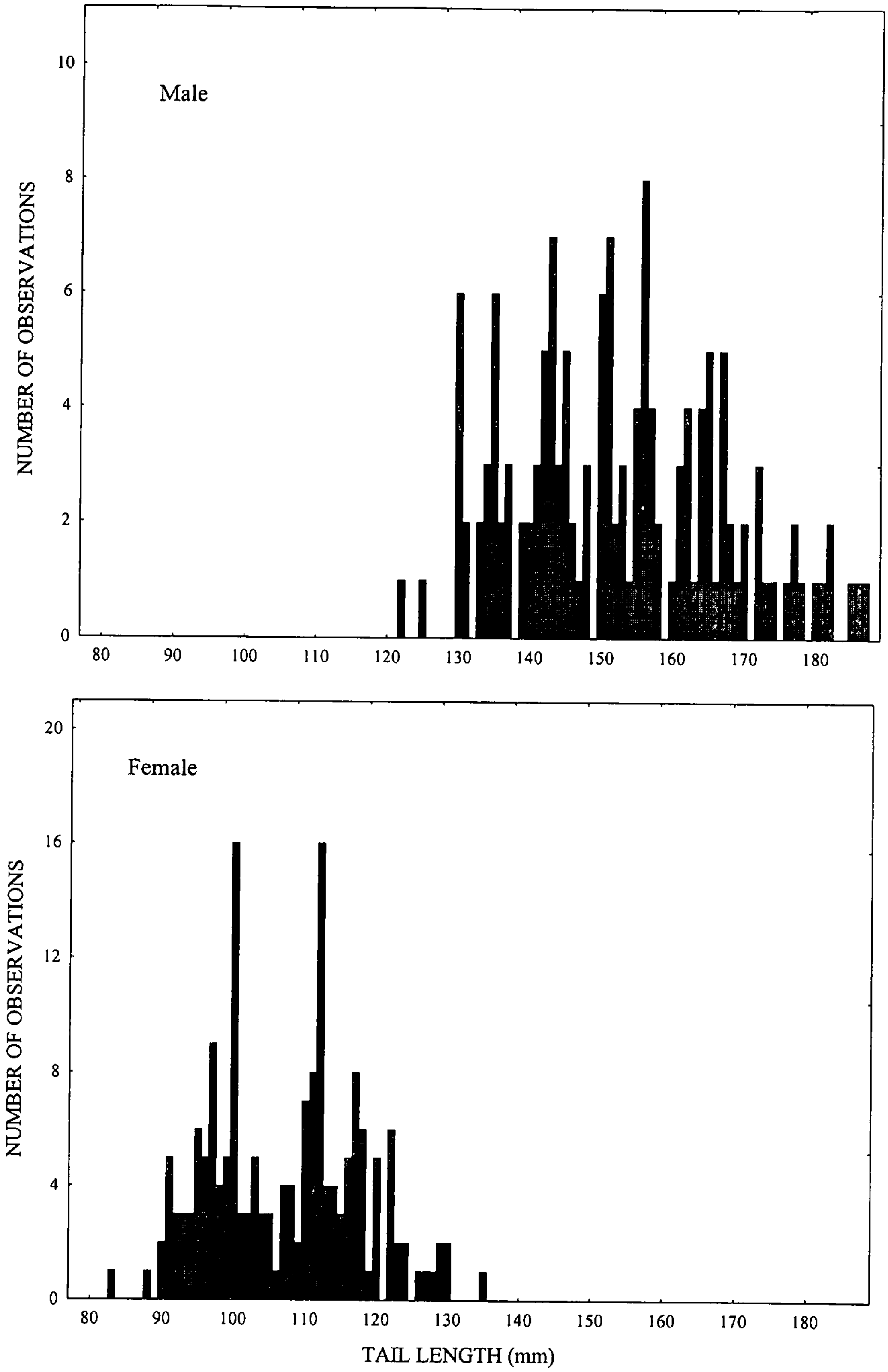


FIGURE 13: Histogram of tail lengths of adult Gurney's Sugarbirds at the Mpumalanga and Free State study sites during the period December 1986 – June 1998.

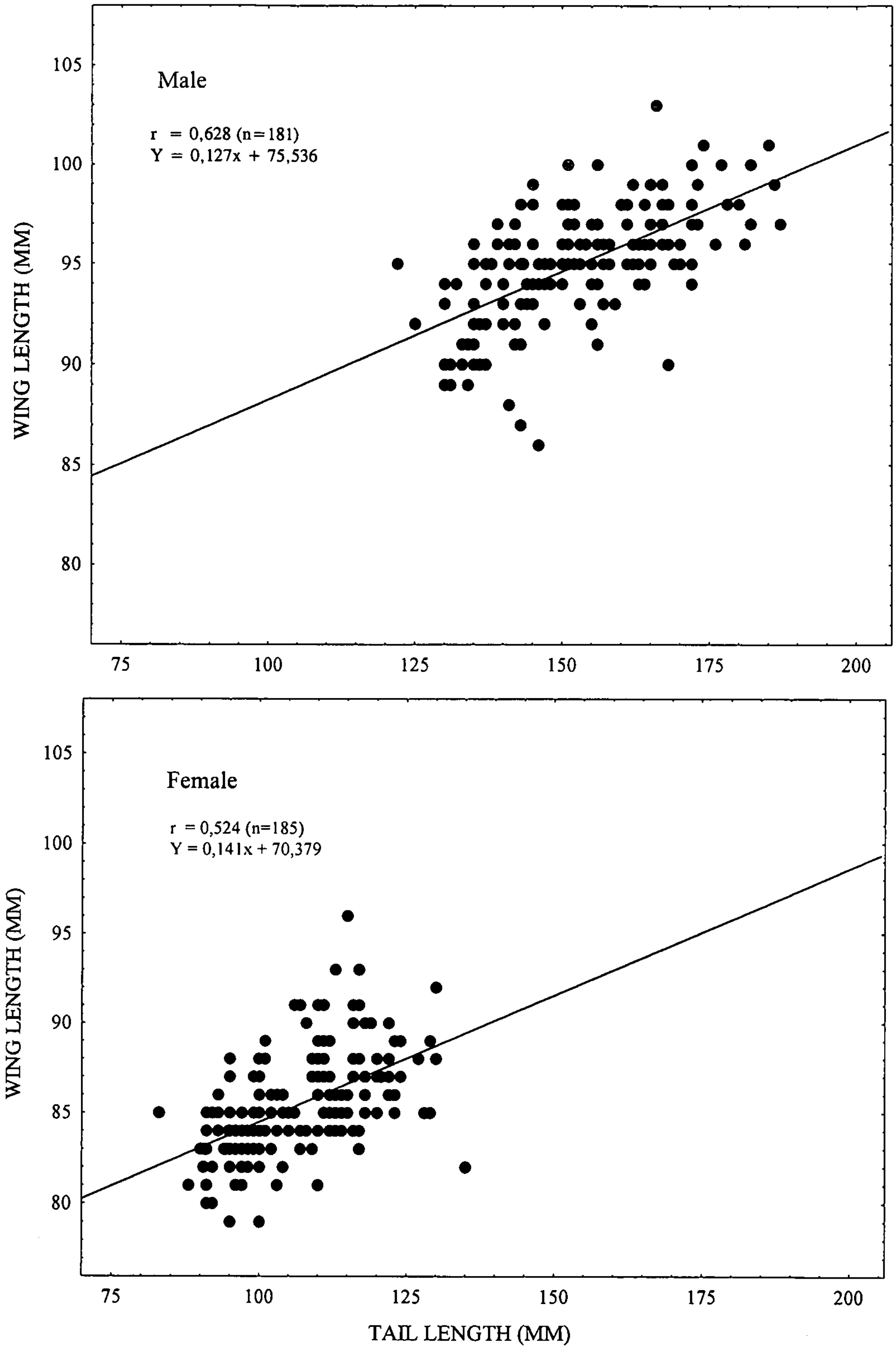


FIGURE 14: Relationship between tail and wing lengths in adult Gurney's Sugarbirds at the Mpumalanga and Free State study sites during the period December 1986 - June 1998.

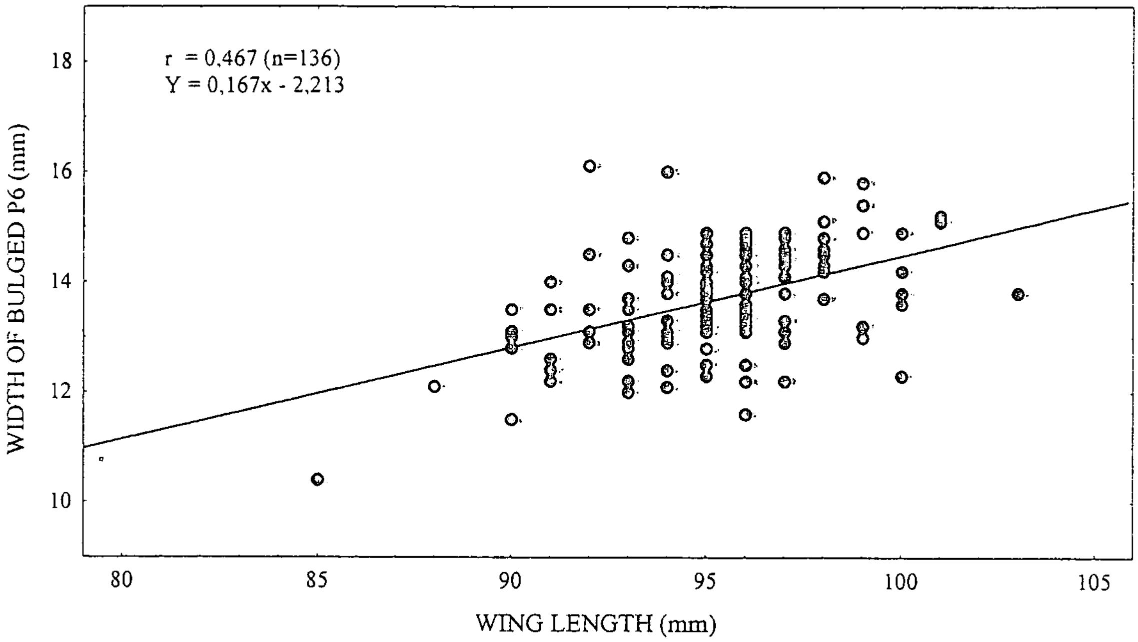


FIGURE 15: Relationship between width of the bulged P6 and wing length in adult male Gurney's Sugarbirds at the Mpumalanga and Free State study sites during the period December 1986 – June 1998.

5.2.1.7. Body mass

Although there was some overlap in the body mass ranges of the sexes (Table 3), the mean mass of adult males was significantly higher than that of females ($t_{413} = 21{,}21$; $p < 0{,}05$). The body mass of adult male sugarbirds is generally above 36,0 g. The body mass of unsexed sub-adults also differs from that of adult males ($t_{315} = 8{,}84$; $p < 0{,}05$), while unsexed juveniles have a lower mean than do adult females ($t_{227} = 5{,}82$; $p < 0{,}05$). Significant monthly variation in body mass was recorded in adult males ($F_{9,217} = 6{,}40$; $p < 0.05$) and females ($F_{9,178} = 2{,}62$; $p < 0{,}05$). Body masses were higher during the November - March breeding season (Fig. 16).

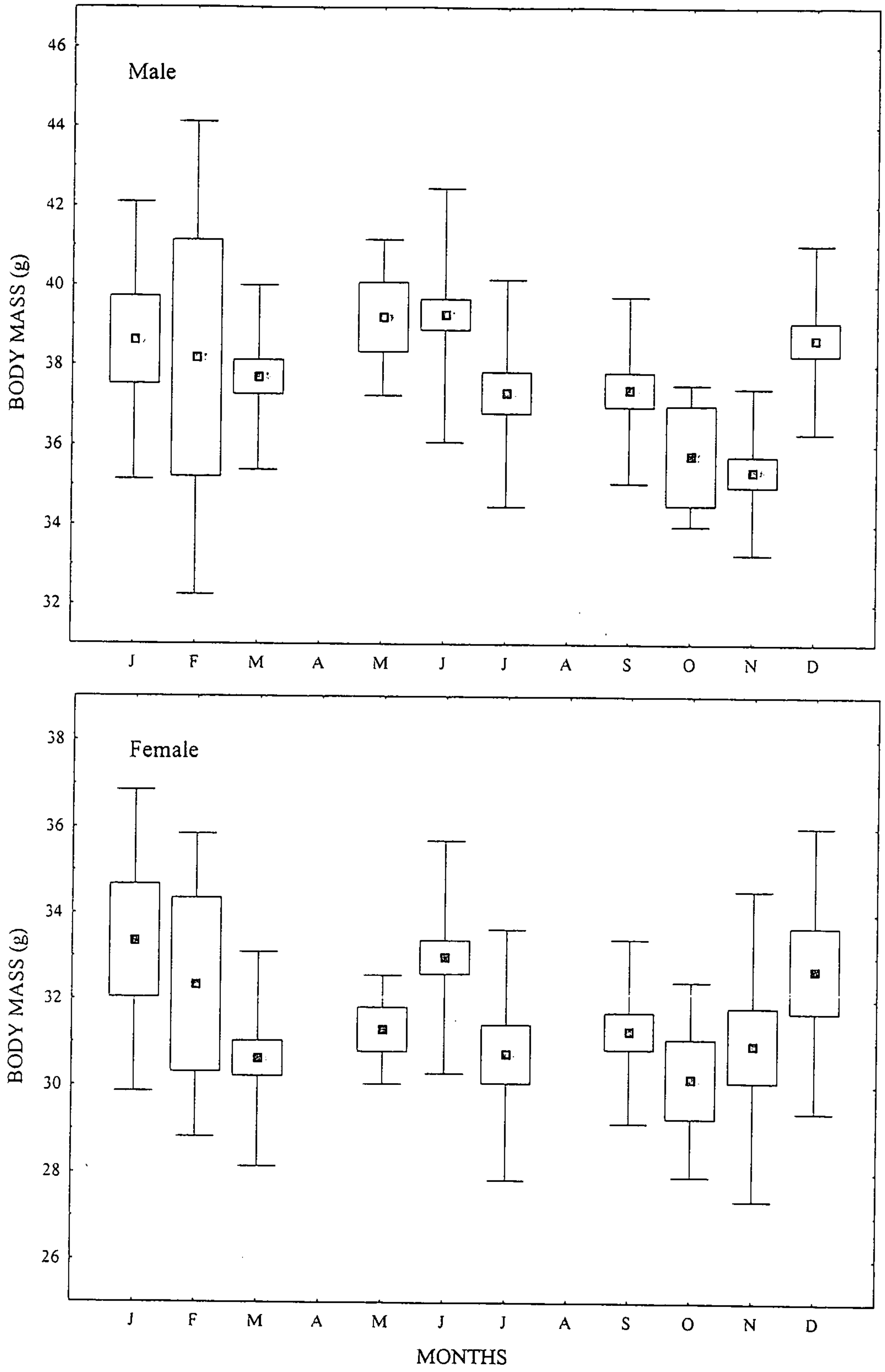


FIGURE 16: Monthly variation in body mass of adult Gurney's Sugarbirds at the Mpumalanga and Free State study sites during the period December 1986 - June 1998. Bold block indicates mean, retangular block the standard error and vertical line the range.

5.2.1.8. Intra-population variation in body and ornament size

The ornament tail and the width of the bulged P6 of Gurney's Sugarbirds at the study sites in and around Lydenburg (excluding the Waterval site U) were significantly more variable than other body size traits (Table 5; $F_{2,8} - _{17,6}$; df = 59 - 181; all $p << 0,05$). No significant variability in width of P6 and culmen, tarsus and total head lengths in adult males was recorded ($F_{1,0 - 1,5}$; df = 102 – 181; $p >> 0,05$). Adult male sugarbird tail ornaments were more variable than those of females ($F_{150, 128} = 1,60$; $p < 0,05$), but not those of sub-adult males ($F_{128, 68} = 1,3$; $p > 0,05$). In adult males, the tail ornaments were significantly more variable than the width of the bulged P6 ($F_{128, 102} = 14,8$; $p < 0,05$). The coefficients of variation values (CV) of sugarbird body size traits of mass, culmen, tarsus, total head and wing lengths in adult male, female and sub-adult sugarbirds averaged 4,6% (range 1,9 - 10,5%). The ornament traits for fully grown tail ornaments averaged 9,4% (range 8,7 - 9,7%) and 6,5% for the bulged P6 (Table 5).

Data of the covariances in body and ornamental traits in male and female Gurney's Sugarbirds are presented in Table 6. Only fully expressed and not significantly abraded wing feathers and tail ornaments were used for analysis. Adult male and female sugarbirds with long, fully grown tail ormanents have longer wings (male: $r_s = 0,621$, $p < 0,001$, n = 131; female: $r_s = 0,555$, $p < 0,001$, n = 164), while such males have wider P6 ($r_s = 0,412$, $p < 0,001$, n = 131). Also in both sexes, birds with longer total head lengths usually have longer bills (males: $r_s = 0,687$, $p < 0,001$, n = 188; females: $r_s = 0,455$, $p < 0,001$, n = 164).

TABLE 5: Summary morphometrics and coefficients of variation (CV) for body and ornament size of Gurney's Sugarbirds at Mpumalanga [excluding those from Waterval (site U)] during the period December 1986 - January 1997. Ornament data from maximum trait size only (unabraded feathers growing or in moult not included).

	Body size traits					**Ornamental traits**	
	Body mass (g)	Culmen length (mm)	Tarsus length (mm)	Total head length (mm)	Wing length (mm)	Tail length (mm)	Width of P6 (mm)
Adult males							
N	188	188	185	162	139	131	105
Mean	38,1	28,9	21,6	54,5	94,5	152,7	13,7
1 S.D.	2,8	1,0	0,9	1,0	3,0	14,1	0,9
Range	30,0-46,5	25,9-31,9	19,0-23,8	50,5-56,9	86,0-101,0	130,0-187,0	12,0-16,1
C.V. (%)	7,3	3,5	4,4	1,9	3,2	9,2	6,5
Adult females							
N	171	171	162	141	171	164	n / a
Mean	31,6	27,5	20,6	51.7	85,3	105,3	
1 S.D.	3,0	0,9	1,2	1,0	2,7	9,1	
Range	23,0-46,0	25,0-29,8	17,0-23,7	47,5-53,5	79,0-96,0	83,0-123,0	
C.V. (%)	9,5	3,3	5,7	2,0	3,1	8,6	
Sub-adult males							
N	75	75	70	66	75	75	n / a
Mean	34,7	28,3	21,2	53,2	88,4	113,8	
1 S.D.	3,6	1,1	1,2	1,2	3,5	10,7	
Range	24,0-44,0	25,8-32,1	18,5-22,1	50,0-55,9	79,0-96,0	88,0-137,0	
C.V. (%)	10,5	3,9	4,4	2,2	4,0	9,4	

TABLE 6: Spearman correlation coefficients for body and maximum (fully grown) ornament size of breeding male (normal print) and female (***bold italics***) Gurney's Sugarbirds.

	Body size traits					**Ornamental traits**	
	Body mass	Culmen length	Tarsus length	Total head length	Wing length	Tail length	Width of P6
Culmen	0,061						
	0,164						
Tarsus	0,093	0,077					
	0,226	***0,216****					
Total head	0,038	0,687**	0,165*				
	0,078	***0,455*****	***0,202****				
Wing	0,192*	0,163*	0,108	0,006			
	0,352**	***0,130****	***0,224****	***0,109***			
Tail	0,050	0,095	0,049	-0,208	0,621**		
	0,265*	***0,034***	***0,238***	***-0,050***	***0,555*****		
Width of P6	0,084	0,210*	0,205*	0,205*	0,412**	0,348**	
	----	----	----	----	----	----	
N	188	188	185	162	139	131	105
	171	***171***	***162***	***141***	***171***	***164***	—

*p < 0,05; **p < 0,001

5.2.2. Ageing and sexing

Gurney's Sugarbirds were sexed using the criteria of tail and wing length, bulging of P6 in males, total head length and body mass (De Swardt, 1990c). Sugarbirds which were previously incorrectly sexed as females based on tail length alone (actually sub-adult), were later recaptured as adult males. Several such cases were handled during the study period. One example is that of a sub-adult (ring no. 4-38925) sexed as a female and recaptured after 24 months as an adult male. Sugarbirds in this study reached adulthood in their second to third year.

Apart from the tail length criterion, the presence or absence of a bulged P6 was also noted in adult sugarbirds. The presence of this primary feather had previously only been described for the Cape Sugarbird. During this study the presence of such a modified primary feather was regularly recorded in adult Gurney's Sugarbirds and I was able to sex them in the hand with great ease (De Swardt, 1992a; Skead, 1967). This modified primary feather probably assists the male sugarbird in its display flights by making a characteristic audible "*frrt-frrt...*" sound. In males the mean width of the bulged feather was 13,6 mm, but only 10,9 mm from a small sample of females (Table 3). The use of the total head measurement was found to be most effective in sexing longer billed species such as nectarivores (M. W. Fraser, pers. comm.). Some difficulty was experienced in sexing sub-adult sugarbirds on the basis of tail and wing lengths or the presence of the bulged P6 alone, but if their total head lengths exceeded 53 mm, they were assumed to be males. They were mostly first classified as sub-adults as their sex could only be confirmed by recaptures. A total of 19 sub-adult sugarbirds were later recaptured, of which 11 were sexed as adult males and three as females. One example is that of an unsexed sugarbird (ring no. 4-38943) captured on 28 November 1987 (site O) which was sexed after subsequent recapture as a male on 27 April 1992. The presence of the bulged P6, the extent of the bulging and the head, tail and wing lengths combined can, therefore, be used to sex Gurney's Sugarbirds with great confidence in the hand. Males are also heavier than females, which can be sexed by the presence of a brooding patch during the breeding season.

Sugarbirds were also sexed on the basis of plumage characteristics. Adult sugarbirds have a deep russet breast and crown as well as a clear, brownish malar stripe. Small pinkish feathers were also found around the eyes, near the malar stripe and on the chin of adults. Furthermore, the secondary remiges are edged whitish in adult sugarbirds, but brownish in juvenile birds. Juveniles retain their yellow gape flange for a few months after leaving the nest. Their undertail coverts are also greenish-yellow and differ from the bright yellow tail coverts of adult birds. In general, the body measurements of juveniles are smaller than those of adult sugarbirds (see Tables 3 and 4).

5.2.3. Moult

A total of 590 sugarbirds (this includes 100 individual recaptures of 90 birds) were examined for moult during the study period at Lydenburg, Mpumalanga and eastern Free State.

5.2.3.1. Primary moult

Sugarbirds in primary moult were recorded mainly during the period November - March, which coincided with their breeding season (De Swardt & Bothma, 1992; Chapter 6) (Fig. 17). Only 23,3% of the sugarbirds examined during the study had moulted primaries. Primary moult was recorded during winter (June) in four males and a female. The moulting pattern in the primaries did not differ from the general sequence described by Ginn & Melville (1983). The primaries were renewed descendantly from P1 to P10.

5.2.3.2. Secondary moult

Of all sugarbirds handled during the study period (n = 590 birds including recaptures), only 15,1% were in secondary moult. The moult pattern of the secondaries occurred mainly during the breeding season (November - March), with only a few winter records. The secondaries are moulted ascendantly from S1 to S8.

5.2.3.3. Tail moult

Tail moult was recorded in 178 individuals (30,2% of total examined) of which 102 individuals were males (57,3%), 53 females and 23 unsexed sugarbirds (Fig. 18). Only a few individuals were in moult between May and July. The replacement of old tail feathers is considered to be important in sexual selection and, therefore, tail moult mainly occurred during the breeding season (November - March) when male sugarbirds defend their territories and display towards females. The tail feathers were dropped centrifugally from T1 to T6. By the time T1 or T2 (longest feathers) are fully grown, the outer tail feathers start breaking through their pins. The longest tail feathers of males were, therefore, replaced first and are already full-grown when the outer feathers have completed moult. A significant correlation was recorded between the primary and tail moult scores in male sugarbirds ($r = 0{,}468$; $p < 0{,}05$; $df = 63$) (Fig. 19).

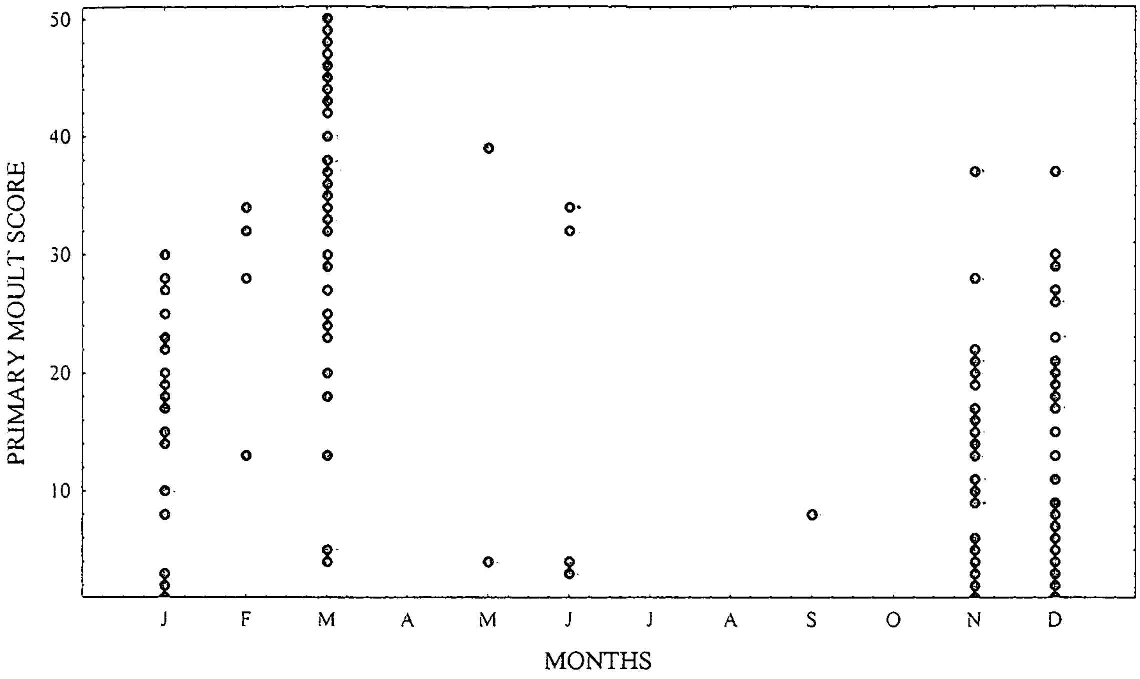


FIGURE 17: Primary moult in Gurney's Sugarbirds at the Mpumalanga and Free State study sites during the period December 1986 - January 1997.

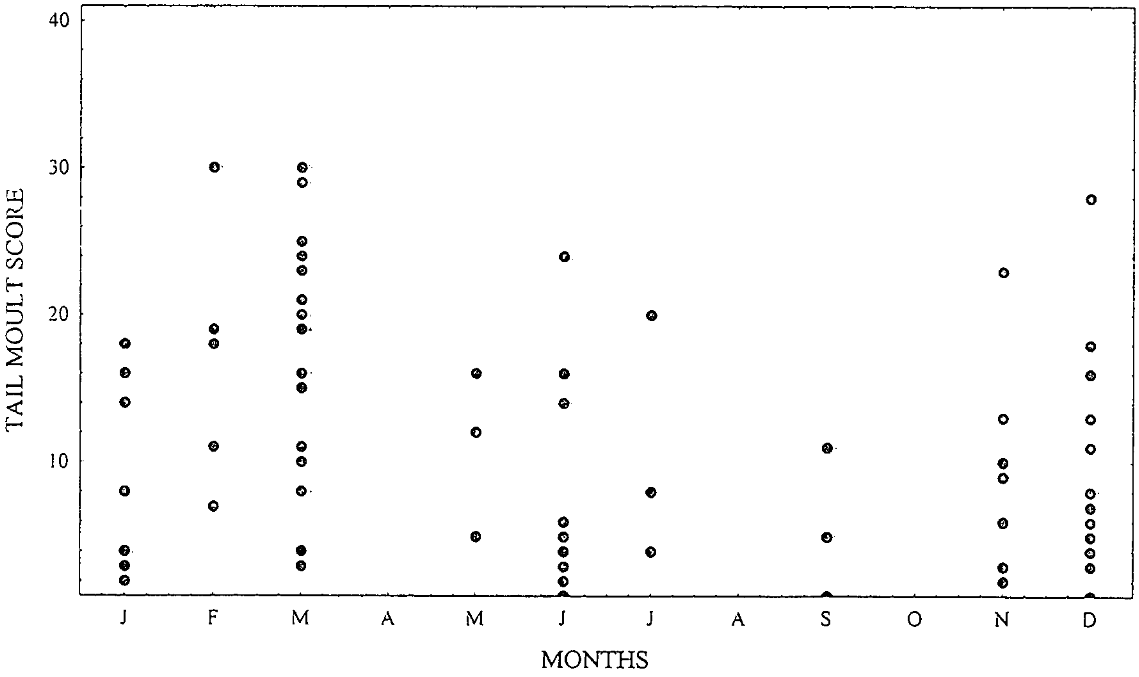


FIGURE 18: Tail moult in male Gurney's Sugarbirds at the Mpumalanga and Free State study sites during the period December 1986 - January 1997.

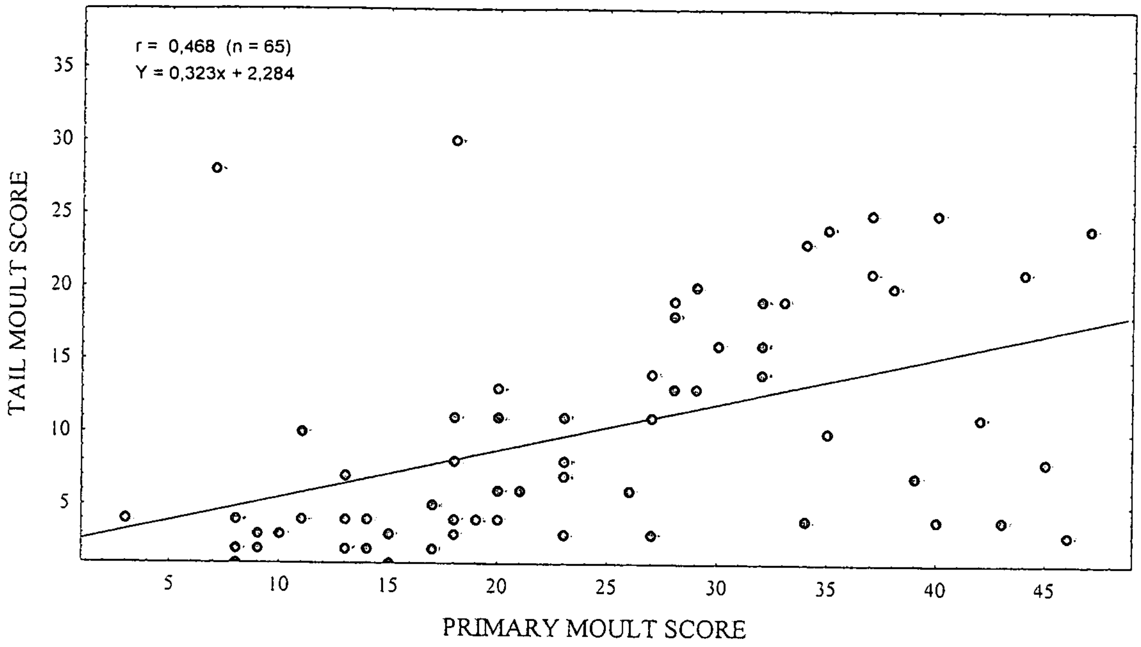


FIGURE 19: Relationship between primary and tail moult in adult male Gurney's Sugarbirds at the Mpumalanga and Free State study sites during the period December 1986 - January 1997.

5.3. DISCUSSION

5.3.1. Biometrics

The biometric data for Gurney's Sugarbird obtained during this study largely agree with those given in Maclean (1993) and McLachlan & Liversidge (1978), with only culmen and tarsus measurements found to be longer. However, the data of this study are from a larger sample than ever published before and represent the most accurate data set for this species. Male Gurney's Sugarbirds were found to be significantly larger than females. As males have to defend their territories (which may include a few *Protea* bushes) from other males in the same area, body size is considered to play an important role. During the breeding season the male usually sits on a specific *Protea* bush advertising his territory by singing and chasing other similar-sized males away. When chasing an intruding male the "*frrt-frrt...*' sound, probably produced by the characteristic bulged P6, is clearly audible. The longer tail of the male is used extensively during the breeding season for territorial displays.

The mean wing length and body mass of Gurney's Sugarbird were found to be similar to those of the Cape Sugarbird (Maclean, 1993; Seiler & Fraser, 1985), although a slight difference was noted by De Swardt (1992a). Culmen lengths of both male and female Gurney's Sugarbirds were shorter than those of the Cape Sugarbird. The differences can probably be related to their feeding preferences and foraging behaviour. Cape Sugarbirds, which inhabit the Cape Fynbos area where *Protea laurifolia* and *P. neriifolia* are abundant, are better able to exploit these species' flowers with their closed involucres (Rebelo, 1995) because of their longer culmen lengths. These Fynbos *Protea* species are replaced by *P. caffra, P. roupelliae,* and *P. subvestita* along the Drakensberg escarpment where Gurney's Sugarbird occurs, and the latter have open involucres; this possibly explains the shorter culmen lengths in Gurney's Sugarbirds. Male Gurney's Sugarbirds with longer culmen and total head lengths can, perhaps, utilise the inflorescences with greater ease than the females, as also suggested by Seiler & Rebelo (1987). This factor probably makes the male a more important pollination vector especially in *Protea* species with closed involucres. Females were observed probing laterally from outside the floral bracts and, therefore, would presumably not cross-pollinate the proteas (De Swardt, 1992a). Because of these differences in bill length between the sexes, Paton & Collins (1989) studied the adaptations in nectarivore bill lengths where different floral resources are exploited by the sexes, and concluded that males with their longer bills can more effectively reach the nectar sources. These sexual differences also reflect differences in bill functions between males and females. Females with their shorter bills do most of the nest building activities and spend more time catching insects, while males are mostly dominant over the females (Collins & Paton, 1989). Sexual differences in foraging behaviour on different floral resources were also observed in hummingbirds and this dimorphism may reflect combined efforts of reproductive role divisions and intersexual food competition, and probably sexual selection (Paton & Collins, 1989; Temeles & Roberts, 1993).

Skead (1967) reported bulged primaries in the Cape Sugarbird and their absence, or small size, in Gurney's Sugarbirds. During this study, however, the bulged P6 was regularly observed in male Gurney's Sugarbirds. As in the Cape Sugarbird, it is suggested that these modified primaries assist in making an audible "*frrt-frrt...*" sound during their display flights (Skead, 1967). This is in contrast to the findings of Sibley & Ahlquist (1974) that no audible sound is produced during displays, as the bulges are small or absent. Male Gurney's Sugarbirds with longer wing and tail lengths were also found to have wider bulged P6 feathers (De Swardt, 1992a). A wider bulged P6 presumably produces a louder sound during display flights and a male sugarbird with a wider P6 and longer wing and tail lengths may be older and therefore it may fulfill a function in sexual selection (Barnard, 1991).

The ornament tail length and width of the bulged P6 observed in Gurney's Sugarbirds were found to be significantly more variable than body measurements, as also found in other nectarivores, such as the Scarlet-tufted Malachite Sunbird (Evans & Barnard, 1995). Both male and female sugarbirds, which have longer fully grown tail ornaments, have longer wings, and males have wider bulged P6 feathers (see results; Table 6). In both nectarivores elongated tails, pectoral tufts and wider bulged P6 are used as sexual signals which are influenced by sexual selection, and these fully expressed male ornaments were significantly more variable than skeletal and wing measurements (Evans & Barnard, 1995). Also, the percentages of coefficient of variation in tail ornaments recorded in Gurney's Sugarbirds (9,7%) and Scarlet-tufted Malachite Sunbirds (12,3%) were also significantly more variable than other body size traits. Evans & Barnard (1995) also found that these fully grown feather ornaments are twice as variable in monogamous species than in polygynous or promiscuous species, and this is attributed to the role of sexual selection (Barnard, 1991). In the Scarlet-tufted Malachite Sunbird the tail ornaments are used as signals in mate choice and the tufts as signals in male-male competition (Evans & Barnard, 1995). This variation in tail ornaments increases in ornament length with age, which is correlated with body size characters (Alatalo *et al.*, 1988). In Gurney's Sugarbird, males with longer tails, wings and wider bulged P6 are probably older (Barnard, 1991; De Swardt, 1992a). Males with longer tails and wider bulged P6 also produce audibly louder sounds during their display flights above their territories. In the Longtailed Widow, males with longer tail lengths were preferred by females above males with shorter tails, and were more successful in raising young (Andersson, 1982). As males invest less time in parental care, the evolution of tails of exaggerated lengths allows individual males advantages in territorial defence and display. The females with their shorter tails, on the other hand, spend more time taking care of the young during the nestling period (De Swardt & Bothma, 1992; Winquist & Lemon, 1994).

5.3.2. Ageing and sexing

Ageing and sexing of individual bird species are widely used during ringing and other avian studies (Underhill, 1994). A relatively large sample of biometric data on the different age and sex classes of Gurney's Sugarbird is presented. The sugarbirds were mainly sexed using of the measurements of the total head, tail and wing length, while the bulged P6, body mass and the presence or absence of a brood patch in females during the breeding season, were also considered (De Swardt, 1990c; Maclean, 1993). Sexing of free-flying sugarbirds can only be done on the basis of their tail lengths, but birds with tails of intermediate lengths can either be females or sub-adult individuals.

De Swardt (1990c) and Maclean (1993) have already described ageing criteria such as plumage, but more detailed descriptions were obtained during this study. Adult and sub-adult sugarbirds are characterised by their deep russet breast and crown with distinctive malar stripes underneath the culmen. In juveniles, their plumage has a downy appearance and their breasts are greenish-russet. Juvenile undertail coverts are greenish-yellow and not bright yellow as in the adults, while their secondaries are edged brownish, which differ from the adults' whitish edged secondary feathers (De Swardt, 1990c). By contrast, juvenile Cape Sugarbirds have no distinctive border between the upper breast and greyish, streaked, lower breast and belly (Seiler & Fraser, 1985) and the undertail coverts are pale brownish (greenish-yellow in Gurney's Sugarbird). In both species the tails are of the same length or shorter than that of females (Maclean, 1993; Seiler & Fraser, 1985). Also, in both species, a yellow gape flange is visible during the birds' first year.

5.3.3. Moult

The timing of primary moult in Gurney's Sugarbird coincides with the breeding season of this species (De Swardt & Bothma, 1992; Maclean, 1993). This is interesting, as a great deal of energy is required for moulting, territorial defence, feeding and breeding. Such an energy budget may be better catered for during this period when more flowers are available for nectar feeding, and when insects are abundant (De Swardt & Louw, 1994). Primary moult is completed by the time the birds undergo seasonal movements after the completion of the breeding season. In most sunbird species, however, interrupted moult is correllated with the winter movements (Craig & Hulley, 1994). Similar to sugarbirds, the Greater Doublecollared Sunbird has a summer breeding moult season and was also observed moving seasonally to suburban areas (De Swardt, 1991b; De Swardt & Schoeman, 1997; Lloyd & Craig, 1989). Malachite Sunbirds moult in an eclipse plumage after their summer breeding season and the occurrence of interrupted moult is an indication that these birds are on migration (Craig & Hulley, 1994; Skead, 1967; unpubl. data.).

The moult pattern in Gurney's Sugarbird was generally the same as in other passerine species such as starlings (Sturnidae), sunbirds (Nectariniidae) and honeyeaters (Meliphagidae) (Hanmer, 1981; Lloyd & Craig, 1989; Paton, 1982a). The moulting pattern of their primaries was descendant and that of the secondaries ascendant. Tail moult occurred both centripetally and centrifugally and also coincided with their breeding season. Tail length plays an important role in sexual selection in birds, especially in the longer-tailed species (Barnard, 1991; Winquist & Lemon, 1994). As the tail feathers are subject to considerable abrasion (mainly during the breeding season), and tail length is important during displaying, the old tail feathers are replaced as soon as they lose condition.

6. BREEDING BIOLOGY

6.1. INTRODUCTION

Pioneer work has been done on the breeding biology and ecology of the Cape Sugarbird in the Fynbos biome of the South-western Cape (Broekhuysen, 1959; Rutherford & Westfall, 1989). Regrettably, little data are available for Gurney's Sugarbird, which occurs in association with *Protea* species, particularly in the summer rainfall areas of southern Africa along the Drakensberg escarpment (De Swardt, 1992a; Maclean, 1993). Skead (1963) studied aspects of the breeding biology of this species for comparisons with the Cape Sugarbird in the KwaZulu-Natal Drakensberg, but his study was not completed prior to his departure from KwaZulu-Natal. For nearly two decades only scant information was available on aspects of Gurney's Sugarbird breeding biology, and descriptions were limited to their breeding season, nest sites, nest dimensions, clutch sizes and egg dimensions - some of those from small sample sizes (Maclean, 1985; McLachlan & Liversidge, 1978; Skead, 1963 & 1967). Although De Swardt & Bothma (1992) provided some new information on the bird's incubation, nesting periods and descriptions of young, additional data on these aspects were obtained during the past few years. These included descriptions of their nests, nest sites, nestling development (including post nestling periods) and breeding successes.

The aim of this chapter is to collate all the data and review the current and historical literature of Gurney's Sugarbird and to compare this with other sunbird species (Family: Nectariniidae) especially the Cape Sugarbird, which is a winter rainfall breeding species (Craib, 1981; Broekhuysen, 1959; Maclean, 1993; Webb, 1996a & 1996b; Winterbottom, 1962).

6.2. RESULTS

Observations on the breeding biology of Gurney's Sugarbird were obtained from 20 breeding attempts in the Lydenburg area, Mpumalanga Province from December 1987 to January 1997. Additional breeding data were also obtained from the Nest Record Card Collection of the Avian Demography Unit, University of Cape Town, and from the Qwaqwa National Park, Free State, during November 1997.

6.2.1. Breeding season

Gurney's Sugarbird breeding season spans the summer months from September to March, while late summer to early winter observations have been observed in KwaZulu-Natal, the Eastern Cape Province and Zimbabwe (Fig. 20). Egg laying peaked in the period between November and December at Lydenburg, which coincided with the peak flowering period of *Protea roupelliae* (De Swardt & Bothma, 1992).

Some mid-winter breeding observations were recorded in the Lydenburg study area. On 10 June 1992 two fledged nestlings, which were still dependent on the adults, were observed and later captured and ringed (ring nos.4A 00038 and 4A 00044) at Paardeplaats (site O). By backdating the incubation and nestling periods of these nestlings, egg laying was estimated to have occurred possibly either during late April or early May. Late breeding attempts, such as in this instance, were possibly triggered by previous conditions after the high rainfall of the past season in the mountainous areas.

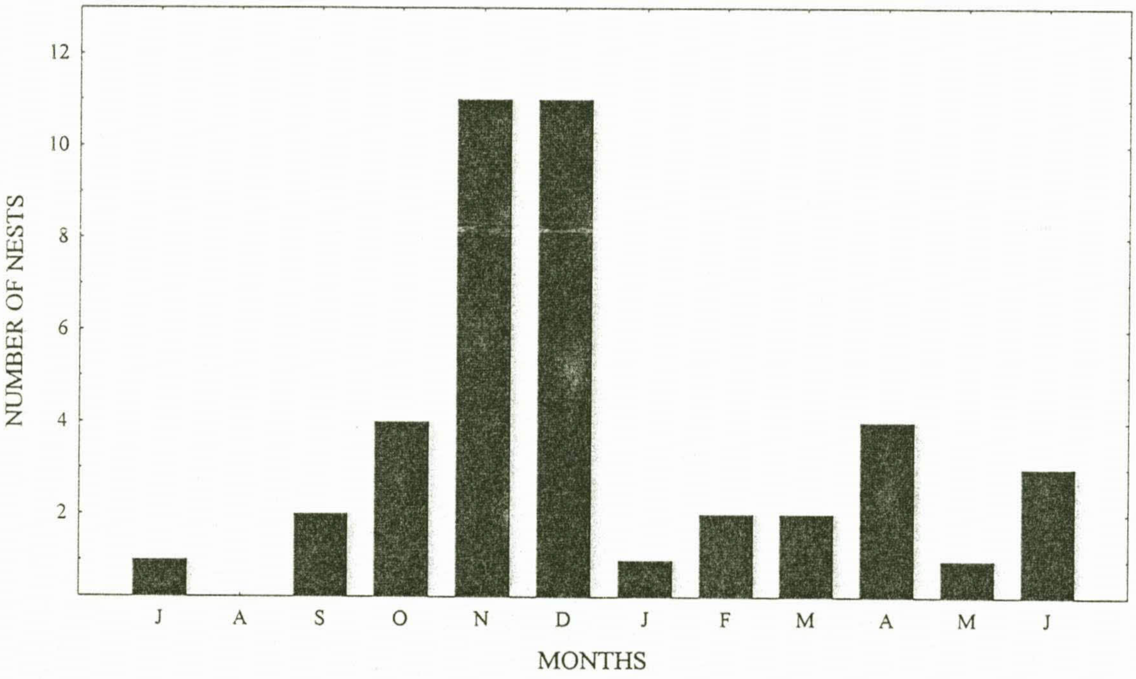


FIGURE 20: Breeding season (egg laying months) of Gurney's Sugarbirds in southern Africa as observed during this study. Data from the nest record card collection (Avian Demography Unit) and from various other sources are included.

6.2.2. Nest site selection

Gurney's Sugarbirds were found to nest mainly in *Protea roupelliae* bushes, however, they also used *P. caffra* and other species (Table 7). In the Lydenburg area the nests were located almost exclusively in *P. roupelliae* bushes, with only one nest observed in *P. caffra*. This preference for *P. roupelliae* over other plant species is probably due to the protection which this tree provides against rain and strong winds, which are common features in mountainous areas.

TABLE 7: Tree preferences for nesting of Gurney's Sugarbirds in southern Africa. NRC, nest record cards.

Plant species	Number of nests	Percentage	Reference
Protea roupelliae	23	60,5	This study, NRC
P. caffra	9	23,8	This study, NRC
Lecosidea sericea	3	7,9	NRC
Leucodendron argenteum	1	2,6	Nevill (1987)
Protea laurifolia	1	2,6	Webb (1996a)
Hibiscus spp.	1	2,6	Webb (1996b)
TOTAL	38	100	

The sugarbirds' nests were mostly situated in solitary trees or on the periphery of a *Protea* clump. In the Lydenburg area, the solitary trees in which the nests were located, were spaced some distances away from surrounding *Protea* trees or were standing in the open grassland. In this area only a few nests were found in the middle of a *Protea* clump, usually where the trees form a thicket. The nests were orientated on the south-western aspect of the *Protea* trees, but in larger trees the nests were centrally positioned. A mean nest height of 1,85 m (range: 0,80 - 4,0 m; n = 19) was recorded.

6.2.3 Description of the nest

The nest of Gurney's Sugarbird is a neat shallow cup which is built mainly with twigs of *Cliffortia linearifolia, Helichrysum* spp., *Pteridium* spp. and *Stoebe vulgaris,* while other available material in the surroundings is also used (De Swardt & Bothma, 1992; Maclean, 1993). The outside rim of one nest, found during December 1996, mostly contained the dry pinnules of *Pteriduim aquilinum* which were growing in the surrounding forest margins and alongside streams. The nests were compactly lined with brown fluffy *Protea roupelliae* seeds collected from old flowers. The sugarbirds probably act as seed dispersal agents as the nests are used only once during a breeding season. The old unused nests are then wind-buffeted out of the tree and the seeds in the nests dispersed by wind, or rain, to germinate.

The nests were mostly well hidden among the *Protea* leaves, either situated in a fork, branch or built on the base of an old infloresence having three to four clustered terminal branches surrounding it. Preference was given to nest sites in bushes which had escaped veld fires, but on 29 December 1991 a nest was found in the lower branches of a *Protea* bush which was burnt during a late winter-spring fire (De Swardt, 1992b) (Fig 21). Nest measurements are presented in Table 8.

FIGURE 21: Nest site of Gurney's Sugarbird among burnt leaves of a *Protea roupelliae* bush at Paardeplaats (site N), Lydenburg, during December 1991.

TABLE 8: Measurements of Gurney's Sugarbird nests obtained in the Lydenburg district, Mpumalanga Province, during the period December 1986 - January 1997.

Measurements (mm)	N	Mean	±SD	Range
Cup depth	7	46,0	10,0	38,0- 65,0
Cup diameter	10	62,1	2,6	57,0- 65,0
Depth of nest	1	84,5	-	-
Diameter of nest	4	111,9	11,6	96,8-125,0

Nest building was mostly conducted by the female, but sometimes the female is assisted by a male, as was noted during December 1995 at the Gustav Klingbiel Nature Reserve (site C) - the nest was located in a *Protea caffra* bush. This was the first confirmed sighting of a male assisting with nest building. However, this breeding attempt was unsuccessful as the nest was blown out of the tree during a thunderstorm a few days later. Nest building was observed to be completed within five days. A female was seen building a nest on 4 December 1990 at Nooitgedacht (site F) and when the nest site was revisited 4 days later, it was found to be complete, without a clutch.

6.2.4. Eggs and clutch size

The eggs of Gurney's Sugarbird are mainly cream, buff or pale brownish, with purple spots, and blotches often concentrated in a ring at the blunt pole of the shell (Maclean, 1993; Skead, 1967). The eggs recorded during this study were generally as described above, but having a more brownish background colour. A mean clutch size of 1,70 eggs (n = 17) was recorded. The eggs measured 22,2 x 16,7 mm (20,8 - 24,1 x 16,3 - 17,6) and weight 2,5 g (n = 4).

6.2.5. Incubation period

An incubation period of 16 - 17 days (n = 3) was recorded in the Lydenburg study area. One nest, containing two eggs, which was found on 22 December 1995 in an isolated *Protea roupelliae* tree at Paardeplaats (1 km from site O), and was revisited on 8 January 1996 had two pulli in the nest. The incubation period of this nest was calculated, by backdating the contents from when first found, as being 23 days after the eggs were laid between 20 or 21 st December 1995. Only the female was observed incubating the eggs, however, there is also a possibility that males assists in incubation. On 29 November 1987, for instance, a female incubating a nest with two eggs at

Sterkspruit (site J), but later on during the day, an individual with a long tail, possibly a male, was seen sitting (incubating?) in the nest.

6.2.6. Nestling period

A nestling period of 21-23 days was established by studying two nests in the Lydenburg area. At one nest during the 1989/90 breeding season, the nestling period was accurately determined to be 23 days as the nestlings were observed leaving the nest on that particular day.

6.2.7. Development of nestlings

The development of nestlings was monitored, at Paardeplaats (site O), during January 1990. Additional observations, obtained from other nests in the study area, were also included in the nestling descriptions.

6.2.7.1. Day 1:

The hatchlings' skin is pinkish with blackish-grey down on the head, back and wing areas. Their eyes are closed and appeared thick. The base of their culmen is a pale orange-flesh colour with a thick yellow gape flange and the tip of the bill blackish.. They weigh six grams (Fig. 22).

6.2.7.2. Day 5:

After 5 days in the nest, their blackish-grey down becomes longer and darker. Their skin also becomes more black and the feather tracts on the wings appear more downy. Their culmen and tarsi are already longer and dull-blackish, with sharp and strong claws on their feet. Their eyes start to open. They weight now between 12 and 14 g.

FIGURE 22: Sugarbird nestling which had hatched recently at Paardeplaats (near site O) on 8 January 1996. At this stage their skin was pinkish with blackish-grey down and their bills had a large swollen gape flange.

6.2.7.3. Day 7 to 9:

From seven to nine days the nestlings' eyes are fully open and they are not as helpless as earlier during the nestling period. Their primary and secondary feathers start to develop from their feather tracts and are already in pin. They weigh approximately 18 g.

6.2.7.4. Day 14:

The nestlings are now much stronger and larger than a few days before and their soft down is replaced by buffy-brown edged feathers. The primary and secondary feathers have already broken through the shafts of the pins and are longer. The scales of the tarsi are fully developed and the colour a brilliant black. The culmen is longer, with the upper mandible blackish and the lower mandible flesh coloured. Their gape flange is bright yellow. Their body mass has doubled to 26 g. (Fig. 23).

FIGURE 23: Sugarbird nestling, showing open wing, at an age of about 14 days at the nest in Gustav Klingbiel Nature Reserve (site S) on 18 December 1989.

6.2.7.5. Day 16:

Body feathers have now replaced the downy feathers. The wing feathers, which have broken through the feather shafts two days before, are now longer. The chin and throat is pure white with two clearly visible distinct black malar stripes on the sides of the chin. Their tarsi look stronger and their claws are longer. The length of the culmen is 16,0 mm and the wings 50,0 mm long. They weigh 28,1 g. This age (14-16 days) is the recommended age to ring sugarbird nestlings in the nest, as they will "jump" out of the nest when larger. The nestlings which were kept under observation in the nest, during January 1990, were ringed on day 16 (ring nos. 4-64911 & 4-64912) (Fig. 24).

FIGURE 24: Sugarbird nestling ringed in the nest at an age of 16 days at Paardeplaats (site O) on 20 January 1990. This is the recommended age to ring precocial passerine species in the nest.

6.2.7.6. Day 19:

The nestlings now look more like sugarbirds. Their primary, secondary and tail feathers are full-grown, with the wax sheets on the base of feathers still visible. Their white chin with two malar stripes and breasts which are now reddish-grey, have the same the russet coloration as the adult birds, are clearly visible.

6.2.7.7. Day 20 to 23:

From day 19 onwards the nestlings become more active, and start to leave the nest between the days 21 to 23. The nestlings have a typical juvenile plumage of downy feathers, russet breast and crown which is reddish-grey, wing feathers which are edged brownish, and body measurements which are significantly shorter than adult sugarbirds (see Chapter 5). The nestlings remain in the nest tree for a few days, where they probably also sleep a night or two, and fly short distances after the adults. Care was taken at this age not to disturb the nestlings unnecessarily in the nest, as they could jump out and not be able to return, thus exposing themselves to predators.

6.2.8. Feeding of nestlings and their behaviour

During the nestling period, both adult birds were observed bringing food to the nest. The nestlings were mainly offered small, winged insects (Hymenoptera species.), but also small beetles (Coleoptera species.). When the adult alighted on the nest, the nestlings responded by craning their necks with their bills wide open, begging for food. When they became larger, they merely stood on their heels. Nectar feeding, when adults inserted their culmens without any insects in their bills into the throats of the nestlings, was often observed (De Swardt & Bothma, 1992). This phenomenon was photographed on several occassions during January 1990.

6.2.9. Post-nestling period

De Swardt & Bothma (1992), previously indicated a post-nestling period of two to three months for sugarbirds. However, recent observations suggest that juveniles become independent within a month. On 8 October 1988 a recently fledged juvenile was captured together with an adult male from which it was still begging for food. They were both ringed, and from measurements taken it was detemined that the nestling (ring no. 4-38974) had left the nest about two weeks earlier (culmen: 23,1 mm, wing: 71,0 mm and weight 27,0 g). A second observation was made on 30 December 1996 when a juvenile (ring no. CC 05493) was captured alongside an adult male, from which it begged for food, and was fed. This juvenile was recaptured 22 days later, 0,5 km from its natal breeding area, while the male (with colour-rings) was observed on the same day in its original territory where it was ringed. These recapture data and observations suggest that young sugarbirds are dependent on the adults for about a month after hatching, after which they disperse from their natal breeding areas.

6.2.10. Breeding success

In the Lydenburg study area the breeding success rate was determined from 17 breeding attempts (excluding the nest that was not used). Of the 29 eggs laid, in mostly two-egg clutches, 12 nestlings fledged successfully. A breeding success rate of 41,4% was recorded between the 1986/87 and 1996/97 seasons in the Lydenburg area and this was compared with Cape Sugarbirds and other sunbird species (Table 9).

TABLE 9: Breeding success of Gurney's Sugarbirds at Lydenburg during the 1986/87 - 1996/97 seasons with comparative data of Cape Sugarbird and sunbird species. NRC, nest record cards.

Species	Number of clutches	Number of eggs laid	Number of chicks reared	% Breeding success	Reference
Gurney's Sugarbird	17	29	12	41,4	This study
Cape Sugarbird	28	55	18	32,7	Broekhuysen (1959)
Malachite Sunbird	487	846	416	49,2	NRC
Orangebreasted Sunbird	93	142	56	39,4	Broekhuysen (1963)
Greater Doublecollared Sunbird	65	109	53	48,6	NRC
Black Sunbird	259	485	191	39,3	NRC
Whitebellied Sunbird	52	94	20	21,7	Earlé (1982)

6.2.11. Causes of breeding failures

During the study period the main causes for breeding failures were nest desertion during rainy, misty and cold days. Thunderstorms, usually associated with strong winds, resulted in nests being blown out of trees. Desertion during nest inspections occurred mostly during such days, mainly when eggs were still in the nests. At two nests located during December 1989 and 1990, a time lapse camera was erected above the nest in order to photograph the incubating females, but in both instances the females were very wary in returning to the nest and the nests were subsequently deserted. Greater success was obtained after the eggs had hatched and when nestlings were present in the nest. As Gurney's Sugarbirds usually nest in inaccessible places in *Protea* woodland habitat, these nests are not easily located and are probably the reasons for the few nests observed in areas other than Lydenburg during the data collecting period for the *Atlas of southern African birds* (De Swardt, 1997).

6.3. DISCUSSION

6.3.1. Breeding season

The breeding season of the two sugarbird species coincide with the flowering periods of the *Protea* species in their distribution ranges, Gurney's Sugarbird a summer and Cape Sugarbird a winter breeder (Maclean, 1993; Winterbottom, 1962). The breeding season for Gurney's Sugarbird was mainly from September to March, with a November - December peak, coinciding with the peak flowering period of *P. roupelliae* (De Swardt, 1991a; De

Swardt & Bothma, 1992). Several late summer to mid-winter breeding observations were, however, noted, particularly in the Lydenburg area, but in other areas also such as the Eastern Cape, KwaZulu-Natal and Zimbabwe (Graham, 1972; Nevill, 1987; Skead, 1964; Webb, 1996 a & b). Skead (1964) found Gurney's Sugarbird breeding during May and June 1963 along with Cape Sugarbirds in the King Williams Town area of the Eastern Cape, and considered these birds to be winter breeders. This was the only breeding data obtained for Gurney's Sugarbirds in the Eastern Cape and as both sugarbird species' distribution ranges have since contracted, no further breeding data are available for this region (De Swardt, 1997).

In the KwaZulu-Natal area, Martin, Martin & Martin (1988) and Nevill (1987) reported late summer to winter breeding observations which are outside the normal September - February breeding season (Skead, 1967). In a study on nectarivore populations in the KwaZulu-Natal area, Daniels (1987) found a peak flowering period for *Protea roupelliae* from February to early May and a earlier summer flowering season for *P. caffra.* The late flowering season of *P. roupelliae,* in these areas, coincides with the late summer breeding observations of the sugarbirds recorded along the Drakensberg escarpment (Martin *et al.,* 1988; Nevill, 1987). The breeding season of Gurney's Sugarbirds in the eastern escarpment (Mpumalanga Province) were observed to coincide with the November - January flowering period of *P. roupelliae* (De Swardt, 1991a; De Swardt & Bothma, 1992).

In Zimbabwe, nests of Gurney's Sugarbirds were observed during the winter months of April, June and July with only two summer records in October and November (Skead, 1967). Recently, nests were also found in suburban gardens in the Chimanimani area of the eastern highlands during April and June (Webb, 1996a & b). These, together with the record of Nevill (1987), were the first records of this species breeding in suburban gardens. The sugarbirds are known to visit suburban gardens during the winter months, and as some of these localities are in close proximity to the mountainous areas, daily movements are possible (De Swardt, 1991a).

The breeding season of the Cape Sugarbird is between March and September, with peak periods from June to August in the Western Cape, April to June in the Eastern Cape, and mainly during the winter rainfall season in the Fynbos biome (Fraser, 1997; Winterbottom, 1962). Like the sugarbirds of the summer-rainfall area, the breeding season of the Cape Sugarbird coincided with the flowering periods of *Protea eximea, P. grandiceps* and *P. nerifolia* which were the nest sites preferred by this species (Burger *et al.,* 1976; Maclean, 1993; Winterbottom, 1962).

Historically, these two sugarbird species were found breeding alongside in thickets of *P. subvestita* in the Amatole Mountains of the Eastern Cape in the late 1950s (De Swardt, 1997; Fraser, 1997; Skead, 1964). These breeding observations were made during April and June, which was during the period when the KwaZulu-Natal observations were made and are the peak winter breeding season for Cape Sugarbirds (Maclean, 1993; Skead, 1967). The ranges of both species have contracted during recent times, but if any re-colonisation should take place, it is possible that they once again will breed in these areas (De Swardt, 1997; Fraser, 1997).

6.3.2. Nest site selection and nest descriptions

The breeding data obtained for Gurney's Sugarbird does not differ much from that already described by Maclean (1985 & 1993) and Skead (1963 & 1967), even though additional data were obtained on nest sites, nest descriptions, incubation and nesting, as well as post-nestling periods. Skead (1963) found nests in the KwaZulu-Natal Drakensberg area where *Protea* trees form small clusters or where they were densely arranged. During this study, most of the nests were located in isolated *Protea* trees, and seldomly where the trees formed a dense clump. The appearance of Gurney's Sugarbirds' nest cups is much neater than that of the Cape Sugarbird, which has an untidy and rugged outside perimeter (Maclean, 1993; Skead, 1967). According to Skead (1963) the base of Gurney's Sugarbirds' nest cups are first laid with an underbark of proteas. This was frequently observed in the nests recorded in the KwaZulu-Natal Drakensberg. During this study, no bark layers were observed in nests recorded in the Lydenburg area. Mostly the nests were built on the old, dry base of a protea floret of previous seasons, with three to four terminal branches supporting the nest.

Nest material used by Gurney's Sugarbirds did not differ from that described by De Swardt & Bothma (1992), Maclean (1993) and Skead (1963). In the Lydenburg area, flowerheads and stalks of *Helichrysum* spp. and *Pteriduim* spp. were used in nest construction. The mean nest height of 1,85 m for Gurney's Sugarbird was found to be higher than the 1,2 m for the Cape Sugarbird. This is of interest as the mean tree heights of *Protea eximia, P. grandiceps* and *P. nerifolia* (in which the Cape Sugarbirds nest), are generally the same as *P. roupelliae* (Burger *et al.*, 1976; Maclean, 1993). Burger *et al.* (1976) found that *Protea* bushes with dense foliage and large leaves are important requirements for nest site protection against cool night temperatures, windy conditions and unfavourable weather conditions. In the main, Cape Sugarbirds selected *P. eximia, P. grandiceps*, *P. nerifolia* and several other fynbos *Protea* species as nest sites to fulfil their needs (Broekhuysen, 1959, Burger *et al.*, 1976). Mostly Gurney's

Sugarbirds were recorded breeding in *P. roupelliae* bushes (see Table 7), which also provided sufficient shelter and protection against weather conditions (De Swardt & Bothma, 1992).

6.3.3. Incubation, nestling and post-nestling periods

The incubation and nestling periods of Gurney's Sugarbirds did not differ greatly from those described for the Cape Sugarbird, even though recorded from smaller sample sizes (De Swardt & Bothma, 1992; Maclean, 1993; Skead, 1967). The post-nestling dependence period for Gurney's Sugarbirds was similar to that observed in Cape Sugarbirds and in some sunbirds (*Nectarinia* spp.) such as the Lesser Doublecollared Sunbird *Nectarinia chaybea* (27 days) and Collared Sunbird *Anthreptes collaris* (24 days) (Broekhuysen 1959; Maclean, 1993; Skead, 1967). Comparative data was not available for the other sunbird species.

6.3.4. Breeding success

Breeding success was measured by recording the number of young surviving to sexual maturity and not by the number of eggs laid (Maclean, 1990). The success of a breeding attempt is affected by several factors that influence the survival of fledglings. In the Cape Sugarbirds, breeding failures resulted mainly from unfavourable climatic conditions (gale force winds, continuous rainy days, etc.), predation on nestlings by Argentine Ants *Iridomyrmex humilis*, snakes and birds (Broekhuysen, 1959; Maclean, 1993). Broekhuysen (1959) calculated a breeding success rate of 32,7 % for the Cape Sugarbird, which is lower than the 41,3 % obtained for Gurney's Sugarbird during this study. Although fewer nests were located in the Lydenburg study area, unsuccessful nest attempts were not as a result of weather conditions, but rather from disturbances at the nest site during the incubation phase. In both species, adverse environmental conditions such as strong winds and heavy rainstorms was a common feature during their breeding season, especially Cape Sugarbirds were more exposed to such conditions during their winter rainfall breeding season (Winterbottom, 1962). The sugarbirds' nests are situated in such way in the *Protea* bushes, that the leaves around the nest protected its contents sufficiently against rain and strong winds (Burger *et al.*, 1976; De Swardt & Bothma, 1992).

The breeding biology of sunbirds differs from sugarbirds with regard to nest structure, nest site, clutch size and their breeding success rates (see Table 9; Maclean, 1993). Whitebellied Sunbirds have a lower breeding success rate and did not associate with *Protea* or fynbos vegetation (Broekhuysen, 1966; De Swardt, 1993b; Earlé, 1982).

Orangebreasted Sunbirds had a higher breeding success rate compared to Cape Sugarbirds, which occured in the same area, a fact which can probably be related to the better protection provided by the closed, rather than open, nests (Broekhuysen, 1963). Malachite and Greater Doublecollared Sunbird nest contents were not as exposed to strong winds and rain as the nests of Gurney's Sugarbirds, although both which occurs in the same *Protea* habitat. A typical sunbird nest, with its side entrance, provides sufficient protection to its contents. Malachite Sunbird nests were found mostly attached to shrubs growing in gullies or on overhanging rocks in the mountainous areas, where they are protected from rain and strong winds (Maclean, 1993).

7. DIET, FORAGING BEHAVIOUR AND INSECTS IN *PROTEA ROUPELLIAE*

7.1. INTRODUCTION

The little information available on the diet of Gurney's Sugarbird refers mostly to proteas, aloes and insects, with no reference to any specific plant species or insect taxa (Maclean, 1993; McLachlan & Liversidge, 1978; Skead, 1967). No detailed accounts are available in the literature of the food plants visited by Gurney's Sugarbirds, excepting for those on cultivated *Leucospermum* spp., *Strelitzia* spp. and *Leonotis leonurus* (Maclean, 1993; Norris, 1989; Skead, 1967; Vernon, 1971). The diet of the Cape Sugarbird has been studied in detail by Mostert *et al.* (1980) and this species was observed utilising both the nectar and the arthropod fauna (which consists of bees, beetles and flies) associated with the Fynbos protea species (Rebelo, 1987).

The importance of sugarbirds and sunbirds as pollinators and their pollination role in protea species are discussed and their efficiency in foraging determined by their culmen lengths and bill curvates which influence the rates of nectar uptake per probe (Paton & Collins, 1989; Rebelo, 1987). These sugarbirds play an important role in the pollination of *Protea* species as the birds have to visit several *Protea* flowers to fulfil their needs (Mostert *et al.*, 1980). The major insect pollinators are the smaller beetles of the Halticidae, Nitidulidae and Staphylinidae while the larger Cetoniinae (Scarabaeidae) are important nectar feeders and these beetle species prefer the deep, cup-like flower heads of *Protea* species (Gess, 1968; Whitehead, Giliomee & Rebelo, 1987). Other insect pollinators in *Protea* species are mainly bees and ants, but the latter serve mostly as seed dispersal agents although their role has not yet been investigated (Whitehead *et al.*, 1987).

De Swardt & Louw (1994) studied the diet and foraging behaviour of Gurney's Sugarbirds when arthropods were collected, from *Protea* inflorescences and sugarbird stomach contents, and food plants visited by sugarbirds in the Lydenburg area. No comparative work, such as this, was previously done on the relationships between birds and plants, excepting for the Cape Sugarbird (Mostert *et al.*, 1980). This chapter reports on the additional information, collected on this species since 1992, which aids in the completion of this study. In the Fynbos biome, the pollination syndromes of insects, in association with the plants, in this region were studied in detail as well as the pollination role of arthropods in *P. repens* and their utilisation by Cape Sugarbirds (Coetzee & Giliomee, 1985; Mostert *et al.*, 1980; Whitehead *et al.*, 1987). Excepting for De Swardt & Louw (1994), no other information was available on the arthropod fauna associated with *P. roupelliae* inflorescences. Additional information has also been collected during the past few years. Pajor (*in litt.*) studied the arthropod fauna in *P. caffra* and *P. roupelliae* in the KwaZulu-Natal Drakensberg. The object of this chapter is to compare the insectivorous diet of Gurney's Sugarbird to that which occur in *P. roupelliae* inflorescences.

7.2. RESULTS

7.2.1. The diet of Gurney's Sugarbird

7.2.1.1. Nectar

In their mountain habitat, Gurney's Sugarbirds were observed foraging mostly on the nectar of *Protea roupelliae*, but they also visited the flowers of *P. caffra*, *Greyia radlkoferi*, *Halleria lucida* and other species (Table 10). The sugarbirds have been observed moving to the *Aloe arborescens* populations, in the cliffs and lower mountain slopes, during the winter months after feeding at the *P. roupelliae* populations during the early morning. It was observed that they left the *Protea* areas, temporally, during the warmer part of the day, although there were still sufficient flowers. Several individuals were captured with *Aloe* pollen on their chins after returning from the *Aloe* populations. In the suburban areas, during the winter months, cultivated *A. arborescens,* in rock gardens and parks, and gardens with *P. nerifolia* and *P. repens* are the main attraction for sugarbirds (Table 10). Other *Aloe* species such as *A. ferox*, *A. pretoriensis* and species such as *Cuphea ignea* and *Callistemon viminalis* provide nectar for the birds during the winter months.

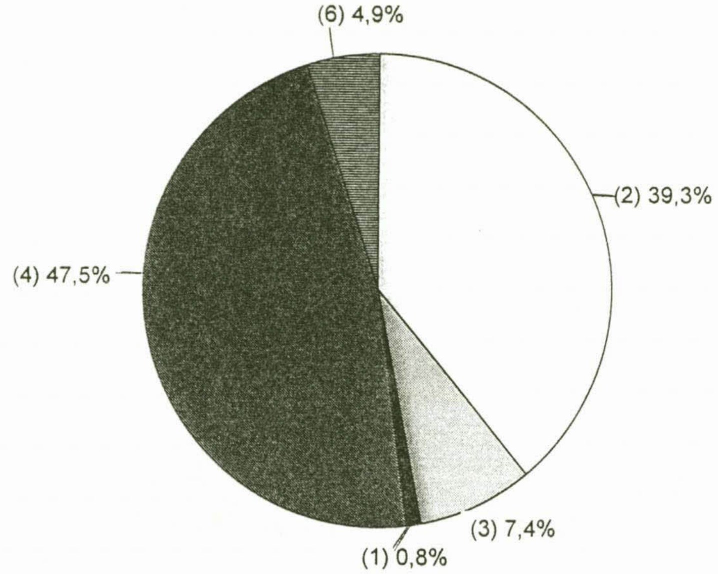
7.2.1.2. Insects

Important insect taxa recorded in the stomach contents of Gurney's Sugarbirds were mostly Coleoptera beetles (39,3%) and Hymenoptera (47,5%), while other arthropod groups such as Arachnida, Hemiptera and Oribati represent only small proportions of the sugarbirds' diet (Fig. 25). Coleoptera beetles, usually found in association with *P. roupelliae* inflorescences (see section 7.2.3.), such as the Apionidae (2,4%), Chrysomelidae (6,5%) and Scarabaeidae (22,9%), were found to be regular items of prey, while bees (Hymenoptera: Apidae; 24,5%) and ants (Hymenoptera: Formicidae; 10,7%) also form a portion of the sugarbird's diet (Table 11).

TABLE 10: Food plants visited by Gurney's Sugarbirds in the Lydenburg area during the period April 1980 - July 1998.

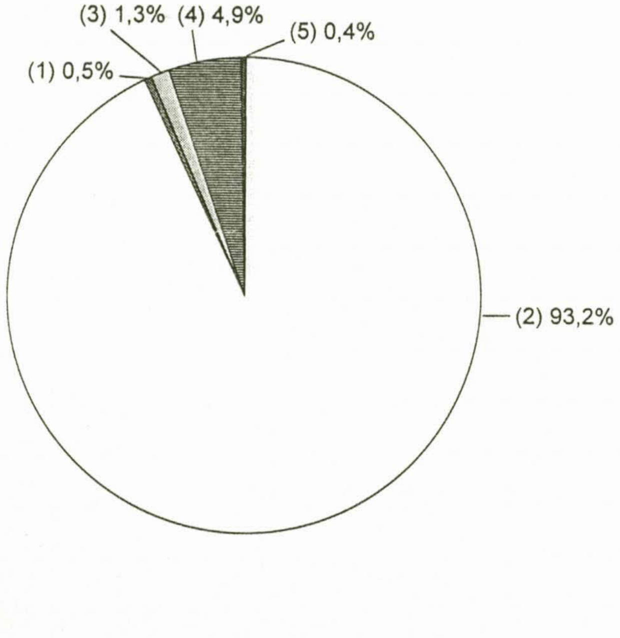
Montane habitat	Suburban habitat
Acacia ataxantha	*Aloe arborescens*
Aloe affinis (winter)	*A. ferox*
A. arborescens (winter)	*A. pretoriensis*
Greyia radlkoferi	*Callistemon viminalis*
Halleria lucida	*Cuphea ignea*
Kniphofia linearifolia	*Eucalyptus* spp.
Protea caffra	*Kniphifia* spp
P. roupelliae	*Protea cynaroides*
Watsonia transvaalensis	*P. exima*
	P. laurifolia
	P. nerifolia
	P. repens

N=14



A

N = 41



B

FIGURE 25: Proportion of insect taxa recorded in Gurney's Sugarbird stomach contents (A) and in *Protea roupelliae* inflorescences (B) at Paardeplaats and Sterkspruit, Lydenburg, during the period November 1992 - January 1997: 1, Arachnida; 2, Coleoptera; 3, Hemiptera; 4, Hymenoptera; 5, Lepidoptera; 6, Oribati.

TABLE 11: Arthropod fauna recorded in Gurney's Sugarbird stomach contents (n = 14) collected at Paardeplaats and Sterkspruit, Lydenburg, during the period July 1990 – December 1992.

Taxa	Number	Percentage composition	Occurrence frequency (%)
Arachnida	**1**	**0,8**	
Araneae			
Salticidae	1	0,8	7,1
Coleoptera	**48**	**39,3**	
Apionidae			
Tanaos sanguineus	3	2,4	21,4
Bostrychidae			
Bostrychinae	1	0,8	7,1
Chrysomelidae			
Eumolpinae	5	4,1	21,4
Galerucinae	3	2,4	7,1
Curculionidae			
Euderes sp.	2	1,6	14,3
Scarabaeidae			
Aphodiinae	4	3,3	7,1
Cetoniinae	15	12,3	14,3
Melolonthinae	3	2,4	14,3
Rutelinae	6	4,9	14,3
Unidentified fragments	6	4,9	28,6
Hemiptera	**9**	**7,4**	
Heteroptera	9	7,4	28,6
Hymenoptera	**58**	**47,5**	
Apoidea			
Apidae			
Apis mellifera	8	6,5	21,4
Apis sp. fragments	22	18,0	57,4
Chalcidoidea	12	9,8	35,7
Formicidae			
Crematogaster sp.	4	3,3	7,1
Formicidae fragments	9	7,4	7,1
Sphecidae			
Ampulex sp.	3	2,4	14,3
Oribati	**6**	**4,9**	
Africoribates sp.	6	4,9	7,1
Total	122		**100,0**

7.2.2. Foraging behaviour

7.2.2.1. Nectar

Data on the foraging behaviour of Gurney's Sugarbirds were obtained on a small *Protea roupelliae* population near the Dorpsdam (site H) outside Lydenburg, during April 1986. Peak foraging periods on *P. roupelliae* inflorescences were during the early morning (06:00 - 10:00) and late afternoon (15:00 - 17:00) (Fig. 26).

When foraging on *P. roupelliae* flowers, a sugarbird perches on the top of it, and with quick movements of its bill probes for nectar inside the flower (Fig. 27). The bird moves clockwise on the flower while feeding, inserting its bill repeatedly into different parts of the flower. The number of probes into a flower varied considerably; from just a few probes up to 17 probes into a single flower. The number of probes could be related to the amount of nectar present, the timing of peak nectar production, and to insect activity in a flower. A few probes, if the sugarbird is not disturbed, is an indication that the nectar resource of that particular inflorescence has been depleted. Mostly the sugarbirds visit several infloresences during these peak feeding times to fulfil their energy requirements and territorial defence and display towards females occurred during these times. Non-territorial sugarbirds were aggressively chased from a *Protea* inflorescence by a territorial male by jumping onto the flower where the interloper was sitting. Malachite Sunbirds were displaced by the same behaviour. During the observation period, nine interactions with sugarbirds and six with Malachite Sunbirds were noted during a 24-hour period.

During a feeding session, birds tend to remain amongst the flowers of a single bush, but will also fly to other *Protea* bushes in the vicinity. Sugarbirds were frequently observed probing for nectar in closed inflorescences by forcing their bills between the floral bracts. This behaviour was observed mainly in females. Males usually foraged on open inflorescences where their longer bills could be inserted deeper into the floret to reach the nectar. When probing *P. nerifolia* for nectar, the sugarbird forces its head into the closed involucles of the inflorescence, so that only the body is visible during the feeding action (Fig. 28). When feeding on *Aloe* species, and other grassland geophytes such as *Watsonia* spp., the bird perches on the peduncle of the flower and probes for nectar by inserting its bill into each downward-pointing corolla, separately (Fig. 29).

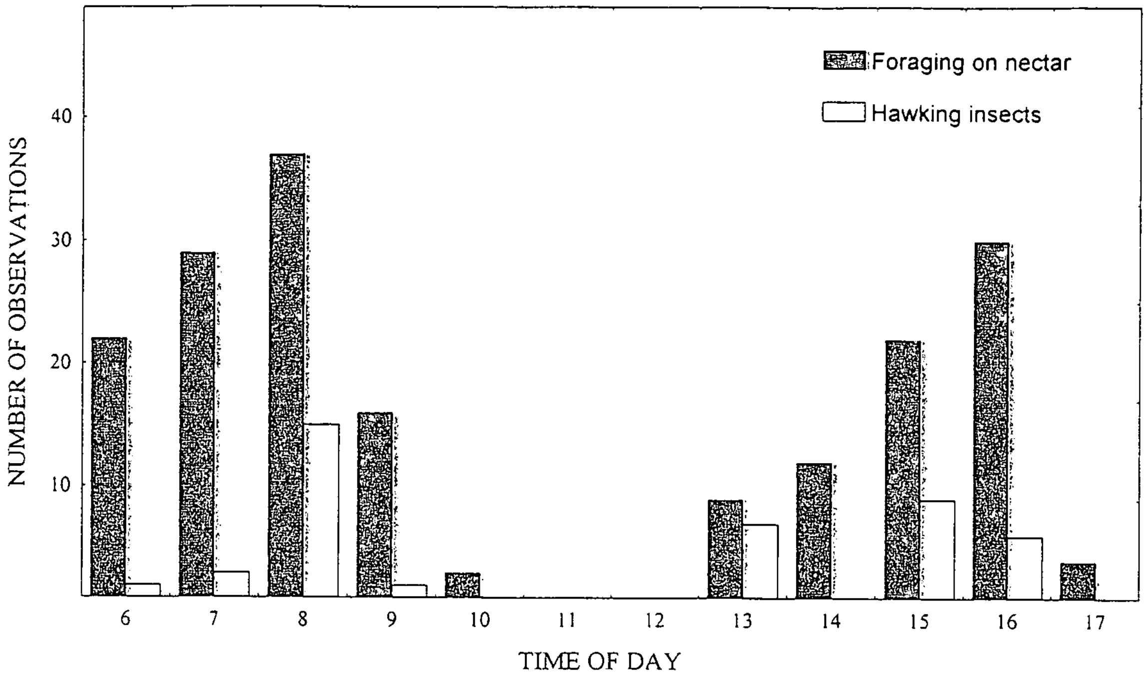


FIGURE 26: Diurnal variation in foraging of Gurney's Sugarbirds near the Dorpsdam, Lydenburg, during April 1986.

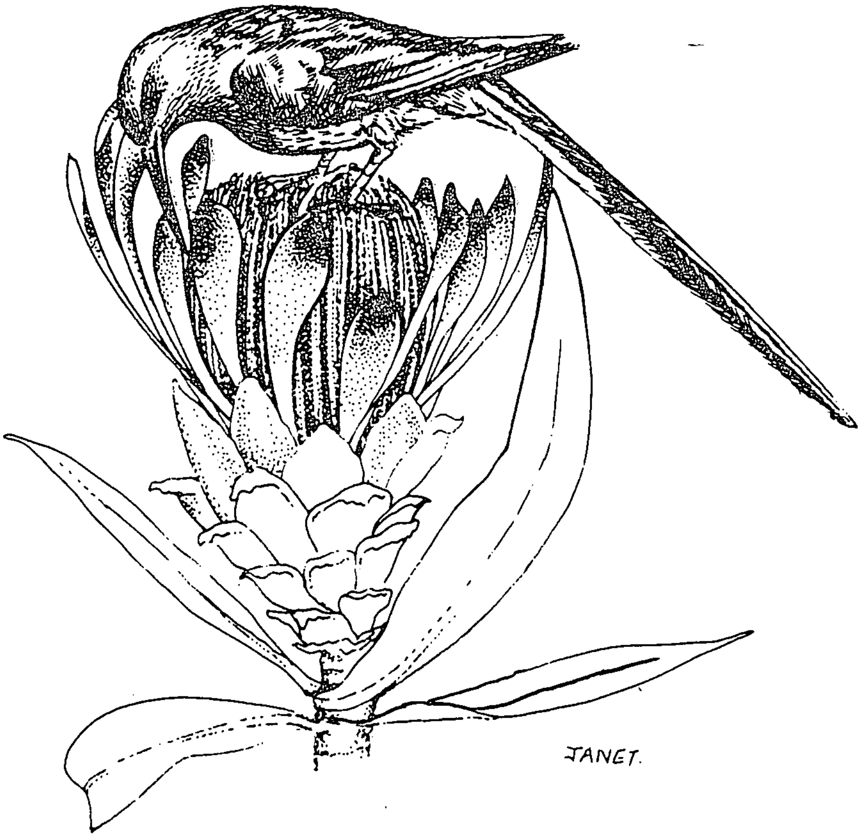


FIGURE 27: Gurney's Sugarbird probing into a *Protea roupelliae* flower with open involucles, perching on top of it.

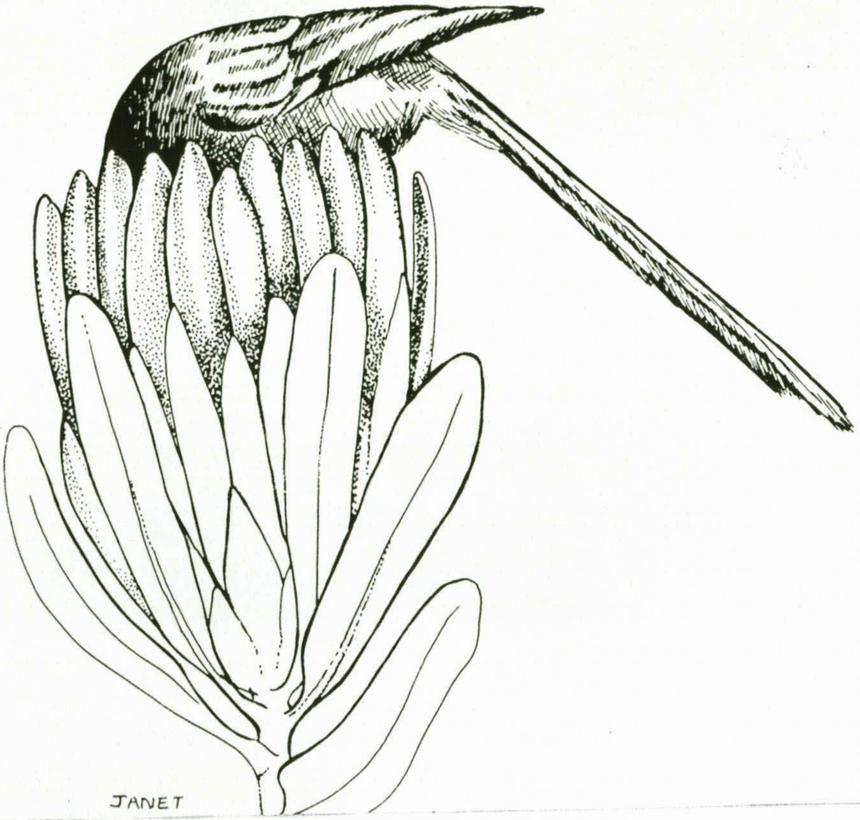


FIGURE 28: Gurney's Sugarbird foraging on closed involucles of *Protea neriifolia*, forcing its head and body into the flower head.

FIGURE 29: Gurney's Sugarbird visting *Aloe arborescens* inflorescences, while perching on the peduncle.

7.2.2.2. Insects

Gurney's Sugarbirds foraged by hawking small flying insects while perching on an inflorescence, or from a low branch of a *Protea roupelliae* bush, and mainly beetles from the flowers. Hawking small flying insects and catching insects were observed usually during the morning (09:00) and late afternoon (14:00 - 17:00) when it was warmer (see Figure 26). While perching on a flower a sugarbird may suddenly flutter into the air, snatch a flying insect and then return to its perch. The bird either consumed the insect while on its perch or flew into a bush and swallow it there. After each feeding action, the bird wiped its bill on a branch using fast to-and-fro movements. Birds were also observed catching small, flying insects which flew in front of them while they were perching on a flower. In the suburban habitat, honeybees were often caught by sugarbirds at *Aloe arborescens* inflorescences and the nectar-feeding of sugarbirds was then temporally interrupted to catch the bee. The bees were caught with a very fast snatching action of the bill, then devenomed on a branch in a similar manner used by bee-eaters (Fry, 1982), and swallowed. Several unidentified Apidae fragments and *Apis mellifera* specimens were recorded in sugarbird stomach contents and in *P. roupelliae* inflorescences, although some escaped collection. Large numbers of bees were observed in *P. roupelliae* inflorecences during December 1996 at Sterkspruit (site L), mostly in the newly opened flowers. Coleoptera beetles (mostly Apionidae and Scarabaeidae) were encountered in large numbers in *Protea* inflorescences and also in sugarbird stomach contents (see Tables 11 & 12). Beetles such as *Tanaos sanguineus* were probably eaten when the sugarbird probed for nectar in the inflorescence and were found in the stomach contents of sugarbirds, and also frequently in *Protea* inflorescences. A sugarbird was also observed removing a beetle, *Cyrtothyrea testaceoguttata*, from a *Protea* inflorescence at Morgenson near Sabie, Mpumalanga Province, during 1983 (R.A. Earlé; pers. comm.).

TABLE 12: Arthropod fauna recorded in *Protea roupelliae* inflorescences (n=41) collected in the Lydenburg study area during the period July 1990 - January 1997. Asterisk indicates specimens escaped from infloresences but caught in nets.

Taxa	Number	Percentage Composition	Occurrence frequency (%)
Arachnida	**4**	**0,5**	
Clubionidae			
Clubiona sp.	3	0,4	7,3
Thomisidae			
Synaema sp.	1	0,1	2,4
Coleoptera	**918**	**93,2**	
Apionidae			
Tanaos sanguineus	35	3,5	31,7
Cocinellidae	2	0,2	4,9
Alticidae	5	0,5	4,9
Histeridae	1	0,1	2,4
Melyridae	1	0,1	2,4
Mordellidae	1	0,1	2,4
Nitididae			
Carpophilus sp.	8	0,8	9,7
Rhizophagidae	370	37,5	85,3
Scarabaeidae			
Cetoniinae			
Artricelaphinus tigrina	6	0,6	12,2
Crytotyrea testaceoguttata	30	3,0	24,4
*Trichostetha fascicularis**	6	0,6	7,3
Melononthinae	3	0,3	2,4
Staphylinidae	450	45,5	68,2
Hemiptera	**13**	**1,3**	
Fulgoroidea	1	0,1	2,4
Lygaeidae	12	1,2	12,2
Hymenoptera	**49**	**4,9**	
Apidae			
Apis mellifera	7	0,7	9,8
Scoliidae	11	1,1	2,4
Formicidae			
Camponotus brevisetosus	11	1,1	12,2
C. irredux	1	0,1	2,4
C. robecci	8	0,8	7,3
C. rufoglaucus	2	0,2	2,4
C. thraso	2	0,2	4,8
Myrmecaria faurei	7	0,7	2,4
Lepidoptera	**4**	**0,4**	
Lycaenidae			
Capys alphaeus larvae	4	0,4	7,3
Total	**988**	**100,0**	

7.2.3. Insects in association with *Protea roupelliae* inflorescences

The insect fauna recorded in the *P. roupelliae* inflorescences comprised mostly Coleoptera beetles (93,2%), while Arachnida, Hemiptera, Hymenoptera and Lepidoptera were also encountered (see Fig. 25). The Coleoptera were represented by the families Staphylinidae (45,5%), Rhizophagidae (37,5%), Scarabaeidae (4,5%) and Apionidae (3,9%) (Table 12). Beetles such as *Artrichelaphinus tigrina, Carpophilus* spp., *Cyrtothyrea testaceoguttata, Tanaos sanguineus* and *Trichostetha fascicularis* were frequently encountered in *P. roupelliae* inflorescences, but some of them escaped collection (mainly *T. fascicularis*).

Hymenoptera in *Protea roupelliae* inflorescences were mostly Apoidea (bees) and Formicidae (ants) (Table 12). Apoidea consisted mainly of bees (*Apis mellifera*) and species of the Scoliidae family which are nectar feeders. Five species of the *Camponotus* genus were recorded in *P. roupelliae* inflorescences of which only *C. brevisetosus* was abundant - this species was previously only known from the Vernon Crookes Nature Reserve, KwaZulu-Natal and Mariepskop, Northern Province (H. G. Robertson, *in litt.*). At Qwaqwa National Park, specimens of *Crematogaster* spp. were recorded in *P. roupelliae* inflorescences during February 1998, while ants were recorded in sugarbird stomach contents at Lydenburg during December 1992.

7.3. DISCUSSION

7.3.1. Nectar diet and foraging

Apart from general information on the diet of Gurney's Sugarbirds, no recent study has focussed, in detail, on flowering plant species visited by this nectarivore. Maclean (1985 & 1993) refers mostly to proteas, aloes, *Eucalyptes* spp. and *Watsonia* spp., while Skead (1967) recorded *Erythrina lysistemon,Greyia sutherlandi* and cultivated *Leucospermum* spp. Vernon (1971) and Norris (1989) recorded *Leonotus leonurus* and *Strelitzia* spp. as food plants visited by Gurney's Sugarbirds. During the study at Lydenburg, sugarbirds were observed visiting a variety of food plants in montane and suburban habitats (Table 10). Gurney's Sugarbirds foraged mainly on the nectar of *P. roupelliae* inflorescences, but also visited *P. caffra*, *Halleria lucida* and *Greyia radlkoferi* inflorescences in the vicinity, always returning to the adjacent *P. roupelliae* clumps.

During winter, when fewer flowers were available after the peak flowering period of *P. roupelliae*, individual sugarbirds of the Lydenburg population were observed dispersing into the valleys and visiting the suburban areas (De Swardt, 1989 & 1991a). During mid-winter (June - July) the resident sugarbirds, in the mountains, were noted moving into the *A. arborescens* clumps in the cliffs and valleys during the warmer parts of the day, but were also observed returning to the *Protea* populations in the vicinity. Some of those that were captured had *Aloe* pollen on their chins. In the KwaZulu-Natal Drakensberg, Daniels (1987) observed them on *A. arborescens* during the winter months and on *Leonotus leonurus* between April and May and, less frequently, on *Greyia sutherlandi* and *Halleria lucida*. In the Lydenburg area, *G. radlkoferi* and *H. lucida* occurred along forest verges, cliffs and in road ecotones where they were visited by sugarbirds, but the birds always returned to the *Protea* clumps in the adjacent mountainous areas (De Swardt, 1991a; De Swardt & Louw, 1994).

Collins & Grey (1988) suggested that the frequency of visits by honeyeaters to food plants is possibly correlated with the number of probes made at each inflorescence, as well as the number of productive inflorescences per plant. Therefore, it was suggested that it would be advantageous for birds to maximize the amount of time spent on inflorescences of particular plants. Gurney's Sugarbirds were observed to move clockwise on *Protea* inflorescences while feeding, probing several times for nectar before moving to the next inflorescence. The number of probes into an inflorescence varied considerably during a feeding session, mainly as a result of their territorial activities, or according to the nectar content of the inflorescence. They visited several flowers in order to fulfil their nectar requirements, giving a few probes in each inflorescence, before moving to the next one. A similar situation has been reported for Cape Sugarbirds where a large number of *P. repens* infloresences had to be visited on a daily basis, for nectar and satellite insects, to fulfil their energy requirements (Mostert *et al.*, 1980).

High sugar concentrations (11,7 g/100 ml) were recorded in *Protea repens* inflorescences which attracted large numbers of satellite insects, which are gleaned by the sugarbirds when probing for nectar (Mostert *et al.*, 1980). Daniels (1987) measured nectar concentrations of *Protea* species in the KwaZulu-Natal Drakensberg and found that *P. roupelliae* had a higher mean nectar concentration than *P. caffra* – the low concentration of 12,5% in *P. caffra* is probably one of the reasons why the sugarbird does not prefer its nectar. It was also observed that Gurney's Sugarbirds were seldomly observed at *P. caffra* clumps and only if these plant species were in the vicinity of *P. roupelliae* populations (De Swardt, 1993b). Other reasons for the sugarbirds preferences for *P. roupelliae* are the structure of the flowers and also the form of the canopy which is important in nest site selection (see Chapter 6). *Protea caffra* flower heads by contrast to those of *P. roupelliae* are flat and open, this allows rainwater to collect in the inflorescences during the rainy season and dilute the nectar and decrease the sugar content which makes *P. caffra* less acceptable to the sugarbirds (I. Pajor, *in litt.*). However, in an experimental study, Downs & Perrin (1996) found that both Gurney's Sugarbirds and Malachite Sunbirds displayed no preferences for the highest concentrations of glucose, fructose and sucrose, but rather selected nectar solutions which gave the greatest energy rewards. It was observed, that Gurney's Sugarbirds preferred *P. roupelliae* above other sources which have higher nectar concentrations, but visited several inflorescences during the day to fulfil their energy requirements (Daniels, 1987; De Swardt & Louw, 1994).

Female sugarbirds were found probing for nectar in closed inflorescences by inserting their bills between the floral bracts. The Greater Doublecollared Sunbirds whose culmen lengths are shorter than those of sugarbirds, were also observed foraging in this manner (De Swardt, 1991b & 1992a). Paton & Collins (1989) proposed that sex-related differences in feeding occur in nectarivore species because of the longer culmens of the males. In general, birds with longer bills were found to be more effective than shorter-billed species in reaching nectar from the base of the flowers, but these interspecific differences are also due to variations in tongue dimensions and body mass (Paton & Collins, 1989). Sex-related differences, in bill lengths, in nectarivores result in females often being forced to utilise the poorer and scattered nectar sources because of their smaller size, while the longer bills of the males are better adapted to probe deeper into the inflorescences (Paton & Collins, 1989). In sugarbirds, male culmen lengths were generally longer than those of the females and thus the males possibly utilised the inflorescences with more ease than the females did (which probe on the side of the flower). This behaviour pattern is also suggested for Gurney's Sugarbirds (De Swardt, 1992a; Seiler & Rebelo, 1987).

7.3.2. Insect diet and *Protea* insect fauna

Excepting for the general statement that sugarbirds feed on beetles, small flying insects and spiders (Maclean, 1993; Skead, 1967), not much detail is known concerning the insect diet of this group. Mostert *et al.* (1980) investigated the food requirements and insect diet of the Cape Sugarbird and found that, during their study, it was predominantly beetles (Coleoptera), bees (Apidae) and flies (Diptera) which were recorded from the stomach contents. Little is known about the insect diet of Gurney's Sugarbird and there is no reference to specific taxa

(Maclean, 1993; Skead, 1967). Three insect orders predominated in the stomach samples of Gurney's Sugarbird, namely Coleoptera (Apionidae, Chrysomelidae and Scarabaeidae), Hemiptera and Hymenoptera which were also present in the flowers of *P. roupelliae* (see Tables 11 & 12). The sizes of the Coleoptera species recorded in sugarbirds stomachs were mainly between 5 mm and 15 mm. The beetle, *Cyrtothyrea testaceoguttata* (11 mm) (Cetoniinae), which forages on the pollen of *P. roupelliae* inflorescences and occurs in large numbers during the flowering period (Holm & Marais, 1992), was also recorded in the diet of Gurney's Sugarbird. Based on these findings it appears that the sugarbirds forage selectively on certain insect species associated with *P. roupelliae* inflorescences. Gess (1968) classifies *Tanaos* spp. (Apionidae) as being permanent residents in proteas, feeding on the involucral bracts of the inflorescences while their larvae bore themselves into the bases of the flowerheads. During this study, *Tanaos sanguineus* (8 mm) was collected in 13 inflorescences (31,7%: n = 41) and in the stomachs of Gurney's Sugarbirds. In *P. repens*, Coleoptera beetles of the families Halticidae (six species), Nitidulidae (eight species) and Staphylinidae (two species) were abundant and these small beetles are the main pollinators of the inflorescences (Coetzee & Giliomee, 1985).

The sugarbirds seemed to avoid the smaller beetles, such as the Rhizophagidae (2 mm) and Staphylinidae (2 mm), which occurred abundantly in *P. roupelliae*. It is expected that it should be easier for sugarbirds, with a bill morphology best suited for nectar feeding (Paton & Collins, 1989), to catch smaller beetles, but in terms of time and energy budgets it may be more efficient to capture larger prey. In Cape Sugarbirds, Chrysomelidae (5 mm) and Staphylinidae (2 mm) were recorded as being the major food items in stomach contents and it is considered that the shape of the birds' bill and tongue structure facilitate the capture of these smaller beetle species - they have also longer bills than Gurney's Sugarbirds (De Swardt, 1992a; Mostert *et al.*, 1980; see Chapter 5). Sugarbirds spend most of their time in *Protea* bushes during the middle of the day, resting and preening themselves while perching on a branch or a flower head (pers. obs.). During this period passing insects, such as beetles and small flying insects (3-5 mm) belonging to the Hemiptera and Hymenoptera insect groups, are mostly hawked in the air. Members of one family, the Scoliidae, were recorded in the inflorescences of *P. roupelliae* during January 1997 and it is possible that sugarbirds hawk them when the insects fly out of the proteas. Hawking of small insects is an alternative means of obtaining protein when small insects cannot be obtained from inside the *Protea* flower heads (Recher & Abbott, 1970; pers. obs.). The Australian honeyeaters (Family: Meliphagidae) forage on both insects and nectar and most insects, which are readily utilisable sources of energy and proteins (Ford & Paton, 1976; Recher & Abbott, 1970), are caught by hawking. New Holland Honeyeaters *Phylidonyris novaehollandiae* forage mostly on nectar and manna for energy and hawk small flying insects to satisfy their energy requirements (Paton, 1982c). These small insects were found to be insufficient to meet their daily energy requirements and they therefore have to spend more time collecting protein from nectar (Paton, 1982c). Other honeyeater species such as *Antochaera chrysoptera,* which have similar diets to the New Holland Honeyeater, catch fewer but larger insects and are are more dependant on insects than on nectar (Pyke, 1980). Both African sugarbird species visit several *Protea* inflorescences during the day to forage on the nectar and remove satellite insects from the inflorescences to fulfil their energy requirements (De Swardt & Louw, 1994; Mostert *et al.*, 1980).

The results on the diet of Gurney's Sugarbirds presented in this chapter, and those of Mostert *et al.* (1980), show that the insect portion of the birds' diet consists mainly of beetles (Coleoptera) which occur in large numbers in *Protea* inflorescences. The sugarbirds and the beetles are both considered to contribute substantially to the pollination of *Protea* species (Collins & Rebelo, 1987; Rebelo, 1987; Wright, 1994; Wright, Visser, Coetzee & Giliomee, 1991). *Cyrtotyrea testaceoguttata* (Coleoptera: Scarabaeidae) usually feed on the pollen of *Protea* spp. and therefore plays an important role in the pollination of this *Protea* species (Holm & Marais, 1992). High numbers of arthropods were recorded as being food sources during the breeding season of Gurney's Sugarbird in the KwaZulu-Natal Drakensberg to their diet (Daniels, 1987). The sugarbirds also spend most of their time searching for flying arthropods, which possibly explains the presence of small bugs in their stomachs.

Ants (Hymenoptera: Formicidae) of the genus *Crematogaster* and a few Formicidae fragments were also recorded, in the stomach contents of Gurney's Sugarbirds. In general, ants do not seem to be a main part of their insect diet, although they occur in large numbers in *P. roupelliae* inflorescences. Coetzee & Giliomee (1985) recorded eight ant species in the inflorescences of *P. repens,* the Argentine Ant was the most abundant while the genera *Camponotus* and *Myrmicaria* were also present. The pollination role of ants are unknown and they are regarded as nectar thieves and for acting more as seed dispersal agents, which studied in the Fynbos biome (Bond & Slingsby, 1983; Coetzee & Giliomee, 1985; Whitehead *et al.*, 1987). During this study five *Camponotus* species and *Myrmicaria faurei* were collected from *P. roupelliae* inflorescences (see Table 12), but were absent from the stomachs of Gurney's Sugarbirds and are avoided because of their unpalatability (S. Louw; pers. comm.). Only in one stomach, specimens of *Crematogaster* spp. were present, although collected from a *P. roupelliae* inflorescence at a different locality. Therefore, it is possible that the sugarbirds forage on certain ants which occur in *Protea* inflorescences. The distribution pattern of *Camponotus brevisetosus* is interesting and it was observed that this ant genera was mainly limited to the eastern parts of the grassland biome, and probably overlap with the distribution of *P. roupelliae* - it is also suggested that they feed on *Protea* nectar and, possibly, flower-inhabiting insects (Staphylinidae) (Robertson & Zachariades, 1997; Rutherford & Westfall, 1986). *Myrmicaria faurei* collected from the Lydenburg area was previously only known from its type locality at Mariepskop, Northern Province (H.G. Robertson; pers. comm.).

8. MOVEMENTS AND SURVIVAL BASED ON MARK-RECAPTURE DATA

8.1. INTRODUCTION

Studies on nectarivore movements are well covered, particularly for the honeyeater (Meliphagidae) and hummingbird (Trochilidae) families. These birds are known to utilise alternative areas after the flowering periods of certain plant species when some of the birds are on their annual migration (Calder & Jones, 1989; Keast, 1968; Pyke, Recher & O'Connor, 1989; Wolf, 1970). In southern Africa, nectarivore studies have mainly concentrated on the fynbos areas of the South-western and Eastern Cape Provinces for the Cape Sugarbirds and for several sunbird species, where these species respond to the flowering seasons of plant species (mostly Proteaceae), and are known to travel considerable distances (Craig & Hulley, 1994; Fraser, McMahon, Underhill, Underhill & Rebelo, 1989; Maclean, 1993). Recently, sunbird movements have also been investigated in the Free State and in Mpumalanga, which, in the main, happened to coincide with this study (De Swardt, 1995; De Swardt & Schoeman, 1997).

Skead (1963 & 1967) reviewed the movements of Gurney's Sugarbirds in southern Africa, which were expected to be after the flowering phenology of *Protea* species where a migration to the KwaZulu-Natal midlands during winter was observed. Skead (1963) specifically inferred that if sugarbird migration is dependent on the flowering of proteas, evidence is needed to support these observations and that a study to unravel their movements is needed. De Swardt (1982) observed a seasonal influx of sugarbirds to the suburban areas of Lydenburg, during the early 1980's which was at the start of a detailed study on their seasonal movements. It appears that the birds left their mountain habitat after the peak flowering period of *Protea roupelliae* and that the subsequent scarcity of nectar obliged them to seek food elsewhere (De Swardt, 1989 & 1991a). The aim of this chapter is to synthesise the movements of Gurney's Sugarbirds and to discuss probable reasons for their movements.

Apart from seasonal movement data that were obtained during the 12 year study period (De Swardt, 1990a & 1991a), significant information on sugarbird survival was also collected. Mark-recapture data can be used to detect survival rates and population size (Clobert *et al.*, 1987; Clobert & Lebreton, 1991). Until recently there have been few attempts to estimate survival rates of African birds from ringing data. Rowan (1964) first used life table methods to estimate adult survival and life expectancy for three ploceids in South Africa, and Oatley (1982) and Hanmer (1984a) used similar methods for Starred Robins *Pogonocichla stellata* and three bulbul species respectively. More recently, Yom-Tov, McCleery & Oatley (1994) used last recapture dates to deduce survival times of 11 southern African passerines but their methods are likely to have underestimated true survival. Robust methods for estimating survival rates from mark-recapture data were first developed during the 1960s (Jolly, 1965; Seber, 1965) and these have recently been extended and incorporated into powerful and flexible computer software packages (Clobert *et al.*, 1987; Lebreton *et al.*, 1992). During this study significant mark-recapture data of Gurney's Sugarbirds were obtained and the Jolly-Seber type method used to estimate survival based on the SURGE mark-recapture model (Lebreton *et al.*, 1992). It is the first time that such a detailed investigation on the movements and survival on this species has been undertaken, as the mark-recapture study was initiated during December 1986 and observations on movements dating back to 1980.

8.2. RESULTS

During the period December 1986 - June 1998, 239 males (43,2%), 193 females (35,0%) and 121 unsexed (21,8%) Gurney's Sugarbirds were captured at study sites in the Lydenburg area. In the corresponding period, a total of 93 individuals yielded 120 recaptures. As shown in Figure 30 the monthly captures and recaptures varied considerably.

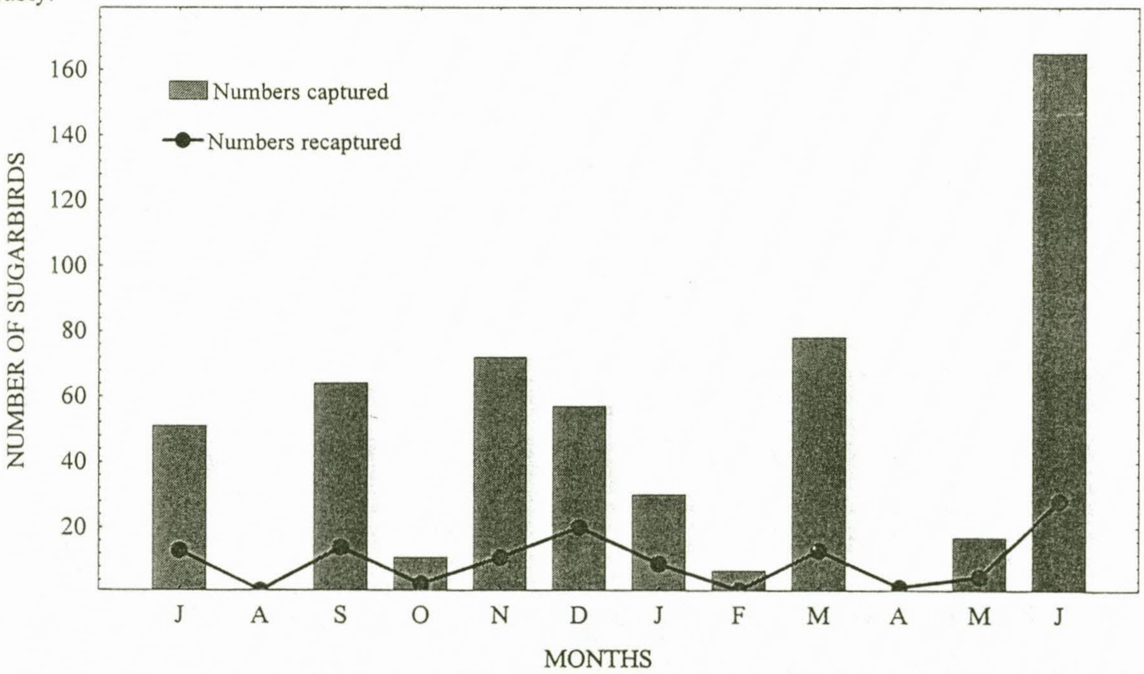


FIGURE 30: Monthly variation in the number of Gurney's Sugarbirds captured and recaptured at the Lydenburg study sites during the period December 1986 - June 1998.

8.2.1. Patterns of movement

Sugarbird recaptures consisted mostly of individuals showing fidelity to *Protea* clump sites, localised (intra-population) movements between *Protea* clumps, seasonal movements between mountainous and suburban areas, and individuals recaptured at wintering sites during different, or even the same, seasons in suburban areas (Fig. 31). Some individuals were recorded to be in more than one of these categories. A recapture rate of 16,8% was recorded.

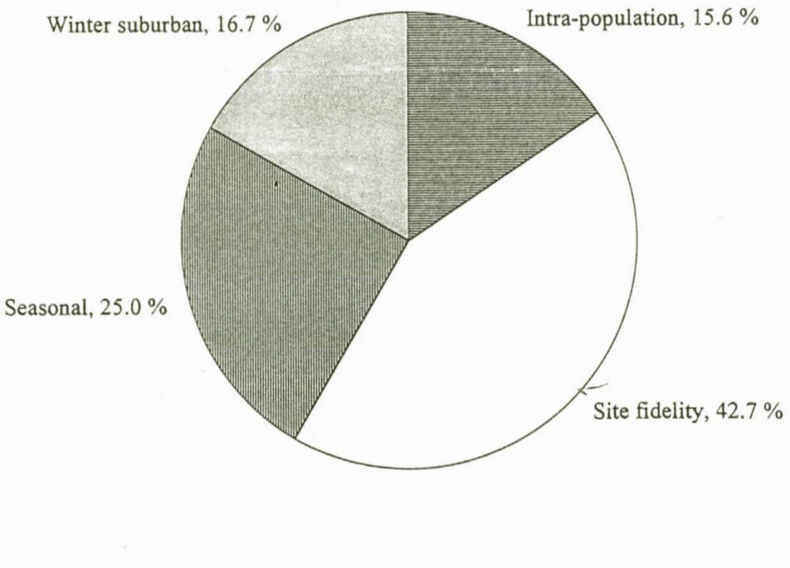


FIGURE 31: Pie-chart of Gurney's Sugarbird mark-recapture data showing proportions of fidelity and movement data.

8.2.1.1. Site fidelity

A total of 41 sugarbirds, 30 males, seven females and four unsexed individuals, were recaptured at the same *Protea* clump sites where they were originally ringed (Table 13). Of these, 15 individuals were captured and recaptured both during the summer and winter seasons, suggesting that they are territorial throughout the year at these sites. Some local movements do take place as other individuals were observed moving between *Protea* clumps or were recaptured in suburban areas, but were later recaptured at sites where they were originally ringed. A male (ring no. 4-38954), ringed at Sterkspruit (site L), moved to a suburban habitat (recaptured at site C) and was twice recaptured at the ringing site in the mountains the following summer. Two other individuals were captured in suburban areas and were later recaptured, more than once, at the same sites in the mountainous habitats (see Table 13).

8.2.1.2. Local movements

Local movements were recorded for 15 (2,7%) sugarbirds which dispersed to adjacent *Protea* clumps in the same valley (Table 14). Of this total ten were males, four females and one unsexed individual - five males and one female were ringed as unsexed individuals. Apparently sub-adults undertake such movements to seek out new breeding territories (natal dispersal). Sub-adults were later recaptured as adult individuals, one ringed (ring no. 4-62157) at Sterkspruit (site L) on 19 September 1989 was recaptured on 2 December 1989 at Paardeplaats (site O). This individual, with a brood patch in evidence, was again recaptured on 2 December 1990, breeding at the same site (De Swardt, 1993b). In another two sugarbirds, natal dispersal was observed after they had been recaptured 74 and 88 months later in *Protea* clumps other than those where they had originally been captured as unsexed sugarbirds. These two individuals (ring no's. 4-62179 and 4-64929) were recaptured as adult males 1,5 and 2,5 km away from their natal areas (see Table 14).

TABLE 13: Details of Gurney's Sugarbirds ringed and recaptured at specific sites in mountainous localities during the period December 1986 – July 1997. Asterisk indicates individuals later recaptured in suburban areas.

Ring number	Sex	Mountain localities	Ringing date	Recapture date	Months elapsed
4-38905	Male	Paardeplaats (O)	87-02-28	87-06-14	4
4-38907	Male	Sterkspruit (J)	87-03-01	88-01-10	10
4-38912	Male	Sterkspruit (I)	87-03-01	89-11-29	33
4-38913	Female	Sterkspruit (I)	87-03-01	89-03-25	25
4-38929	Female	Paardeplaats (O)	87-09-05	89-03-22	19
4-38941	Male	Paardeplaats (O)	87-11-28	89-06-28	19
4-38949*	Male	Sterkspruit (L)	88-01-09	90-03-11	27
4-38951	Male	Sterkspruit (L)	88-01-09	89-12-19	24
4-38954*	Male	Sterkspruit (L)	88-01-09	90-03-11	27
4-38957	Female	Paardeplaats (N)	88-03-26	91-10-04	43
4-38960*	Male	Sterkspruit (L)	89-09-18	89-12-19	3
4-38979	Male	Paardeplaats (N)	89-03-22	90-12-08	21
4-38982	Male	Waterval (U)	89-03-23	89-09-20	6
4-38983	Male	Waterval (U)	89-03-23	89-09-20	6
4-38991	Unsexed	Waterval (U)	89-03-24	89-09-21	6
4-38996	Male	Waterval (U)	89-03-24	89-09-20	6
4-62121	Male	Paardeplaats (O)	89-06-28	89-11-25	5
4-62123	Male	Paardeplaats (O)	89-09-16	92-06-11	33
4-62133	Male	Paardeplaats (N)	89-09-16	90-07-14	10
4-62138	Female	Sterkspruit (L)	89-09-18	90-03-11	6
4-62144	Male	Sterkspruit (L)	89-09-18	89-11-30	3
4-62148	Male	Sterkspruit (L)	89-09-18	90-03-11	5
4-62165	Male	Gustav Klingbiel (S)	89-09-22	92-11-20	38
4-62169	Male	Gustav Klingbiel (S)	89-09-22	90-12-03	15
4-64174	Male	Paardeplaats (O)	89-11-25	89-12-28	1
4-62175	Unsexed	Paardeplaats (O)	89-11-25	90-03-14	4
4-62176	Unsexed	Paardeplaats (O)	89-11-25	89-12-18	1
4-62190	Female	Sterkspruit (L)	89-11-30	90-03-11	3
4-64969	Male	Paardeplaats (N)	90-07-10	90-12-08	5
4-64975	Male	Nooitgedacht (Q)	90-07-10	90-12-04	5
4-64978	Male	Nooitgedacht (Q)	90-07-11	91-12-23	8
4A00028	Male	Paardeplaats (N)	91-10-04	96-06-05	55
4A00036	Male	Paardeplaats (N)	91-12-29	92-11-26	12

TABLE 13 (continued)

4A00055	Male	Paardeplaats (N)	92-06-11	92-11-22	6
4A00058	Male	Paardeplaats (N)	92-06-11	92-12-30	7
4A00079	Male	Gustav Klingbiel (S)	92-11-20	92-12-29	1
CC05344	Unsexed	Paardeplaats (O)	95-12-22	97-06-19	18
CC05349	Male	Paardeplaats (N)	95-12-22	96-06-06	6
CC05476	Female	Paardeplaats (N)	96-06-05	97-01-21	8
CC05477	Female	Paardeplaats (N)	96-06-05	97-01-22	8
CC05494	Male	Paardeplaats (N)	96-12-30	97-01-22	1
				Mean (n=41)	13,2

TABLE 14: Details of intra-population movements of Gurney's Sugarbirds at mountainous localities in the Lydenburg study area during the period December 1986 – June 1997. a, ringed as a sub-adult but recaptured as a breeding female; b, natal dispersal (recaptured as an adult male at a different site); c, post fire dispersal.

Ring number	Ringing location	Ringing date	Recapture location	Recapture date	Time elapsed	Distance moved
4-38938	Sterkspruit (I)	87-09-06	Sterkspruit (L)	88-01-09	5	1,8
4-38940	Sterkspruit (M)	87-09-06	Sterkspruit (I)	89-11-29	27	0,7
4-38944	Paardeplaats (O)	87-11-28	Paardeplaats (N)	89-09-16	22	0,5
4-62119	Paardeplaats (O)	89-06-28	Paardeplaats (N)	91-10-04	28	0,5
4-62157[a]	Sterkspruit (L)	89-09-19	Paardeplaats (O)	90-12-01	14	2,5
4-62179[b]	Paardeplaats (O)	89-11-26	Paardeplaats (N)	96-01-11	74	1,5
4-62183	Sterkspruit (I)	89-11-29	Sterkspruit (J)	90-03-12	3	0,7
4-62184	Sterkspruit (I)	89-11-29	Sterkspruit (K)	90-12-06	12	1,5
4-64902	Paardeplaats (0)	89-12-28	Paardeplaats (N)	90-07-09	7	0,5
4-64929[b]	Gustav Klingbiel (S)	90-03-11	Paardeplaats (O)	97-06-21	88	2,5
4-64984[c]	Nooitgedacht (Q)	90-07-11	Paardeplaats (P)	92-11-25	29	1,5
4A00002	Paardeplaats (O)	90-07-14	Paardeplaats (N)	93-01-04	30	0,5
4A00033	Paardeplaats (O)	91-12-29	Gustav Klingbiel (S)	92-07-01	6	2,3
4A00063	Paardeplaats (O)	92-06-13	Paardeplaats (N)	95-12-22	43	0,5
CC05493	Paardeplaats (O)	96-12-30	Paardeplaats (N)	97-01-21	1	0,5
				Mean (n=15)	26	1,2

8.2.1.3. Seasonal movements between mountainous and suburban areas

Sugarbirds normally begin their altitudinal migration from mountainous to suburban habitats between March and April. The earliest observation dates were on 26 March 1991 and 29 March 1993 (Table 15) when individuals were captured and ringed in the suburban areas. In practice the timing in seasonal occurrence varied considerably, and, in some years, the birds were only been observed for the first time during late May or early June. The peak time of occurrence is during late May to July, usually coinciding with the flowering of *Aloe arborescens*. However, not all sugarbirds moved to suburban habitats in winter and several unmarked individuals were sighted at *Protea roupelliae* clumps in which some flowers were available, or were seen seeking *Aloe* nectar at nearby cliffs and visiting *Buddlea salviifolia* and *Halleria lucida* along the roadside vegetation (De Swardt, 1991a).

Seasonal movements between mountainous and suburban habitats were recorded for 24 sugarbirds (4,3%) (Table 16). Most of the individuals were recaptured a season or more later in the same mountainous localities. Twenty of these were ringed in the mountains and recaptured in the town, while the remainder were recaptured at the Gustav Klingbiel Nature Reserve (site S) and Sterkspruit (site L). An overall mean distance of 7,2 km (range 6,0 - 9,3 km) was calculated for the seasonal movements of the birds (Table 16).

Two movement routes (Figs. 32 & 33) are proposed for Gurney's Sugarbirds based on the recapture data obtained during this study. The topography of the mountains with their cliffs and valleys could be a factor giving rise to the different routes. The plateau along the Long Tom Pass divides the Gustav Klingbiel/Potloodspruit and Sterkspruit and study sites into two distinct areas. The Fisheries Institute/Lydenburg Hospital and suburban town localities in the low-lying areas are linked, each by a separate valley, to the corresponding higher-lying mountain localities. A downward migration pattern, from the higher mountainous to the lower suburban areas in winter, is involved. In summer the direction is reversed. A mean distance of 7,3 km ($n = 15$) was recorded for sugarbirds moving between the Gustav Klingbiel/Potloodspruit (including birds from Paardeplaats and Sterkspruit) and town areas, while the distance between the Fisheries Institute/Lydenburg Hospital and Sterkspruit areas was shorter at 6,9 km ($n = 9$). These two distances did not differ sigificantly ($t22 = 0{,}74$; $p > 0{,}05$).

TABLE 15: Seasonal occurrence of Gurney's Sugarbirds in the suburban areas of Lydenburg over a period of 18 years.

Year	First observation	Last observation
1980	8 April	31 August
1981	19 April	10 September
1982	18 April	15 September
1983	±15 April	11 August
1984	±29 April	31 July
1985	11 April	15 August
1986	20 April	14 August
1987	24 May	21 August
1988	10 May	13 August
1989	16 May	30 August
1990	29 April	10 July
1991	26 March	24 August
1992	13 March	7 August
1993	29 March	Date unknown
1994	11 April	8 July
1995	Date unknown	Date unknown
1996	3 June	5 August
1997	12 March	10 July
1998	25 May	28 August

TABLE 16: Details of seasonal movements of Gurney's Sugarbirds between mountainous and suburban habitats at Lydenburg during the period December 1986 – June 1998.

Ring number	Ringing location	Ringing date	Recapture location	Recapture date	Months elapsed	Distance moved
4-38902	Paardeplaats (O)	87-02-28	Town (C)	88-05-31	15	9.3
4-38906	Paardeplaats (O)	87-02-28	Town (B)	87-06-14	4	8.8
4-38911	Sterkspruit (I)	87-03-01	Town (D)	89-06-18	28	6.0
4-38943	Paardeplaats (O)	87-11-28	Town (D)	92-04-27	53	8.8
4-38947	Sterkspruit (I)	87-11-29	Town (C)	90-07-07	31	6.5
4-38949	Sterkspruit (L)	88-01-09	Fisheries Inst. (G)	92-06-09	54	6.5
4-38952	Sterkspruit (L)	88-01-09	Fisheries Inst. (G)	89-06-21	18	6.5
4-38953	Sterkspruit (L)	88-01-09	Town (C)	89-04-30	16	7.0
4-38954	Sterkspruit (L)	88-01-09	Town (C)	89-07-23	19	7.0
4-38960	Town (C)	88-05-29	Sterkspruit (L)	89-09-18	16	7.0
4-62109	Fisheries Inst. (G)	89-06-21	Sterkspruit (L)	89-09-19	3	6.5
4-62116	Town (B)	89-06-27	Gustav Klingbiel (S)	89-09-23	3	6.8
4-62143	Sterkspruit (L)	89-09-18	Fisheries Inst. (G)	94-07-08	57	6.5
4-62151	Sterkspruit (L)	89-09-18	Fisheries Inst. (G)	94-07-08	57	6.5
4-62152	Sterkspruit (L)	89-09-18	Fisheries Inst. (G)	92-06-09	32	6.5
4-62193	Sterkspruit (L)	89-11-30	Town (B)	92-06-07	30	6.8
4-64952	Potloodspruit (R)	90-03-12	Town (F)	97-06-19	88	6.8
4A00008	Paardeplaats (O)	90-12-02	Fisheries Inst. (G)	92-07-23	8	8.0
4A00018	Sterkspruit (K)	90-12-06	Fisheries Inst. (G)	94-07-08	43	7.0
4A00039	Town (E)	92-06-07	Gustav Klingbiel (S)	92-11-20	6	6.5
4A00068	Gustav Klingbiel (S)	92-11-20	Fisheries Inst. (G)	94-08-21	21	6.7
4A00078	Gustav Klingbiel (S)	92-11-20	Town (C)	94-05-23	18	7.0
CC05304	Sterkspruit (K)	92-11-23	Hospital (A)	93-06-07	7	8.7
CC05460	Gustav Klingbiel (S)	96-01-10	Hospital (A)	98-06-22	30	8.5
				Mean (n=24)	27,4	7,2

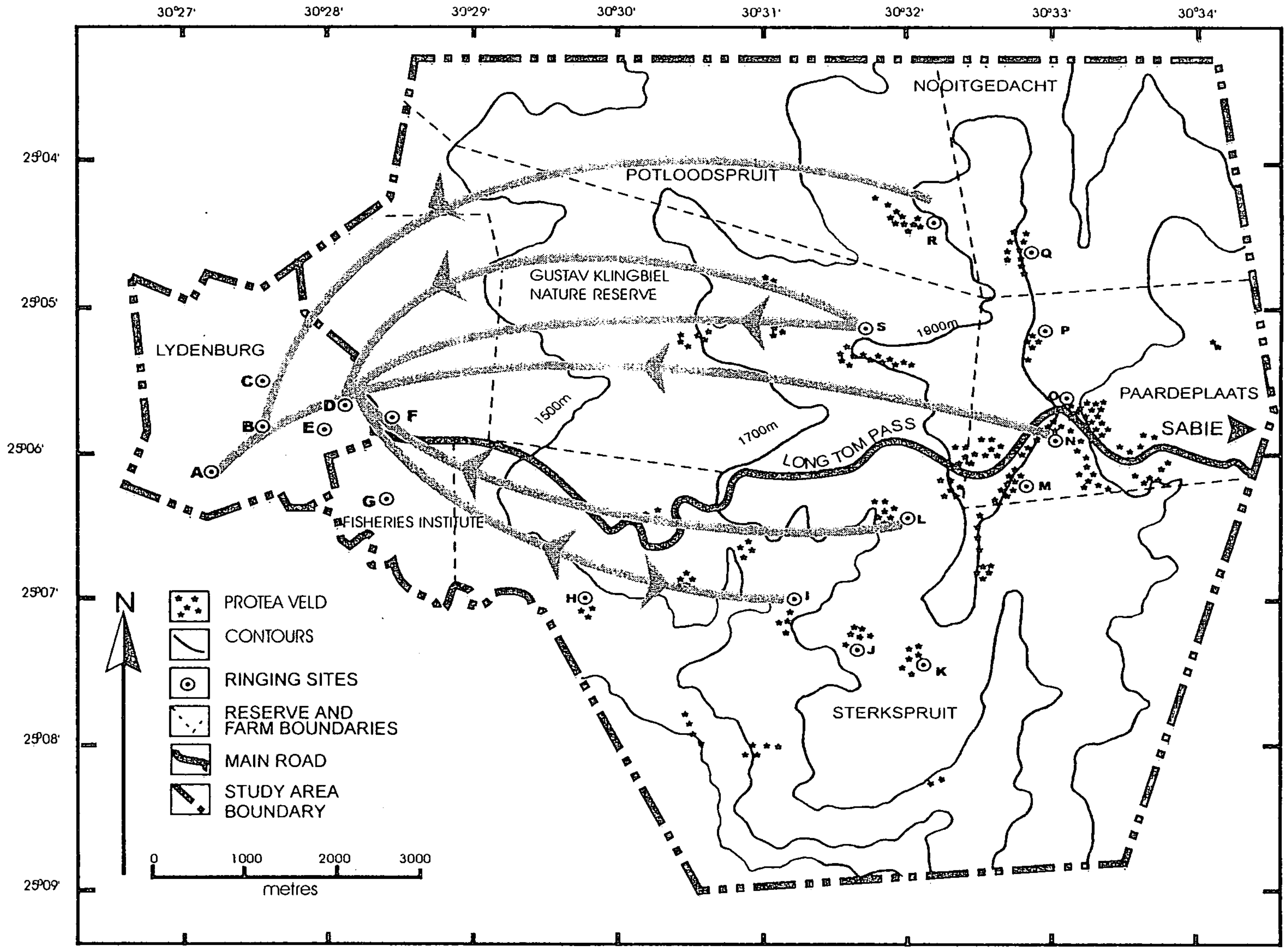


FIGURE 32: Seasonal movement routes of Gurney's Sugarbirds between the Gustav Klingbiel/Potloodspruit and the Lydenburg town localities.

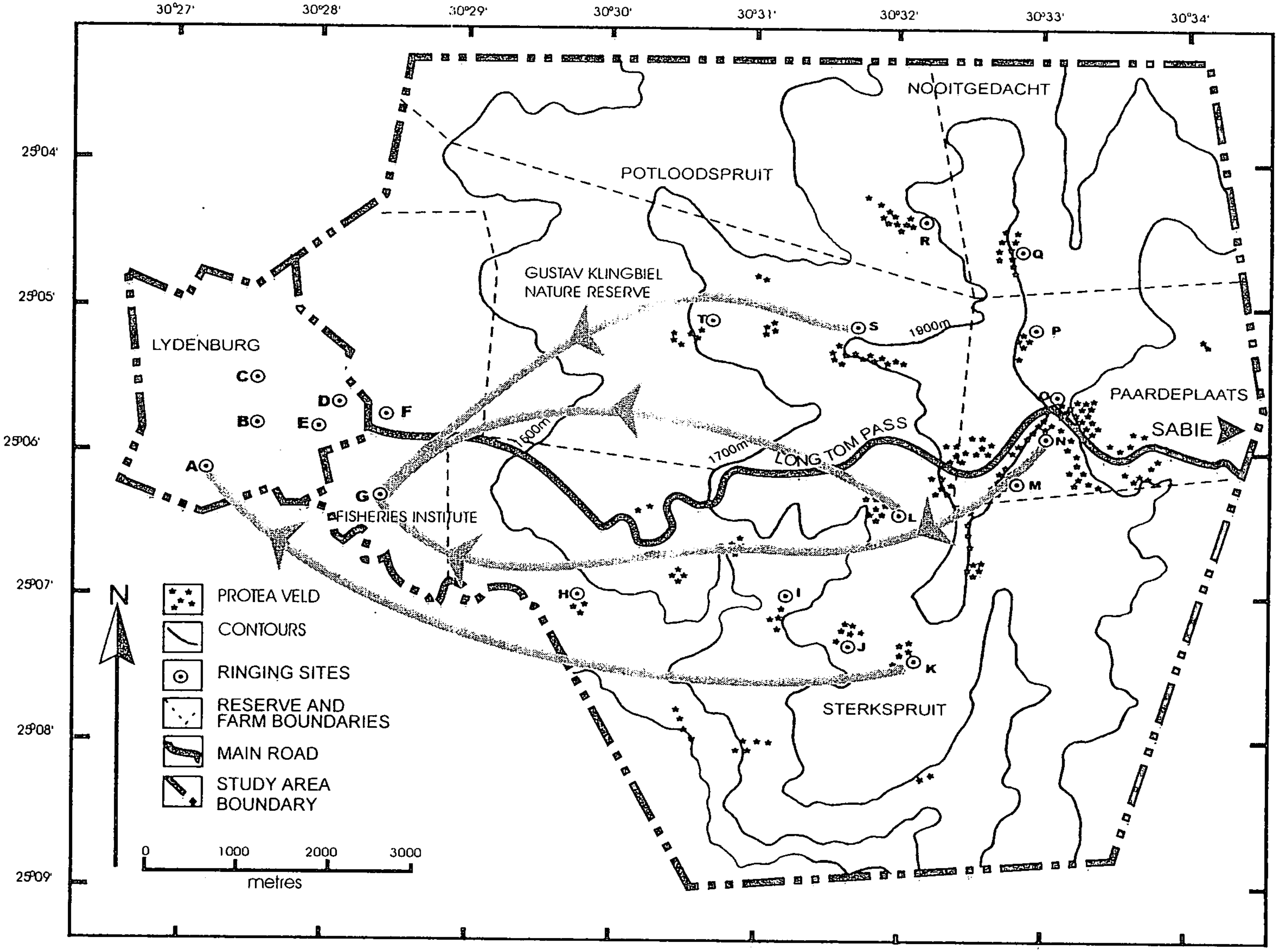


FIGURE 33: Seasonal movement routes of Gurney's Sugarbirds between the Fisheries Institute/Lydenburg Hospital and the Sterkspruit localities.

Of the 553 sugarbirds captured, only 119 (21,5%) were ringed in suburban habitats. Sixteen (13,5%) of these were recaptured during the same, or successive seasons, at the same localities or very close to them (Table 17). Several sugarbirds ringed in a town locality were later recaptured at the Fisheries Institute (site G) or at the Lydenburg Hospital (site A). One male (ring no. 4-38925), for instance, was ringed in a town park (site B) and recaptured two seasons later at the Fisheries Institute (site G), while another (ring no. 4A00049) was recaptured 60 months later at the Fisheries Institute (site G) after being ringed at the Lydenburg Hospital (site A) (Table 17).

TABLE 17: Details of Gurney's Sugarbirds ringed and recaptured during winter at suburban localities of Lydenburg during the period December 1986 – June 1998. Asterisk indicates an individual previously recaptured at the Hospital (site A).

Ring number	Ringing location	Ringing date	Recapture location	Recapture date	Months elapsed	Distance moved
4-38921	Town (C)	87-06-28	Town (C)	88-03-27	9	0
4-38925	Town (B)	87-06-28	Fisheries Inst. (G)	89-06-20	24	1,2
4-38963	Town (C)	88-05-29	Town (D)	89-06-17	13	0,5
4-38965	Fisheries Inst. (G)	88-05-30	Town (B)	89-06-19	13	1,2
4-38967	Fisheries Inst. (G)	88-05-30	Fisheries Inst. (G)	89-06-21	13	0
4-62108	Fisheries Inst. (G)	89-06-20	Fisheries Inst. (G)	94-05-28	59	0
4-62111	Fisheries Inst. (G)	89-06-21	Fisheries Inst. (G)	92-06-16	37	0
4A00047*	Fisheries Inst. (G)	92-06-09	Fisheries Inst. (G)	94-07-08	25	0
4A00049	Hospital (A)	92-06-10	Fisheries Inst. (G)	97-06-03	60	2
4A00051	Hospital (A)	92-06-10	Town (D)	92-06-26	1	1,9
CC05314	Hospital (A)	93-06-07	Hospital (A)	94-05-28	12	0
CC05321	Fisheries Inst. (G)	93-06-08	Fisheries Inst. (G)	94-07-08	13	0
CC05322	Fisheries Inst. (G)	93-06-08	Fisheries Inst. (G)	94-07-08	13	0
4-98402	Town (C)	93-03-29	Fisheries Inst. (G)	93-06-08	2	0
4-80667	Fisheries Inst. (G)	94-05-27	Town (C)	94-06-22	1	0
4-80693	Fisheries Inst. (G)	94-06-16	Fisheries Inst. (G)	98-06-19	48	0
				Mean (n=16)	21,4	0,4

8.2.2. Reasons for seasonal movements

8.2.2.1. Movements after the flowering period of Protea roupelliae

As the sugarbirds were observed leaving the mountainous areas at the end of the flowering period of *P. roupelliae*, the flowering phenology of this protea was determined. A flowering peak during the period November – January was recorded at Paardeplaats from December 1986 to August 1990 (Fig. 34). Closed inflorescences were abundant buring November and December, coinciding with the early breeding season of sugarbirds (De Swardt & Bothma, 1992). Fully opened inflorescences occurred a little later (December and January) and probably provided the birds with sufficient nectar during the later stages of breeding when large numbers of nestlings are present. During seasons with high rainfall months, the flowering season of *P. roupelliae* is, apparently, extended later into the winter, but this varied between *Protea* clumps (De Swardt, 1993b).

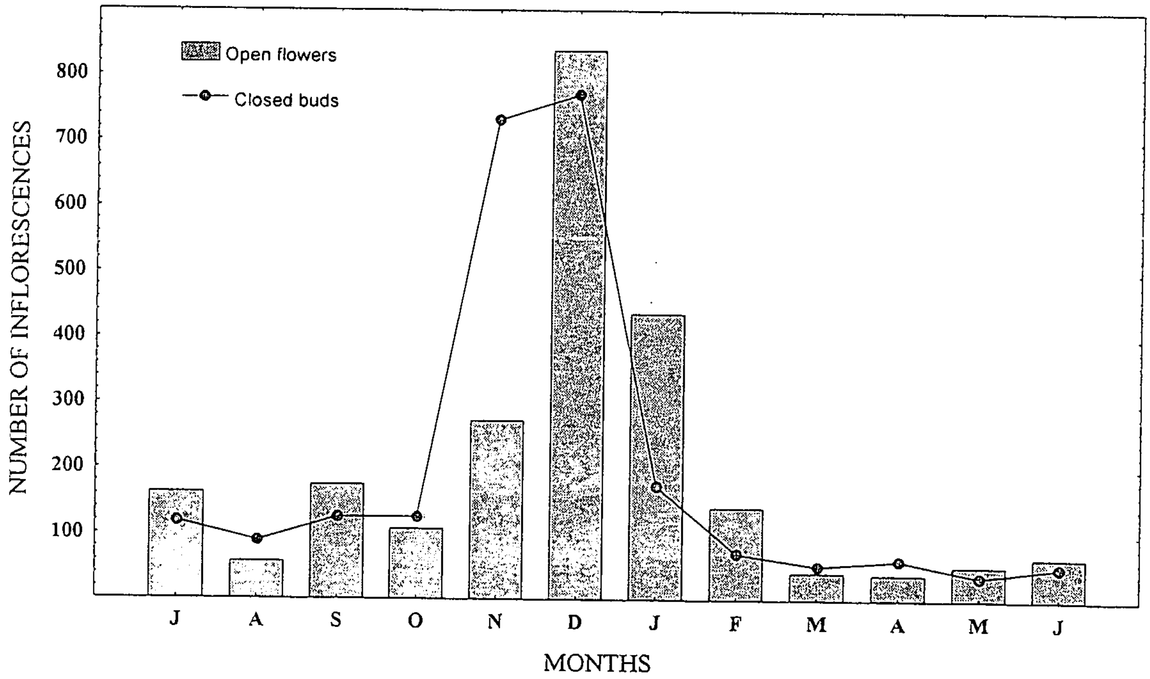


FIGURE 34: Monthly availability of *Protea roupelliae* inflorescences at Paardeplaats (sites N & O), Lydenburg, during the period December 1986 – August 1990.

8.2.2.2. Sugarbird responses after fires in Protea *woodland*

Adult sugarbirds were found to disperse after their *P. roupelliae* breeding territories were destroyed by veld fires. An individual (ring no. 4-64984) ringed at Nooitgedacht (site Q) on 11 July 1990 was, for example, recaptured at a *Protea* clump higher up in the same valley (Paardeplaats, site P) after the occurrence of a fire in late July (De Swardt, 1993b). Subsequent visits to the burnt site (in December 1990 and October 1991) were characterised by the absence of sugarbirds and the presence of only a few flowers on those protea bushes which were not completely destroyed by the fire. Similarly, sugarbirds ringed at Sterkspruit (site L) during January 1988 and in September and November 1989 were recaptured during June 1992, in suburban Lydenburg, after a fire occurred at the original ringing site in October 1991. During December 1992, unringed sugarbirds were also observed in *P. caffra* woodland near Sterkspruit (site L). These individuals probably came from a burnt site lower down in the valley. Considerable movement has also been recorded between other sites at Sterkspruit (sites I, J and L), possibly as a result of fires during 1988 (see Table 14).

8.2.2.3. Seasonal rainfall as climatic factor.

Although sugarbirds were found to move away from *Protea* clumps, after the peak flowering period of *P. roupelliae* (see De Swardt, 1991a and previous section), rainfall is also suggested as being a reason for these movements. High rainfall seasons secured a prolonged *Protea* flowering period into the winter months, while in years of lower rainfall, fewer flowers are available and the sugarbirds were observed dispersing more widely. Whenever the annual rainfall in the Long Tom Pass dropped below average, or during a severe drought (*e.g.* 1991/92 – see Fig. 2), there was a greater influx of sugarbirds to the suburban areas of Lydenburg. No significant correlation could, however, be demonstrated between the number of sugarbirds observed and captured in the suburban areas during winter and the ammount of rainfall in the Long Tom Pass during the previous season (September – March) (Table 18; $r = 0,153$; $p > 0,05$; $df = 12$). Neverthless, the scarcity of sugarbirds in the suburban areas during winters, following wet years (1995 – 1997), is in contrast with the high influx of birds during the relatively dry years of 1985/86, 1986/87 and 1988/89 (see Fig. 2). A similar phenomenon was observed for the 1997/98 season (dry cycle) when 16 sugarbirds were captured and several unringed individuals observed.

TABLE 18: Relationship between number of Gurney's Sugarbirds observed, captured and/or recaptured in the suburban areas during winter and rainfall during previous seasons (September – March) on the Long Tom pass (LTP) between the 1985/86 – 1997/98 seasons.

Seasons	Rainfall at LTP	Number of sugarbirds
1985/86	679,9	20
1986/87	726,0	33
1987/88	753,0	35
1988/89	604,0	48
1989/90	748,0	29
1990/91	969,0	52
1991/92	474,0	37
1992/93	852,0	28
1993/94	698,1	18
1994/95	723,5	2
1995/96	945,4	7
1996/97	1078,0	9
1997/98	588,3	24

Although individual sugarbirds were present in the mountains during the winter months, they were fewer in number than during the summer months. During the 1995/96 and 1996/97 season the annual rainfall in the Long Tom Pass exceeded 1 000 mm (see Fig. 2) with the result that the flowering period of *P. roupelliae* was probably prolonged into the season with more inflorescences available. In June 1996 and 1997 several were actually captured at Paardeplaats (site O) with *Aloe* pollen on the feathers of their foreheads and chins. These individuals probably visited the *Aloe* species lower down the valley, returning to the *Protea* clumps only later during the day. Several sugarbirds were also observed foraging on *A. arborescens* nectar during the late morning and midday of 5 June 1996. The relative absence of sugarbirds in the suburban areas was especially noticeable during this period. Only a few individuals were observed in some gardens between 1995 and 1997 compared to the large numbers which congregated on the different *Aloe* clumps during the winter of 1994. Likewise, an influx of sugarbirds to suburban areas was experienced following the dry season of 1997/98. The absence of *Aloe* pollen on several sugarbirds captured in *P. roupelliae* clumps at Paardeplaats (site O), during this time, suggests that the *A. arborescens* populations in the surroundings were already past their flowering seasons and that this aspext is the probable reason for the birds' dispersal to the suburban areas.

8.2.3. Survival estimates based on mark-recapture data

Survival estimate figures of individual male and female sugarbirds were analysed from recaptures and resightings obtained during the study period (See this chapter - section 8.2.1.). Only the recaptures of more than a year were considered for analysis on the SURGE mark-recapture model; recaptures of movements within ten months were published elsewhere (De Swardt, 1991a; this chapter). The survival analyses was therefore based upon 227 ringed males and 177 ringed females caught during the period December 1986 – June 1998, of which 43 and 13 respectively were retrapped more than one year later (Table 19 and 20). Recapture data indicated that Gurney's Sugarbirds can survive beyond seven years of age, with two individuals being retrapped 88 months, and one 74 months, after initial capture. A further three ringed juveniles (recaptured as adult males) and four adult males were recaptured more than four years later. An average expectation of a further 4,7 years of life was calculated for this species.

TABLE 19: Capture histories of 43 male Gurney's Sugarbirds captured at the Lydenburg study sites during the 1986/87 – 1997/98 seasons.

Year	No	Recapture year										
	Ring	87/88	88/89	89/90	90/91	91/92	92/93	93/94	94/95	95/96	96/97	97/98
1986/87	17	3	3	1	-	-	-	-	-	-	-	-
1987/88	14	-	10	7	3	2	-	-	-	-	-	-
1988/89	19	-	-	3	3	2	1	1	-	-	-	-
1989/90	52	-	-	-	10	7	5	4	4	2	1	-
1990/91	29	-	-	-	-	5	4	1	1	-	-	-
1991/92	21	-	-	-	-	-	5	4	4	3	1	-
1992/93	37	-	-	-	-	-	-	4	2	-	-	-
1993/94	2	-	-	-	-	-	-	-	1	1	1	1
1994/95	3	-	-	-	-	-	-	-	-	-	-	-
1995/96	23	-	-	-	-	-	-	-	-	-	2	1
1996/97	10	-	-	-	-	-	-	-	-	-	-	-

TABLE 20: Capture histories of 13 female Gurney's Sugarbirds captured at the Lydenburg study sites during the 1986/87 – 1997/98 seasons.

Year	No	Recapture year										
	Ring	87/88	88/89	89/90	90/91	91/92	92/93	93/94	94/95	95/96	96/97	97/98
1986/87	11	2	1	-	-	-	-	-	-	-	-	-
1987/88	21	-	6	2	1	1	-	-	-	-	-	-
1988/89	19	-	-	1	1	1	-	-	-	-	-	-
1989/90	49	-	-	-	3	2	1	1	1	1	1	-
1990/91	19	-	-	-	-	-	-	-	-	-	-	-
1991/92	14	-	-	-	-	-	-	-	-	-	-	-
1992/93	21	-	-	-	-	-	-	1	1	-	-	-
1993/94	0	-	-	-	-	-	-	-	-	-	-	-
1994/95	3	-	-	-	-	-	-	-	-	-	-	-
1995/96	16	-	-	-	-	-	-	-	-	-	-	-
1996/97	4	-	-	-	-	-	-	-	-	-	-	-

The survival modelling process is summarised in Table 21. All attempts to simplify recapture probability failed, indicating significant variation in recapture rates, both between years (LRT between models 7 and 8 in Table 21: χ^2 = 46,3; df = 20; p < 0,001) and between the sexes (LRT between models 7 and 9: χ^2 = 27,2; df = 11; p < 0,005). The pattern of temporal variation, in recapture rates, differed between males and females. Survival rate did not differ between years (LRT between models 6 and 7: χ^2 = 7,2; df = 10; p > 0,5) or between the sexes (LRT between models 5 and 7: χ^2 < 0,1; df = 1; p > 0,5), and there was also no evidence that survival during the first year after capture differed from subsequent survival (LRT between models 7 and 11: χ^2 = 1,5; df =1; p > 0,15; Table 21). The model providing the best description of the sugarbird survival, therefore, one in which recapture rates differed between years and between the sexes, and survival was the same in all years for both males and females (model 7). Under this model, annual survival was estimated as 80,7% (se 5,9%; 95% confidence limits 66,6 – 89,7%). Recapture rates varied between 0 - 31% (mean 8,7%) for males and between 0 - 21% (mean 4,3%) for females, and this probably reflects the variable quantities of fieldwork conducted in each year of the study.

TABLE 21: Modelling survival (S) and recapture rates (p) of Gurney's Sugarbirds in terms of sex (s), year (t) and age (a). The age effect separates survival during the year after ringing with that of subsequent years. Also shown are the number of identifiable parameters for each model (np), the relative deviance (provided by program SURGE), and Akaike's Information Criterion (AIC).

Model	np	dev	AIC
Starting model			
1) Ss*t, p s*t	42	485,0	569,0
Attempting to simplify recapture rate			
2) Ss*t, ps	24	514,7	562,7
3) Ss*t, pt	33	495,0	561,0
4) Ss*t, p	23	515,5	561,5
Attempting to simplify survival			
5) Ss, ps*t	24	493,4	541,4
6) St, ps*t	33	486,2	552,2
7) S, ps*t	23	493,4	539,4
Further checks on recapture rate			
8) S, ps	3	539,7	545,7
9) S, pt	12	520,6	544,6
10) S, p	2	550,8	554,8
Checking for the effect of age on survival			
11) Sa, ps*t	24	491,9	539,9

8.3. DISCUSSION

8.3.1. Patterns of movements

Local seasonal movements in birds are usually stimulated by a chance in food availability such as the seasonal flowering of their food plants (Rebelo, 1987; Wolf, 1970). Prior to this study, movements of Gurney's Sugarbirds have been reported in KwaZulu-Natal where they were believed to leave the *Protea* areas their period of flowering, however, most of these observations were speculative with no occurrences being definitely concluded (Skead, 1963 & 1967). Other authors only mentioned that they observed seasonal occurrences of Gurney's Sugarbirds when the birds were observed to be absent from the *Protea* covered hillside habitats (Craib, 1981; Manson, 1985). De Swardt (1989 & 1991a) was the first who attempted to unravel the movements of Gurney's Sugarbird and to observe a regular seasonal movement between two distinct areas, based on results obtained during a mark-recapture study.

These movements were found to be in a 10 km radius in the Lydenburg area, and because *Protea* clumps in their mountainous habitats are widely distributed with supplimentary *Aloe* nectar available during the winter months, no known long distance movements have been recorded (De Swardt, 1993b). Although no recoveries from other areas have been reported, such movements may, neverthless, take place. Sightings obtained during the winter of 1994 at Bosbokrand and in the Kruger National Park (Skukuza and Berg-en-Dal) are indications that long distances are possible (Gouws, 1994; Lawson, 1994). The birds observed at these localities (foraging on aloes) probably originated from the escarpment area, which is nearest to these localities, a movement involving a distance of more than 80 kilometers! In contrast with Cape Sugarbirds, only short movement distances have yet been recorded for Gurney's Sugarbirds in the Lydenburg area (De Swardt, 1991a). The movements of Cape Sugarbirds in the western Cape are well studied, and movements of ringed individuals between Helderberg Nature Reserve, Kirstenbosch, Somerset West and Teeberg (Cape of Good Hope Nature Reserve) have been reported, mainly after the flowering peak of fynbos Proteaceae, and in response to fire or the avoidance of burnt areas (Fraser *et al.*, 1989; Fraser, 1997; Oschadleus & Fraser, 1988). Ringed Cape Sugarbirds were found to move over long distances, up to 160 km has been recorded, some crossing the Cape Flats (Fraser *et al.*, 1989).

Payne (1990) described natal dispersal as the movement between the site of birth and the site of breeding. According to Warkentin & James (1990) natal dispersion involves a permanent movement to a new location, irrespective of whether the birds reproduce after dispersal, and adds that young birds have been forced to disperse farther in response to the movements of adjacent adult males, or to locate potential mates. During this study considerable localised movement was recorded in the population of the Long Tom Pass study area and natal dispersal is suggested as following the description given. Of the 15 sugarbirds which were observed to disperse, six were captured as juveniles and later recaptured as adult individuals, some breeding (see results and Table 14). Site fidelity observed in Gurney's Sugarbirds is unique, probably resulting from the fact that *Protea* clumps form small "islands" of suitable habitat which provide nest sites, food and shelter in an otherwise montane grassland habitat (De Swardt, 1992a).

8.3.2. Reasons for seasonal movements

The main aim of this study was to investigate the seasonal occurrence of Gurney's Sugarbirds between two different areas and to ascertain the reasons for any movements (see De Swardt, 1991a & 1993b). The birds were found to move mainly as a result of changes in the availability of food, after the peak flowering period of *Protea roupelliae*, and after the incidences of fires and the effects which seasonal rainfall (wet and dry seasons) have on the flowering seasons of *P. roupelliae*. Catastrophic changes to the environment, after a veld fire, forced the birds to abandon a site and to congregate at food sources in other sites (Fraser & McMahon, 1992). A similar situation was observed in Cape Sugarbirds where they switched habitat from Mountain Fynbos to Strandveld *Leonotis* after fire (Fraser & McMahon, 1992). Because of such fires, sugarbirds in the Lydenburg area, were observed dispersing away from *Protea* clumps (see De Swardt, 1993b). Fraser & McMahon (1992) also noted that fire-related responses, in Cape Sugarbirds, may be masked by normal seasonal movements, but in Gurney's Sugarbirds, movements were mainly in response to changes in the avialability of food (De Swardt, 1991a). However, some birds were probably forced to move to the suburban areas after fires destroyed the *Protea* clumps where they had been resident (breeding) (De Swardt, 1993a).

Studies on the seasonal effects of rainfall (wet and dry years) on bird populations have been paid scant attention. In Zimbabwe, Gargett, Gargett & Damania (1995) found that variations, in rainfall seasons, affect the breeding populations of Black Eagles *Aquila verreauxi* and during years of high rainfall, increases in resident breeding pairs were observed when prey was abundant. During low rainfall seasons, when food was scarce, decreases in breeding pairs were observed. During the study on Gurney's Sugarbirds, influxes to the suburban areas of Lydenburg were observed after the peak flowering of *P. roupelliae* (De Swardt, 1991a). It was also observed that years of high and low seasonal rainfall have secondary effects on the flowering seasons of *P. roupelliae*. During seasons of high rainfall, the flowering season of the proteas was prolonged into the winter months, while during dry years a shorter flowering season was observed. It was mainly during the early 80's, when low to average rainfall seasons were recorded, that large seasonal influxes were observed in the suburban areas (De Swardt, 1982 & 1990a). Groups of up to ten individuals were observed to be present, in suburban gardens, from early April until late July (De Swardt, 1990a). An explanation for the absence of sugarbirds in suburban areas, during the winters of 1995 to 1997, can mainly be attributed to the high rainfall experienced in the Lydenburg area during the 1994/95 to 1996/97 seasons. Excepting for several localities which were burnt by veld fires, and from which the resident populations dispersed, the flowering seasons of *P. roupelliae* were extended into the winter months and more sugarbirds were observed in the mountains, mainly as a result of high rainfall seasons (De Swardt, 1993b).

8.3.3. Survival estimates based on mark-recapture data

The estimate of annual survival for Gurney's Sugarbird should be regarded as minimum value because the analysis cannot distinguish between mortality and permanent emigration out of the area. The annual survival rate of Gurney's Sugarbirds, reported during this study, were found to be higher compared with some southern African passerine species such as Cape Sparrows *Passer melanurus* (Dean, 1978), ploceid weavers (Hanmer, 1984b; Rowan, 1964) and bulbuls (Hanmer, 1984a), and lower than that for Starred Robins (Oatley, 1982) and some tropical forest birds in Malawi (Dowsett, 1985). The estimate of survival is also much higher than for most passerines from northern temperate regions (Johnston *et al.*, 1997). It is well known that many African and Australian passerines have higher survival rates than their northern hemisphere counterparts (Yom-Tov *et al.*, 1994; Yom-Tov, McCleery & Purchase, 1992). These higher survival rates have been attributed to the less extreme and variable environmental conditions which prevail in the tropics and Australia, in contrast to northern temperate regions where cold winters weather coincides with food shortage, and can cause severe mortality among small passerines (Cawthorne &

Marchant, 1980). Over a 20-year period in England, low survival rates of adult Wrens *Troglodytes troglodytes* averaged only 31%, and mortality rates during three particularly cold winters were probably close to 100% (Peach, Du Feu & McMeekings, 1995). High adult survival rates are often associated with smaller clutch size and this probably reflects life histoty trade-offs between fecundity and survival (Saether, 1988; Linden & Moller, 1989). Factors such as the length of the breeding season, effects of predators and seasonality of food supplies affect clutch sizes. By laying smaller clutches during the breeding season, the changes of nestling survival is ensured as the species don not need to invest large amounts of energy on a single large clutch (Faaborg & Arendt, 1995). This was observed to be similar for Gurney's Sugarbirds and Starred Robins, which also lay smaller clutch sizes (2-3 eggs per clutch), and have high survival rates (De Swardt & Bothma, 1992; Maclean, 1993; Oatley, 1982). An average sugarbird can survive for 5 breeding seasons, so it is more 'profitable' in an evolutionary sense to raise relatively few young per breeding season, thus minimising any cost of repoduction, and therefore maximising the changes of surviving for more breeding seasons.

The higher recapture rates recorded in male (8,7%) versus female (4,3%) sugarbirds are mainly attributed to the more aggressive and territorial behaviour of males, especially during the breeding season (defending feeding and nest sites), which made them easier to trap than the females (see De Swardt & Louw, 1994). The low and variable retrap rates are also as a result of trapping effort, as the latter part of the study (1994 - 1998) was not so intensely conducted as the first few years (1987 - 1993) (De Swardt, 1991a). Although most of the sites were visited during the study to obtain recapture data, only a small percentage of the sexes were recaptured, and of the 434 sugarbirds which were ringed at the mountain localities, only 41 (9,4%) were recaptured at their original capture sites (see 8.2.1.1.). Oatley & Underhill (1993), in developing methods of survival estimates, assumed that individuals in a population can either be recaptured, recovered or (like in this study) never be seen after being ringed and released. In the Lydenburg study area, only a small percentage of the sugarbirds were recaptured during this study, suggesting that the birds move in responses to local conditions such as flower availability, rainfall, periodic fire regimes and their association with a specialised vegetation type (Bredenkamp *et al.*, 1996; De Swardt, 1992a). These absences could also be due to mortality, dispersal, birds moving into new breeding territories in the study population, or the replacement of older sugarbirds that move out of the population (De Swardt, 1993b). Recent recaptures of sugarbirds after periods of 74 and 88 months are examples of recapturing individuals when not expecting to find them again. The high survival rates recorded for Gurney's Sugarbirds is interesting when the environmental conditions in which they must survive, such as fires in *Protea* veld (which destroys breeding areas), low rainfall seasons, flowering periods of nectar food sources and competition for breeding space with other individuals of the same species, are taken in account.

Hanmer (1984a) calculated annual rates of changes in populations rates of Sombre Bulbul *Andropadus importinus* and Terrestrial Bulbul *Phyllastrephus terrertris* and estimated that breeding only takes place when the birds are at least two years old. It is, therefore, possible that sugarbirds only commence breeding during their second to third year of life (De Swardt, 1990c). Recaptures of ringed adult individuals (two males and a female) after more than seven years, and seven after four years, suggests a longevity beyond seven years for this species. Further life expectation (4,7 years) and the longevity of Gurney's Sugarbirds are comparable to the oldest sunbird records in the SAFRING database: Malachite Sunbirds (10 years), Black Sunbirds *N. amethystina* (7,3 years) and Greater Doublecollared Sunbirds (6,2 years) (Oatley & Best, 1997; T. B. Oatley, *in litt*). Malachite and Black Sunbirds were recaptured after five years in the Lydenburg study area, where they were originally ringed as adults (De Swardt & Schoeman, 1997).

9. CONSERVATION AND HABITAT MANAGEMENT

9.1. INTRODUCTION

Gurney's Sugarbirds are endemic to southern African and occur in close association with *Protea* species along their distribution range in the summer rainfall regions along the Drakensberg escarpment (Clancey, 1980; De Swardt, 1993b; Chapter 4). Siegfried (1985) argued that Gurney's Sugarbird deserves a high-priority rating for conservation attention because of their association with *Protea* species and any extinctions of this sugarbird would trigger further extinctions of proteas and other plants. Siegfried (1985) also pointed out that the survival of Gurney's Sugarbird could only be assured by maintaining the ecological functioning of the biotic community of which this sugarbird species is an essential component. Their association are further supported by the recent study of Harrison *et al.*, (1994) which considered this species to be a primary indicator of *Protea* schrub habitats in their distribution range. This relationship can be used in conservation decisions in environmental consultancy and planning.

The recent *Atlas of Southern African Birds* was the first publication to address the conservation status of all bird species that occurring in the sub-region (Harrison, Allan, Underhill, Herrenmans, Tree, Parker & Brown, 1997). As a result of this, the urgency for the conservation and management of bird habitats has been realised, for the first time, and management recommendations provided for some species. Harrison & Martinez (1995) and Harrison *et al.* (1994) analysed this atlas' data which supplies important guidelines for conservation planning for species within a specific biome or habitat. Rebelo & Tansley (1993) were the first to identify priority conservation areas for rare *Protea* species in the south-western Cape, using the geographical distribution of rare species to determine priority areas for conservation attention. Here, I investigate the importance of *Protea roupelliae* woodland habitats for Gurney's Sugarbirds and the conservation importance of this plant species (De Swardt, 1993b).

Currently the main threats for both sugarbird and *Protea* species in the grassland biome is the occurrence of uncontrolled fires (De Swardt, 1993b; Rutherford & Westfall, 1986). Although these fires occur with regular frequency and intensity, little is yet known of their effect on woody species (including *Protea* species) and to what extend repeated burning affects the recovery of these species (Van Wilgen, Everson & Trollope, 1990). Most studies were concentrated on fynbos species and very little is known about summer-rainfall proteas and fire (B. W. Van Wilgen, *in litt.*). The *Protea* species in the Western Cape fynbos are mostly killed by fire and regenerate from canopy-stored seeds and very few resprouts. These fires mostly occurrs mostly in intervals of up to 15 years and are used as a management tool for bird species in their habitat (Le Maitre & Midgley, 1992). The fire regime in grassland areas is between 2-5 year intervals (and most sprout after fire) and were mainly determined by the climate and available fuel and it is mostly these factors which have an effect on *Protea* species (De Swardt, 1993b). In this chapter I provide data that were collected during the past 10 years on the effect of fire on *P. roupelliae* woodland habitats. The effect of different seasons on regeneration of trees in considered. Recommendations for the management of *Protea roupelliae* woodland habitats using firebreaks and blockburns is discussed. I also document the cutting of *Protea* trees for firewood as another possible threat to bird and protea populations.

9.2 RESULTS AND DISCUSSION

9.2.1. Grassland fires in *Protea* veld

The effects of grassland fires in *P. roupelliae* woodland has been observed in the mountainous areas around Lydenburg, Mpumalanga Province. At Lydenburg the effect of fires in the *Protea* populations was monitored when accidental fires occurred near the Dorpsdam (site H; October 1986), at Nooitgedacht (site Q; late July 1990), Sterkspruit (Site L; October 1991) and Gustav Klingbiel Nature Reserve (including sites S & T; August 1996). These are compared to the mountain catchment areas managed by regular block burns in the nearby Makobulaan Plantations and Sterkspruit Nature Reserve. The effects of these fires on the *Protea* trees varied from a mild scorching to severe damage (total crown burn) and bird responses and re-establishment of trees were noted (see Chapter 4 for more detailed descriptions).

Late season burns during dry conditions in October 1986 and 1991 and in August 1996 had negative effects on *P. roupelliae* populations and damage to crowns of bushes were observed. As the grass cover in these areas were mostly long, and the fire chased by strong winds, the fire intensities were very high and the *Protea* trees were severely damaged: 90 – 95% of the trees in the clumps were killed, some trees burning off at the base of their trunks (Figs. 35 & 36). Only a few isolated trees growing in sheltered places amongst rocks and on the periphery of clumps, were not burnt up to their crowns and survived. The lower branches of the bushes were burnt, but flames did not reach the canopies. Site L was revisited to monitor seedling re-establishment and regrouth in December 1993 and December 1995. No crown burned trees resprouted. Re-establishment did occur from seed banks which possibly germinate after the rainfall of the 1995/96 season (Fig. 37).

FIGURE 35: Damage to a *Protea roupelliae* community at Sterkspruit (site L), Lydenburg, during October 1991 when grassland along Long Tom Pass was burnt in an accidental fire. The *Protea* trees experienced a total crown burn and were completely destroyed by the fire.

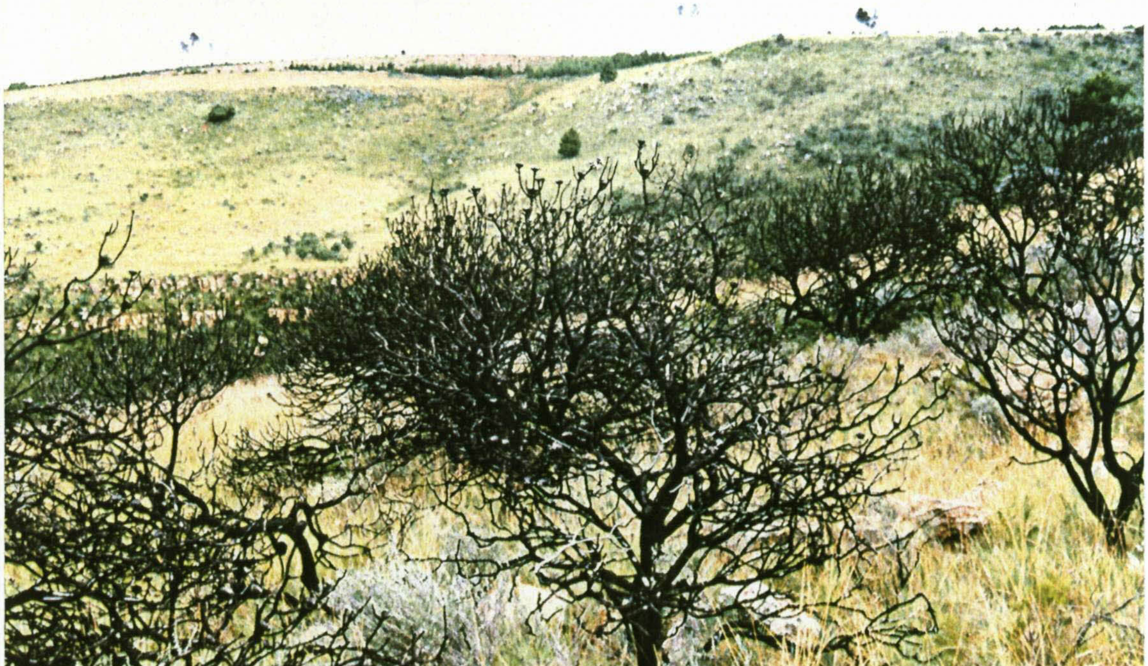


FIGURE 36: A close-up view of a *Protea roupelliae* tree burnt off at its stem in a fire at Sterkspruit (site L), Lydenburg, during October 1991.

FIGURE 37: Germination of *Protea roupelliae* seedling at Sterkspruit (site L), Lydenburg, during December 1995 after the fire of October 1991.

At Makobulaan, block burns were made during autumn (April/May to June) on a three-year rotation basis and at nearby Sterkspruit Nature Reserve, after the first spring rains of August/September. The densities of the *Protea* trees in clumps at Makobulaan were higher than at Sterkspruit Nature Reserve (inter-bush distances larger) as the autumn burns damaged *Protea* trees than the spring burns which experience hot and windy conditions (A. Lindströhm, pers. comm). Firebreaks next to the road on the Long Tom Pass at Paardeplaats (sites N & O) were mainly made during June/July, and these biennial burns have led to the seed-set of several *P. roupelliae* trees which grows in these firebreaks. Near site O several small *Protea* bushes (15+) have germinated from seeds which were dispersed from the tree in the firebreak (pers. obs.). Regular, biennial fires would probably stimulate seed-set of *P. roupelliae* trees in the grassland. At Honingkloof and Qwaqwa Mountain (Qwaqwa National Park) fires were observed after the first spring rains during September 1993 and during June/July 1997. These were mostly mild fires which caused no severe damage to *Protea* trees, and only a few were destroyed. As the grass cover was relatively short, the intensity of the fires was not high - both occurred during a high rainfall period (see Fig. 5; Chapter 2). Re-establishment of *Protea* trees was mainly from unburnt leaf buds of branches which were not burned (Fig. 38). As a consequence, crown fires killed trees.

FIGURE 38: Regrowth of *Protea roupelliae* branches during February 1998 following a fire at Qwaqwa National Park during the winter of 1997. The canopy escaped the fire and regrouth started from the unburned leave buds.

The trunk of *Protea roupelliae* is protected by a thick, corky bark which are a survival strategy of grassland Proteaceae that grow taller than the surrounding grasses (Rourke, 1982). *P. roupelliae* recovers only from leave buds not damaged by the fire. Damage to *Protea* trees varied from severe, where large sections of the population were destroyed by the fire, to mild scorching. The Lydenburg fire (site L; October 1991) was followed by a very dry period (see Fig. 2; Chapter 2). It must be noted that *Protea* species of the fynbos biome regenerate from canopy-stored seeds and will establish from its soil stored seeds sometime after the fire, which differs from the Drakensberg *Protea* species, which are little understood (Le Maitre & Midgley, 1992).

Fires are a regular occurrence in grassland areas and are mostly caused by natural causes such as lightning, but mostly deliberately or accidental by human interference - large areas of *Protea* veld have been destroyed during the past in the Eastern Cape (Skead, 1987). Correct management using fire breaks and blockburning can play an important role in protecting these *Protea* habitats. During conditions of low fuel availability (during autumn), with or without any grazing, fewer mature trees are destroyed by the fire. As only large trees in the population survive the fire, with no young trees. The ideal situation is to having a good selection of mature and large trees, but this can be influenced differently during dry and wet years. In *Protea* veld which is excluded from grazing (short grass) and burnt in spring–summer during dry years, the adult trees in the population are killed, but in wet years, the seedlings survive the fire. If *Protea* veld is heavily grazed, few mature trees are killed because of the shorter grass cover and sufficient adult trees and seedlings remains. During wet years, the seedlings survive fires and will develop in dense *P. roupelliae* forests with less grass for grazing. The use of block burns during autumn (May/June) is recommended to establish dense stands of *Protea* bushes which, however, must be protected from accidental fires by bordering firebreaks. Accidental fires during dry conditions and when the grass layer is long make better conditions for destructive crown fires. As montane grassland areas consist mostly of short grass, the use of regular block burns, which can be rotated annually, and fire breaks ensure less damage to trees during accidental fires.

Protea roupelliae woodland habitats are preferred by Gurney's Sugarbirds and other nectarivore species and therefore the correct management of this habitat type is a priority (De Swardt, 1993b; De Swardt, 1997). The prescribed burning season for grassland areas is mostly fires during May (early winter) and June-July (winter), which can be annually rotated (Van Wilgen *et al.*, 1990). Everard, van Wyk & Viljoen (1994) recommended the same early winter burn as grasses are mostly dormant and less damaged by fires. Patch burning (or block burning) also faciliates a mosaic of burnt and unburnt patches (Everard *et al.*, 1994). At the Makobulaan Plantation, where block burns such as these were applied, the densities of *Protea* bushes were higher in areas burnt during autumn than in spring (A. Lindströhm, pers. comm.). The ideal burning period for *P. roupelliae* woodland is thus during the dry winter months (June-July) which lead to an increased number of seedlings, or else after the first spring rains (Mentis, Meiklejohn & Scotcher, 1974). These grassland fires may also be rotated during early spring, but opportunities are limited by hot, dry and windy conditions which form the main fire danger period (Van Wilgen *et al.*, 1990).

9.2.2. Logging of *Protea roupelliae* trees

At Qwaqwa National Park the cutting of *Protea* trees for firewood was observed in remote areas of the Park. This occurred adjacent to the settlements of Hlatseng, Mononthsa and Phuthadlitjhaba, during 1992 –1994 (period after proclamation of the Park) (De Swardt & Van Niekerk, 1996). At one *P. roupelliae* clump, several trees were cut down or sawn off at the bases of their stems (Fig. 39). Fire killed trees were left, but rather unburned bushes were preferred. This occurs commonly in the Drakensberg areas, mainly in the Qwaqwa area (A. J. Botha, pers. comm.).

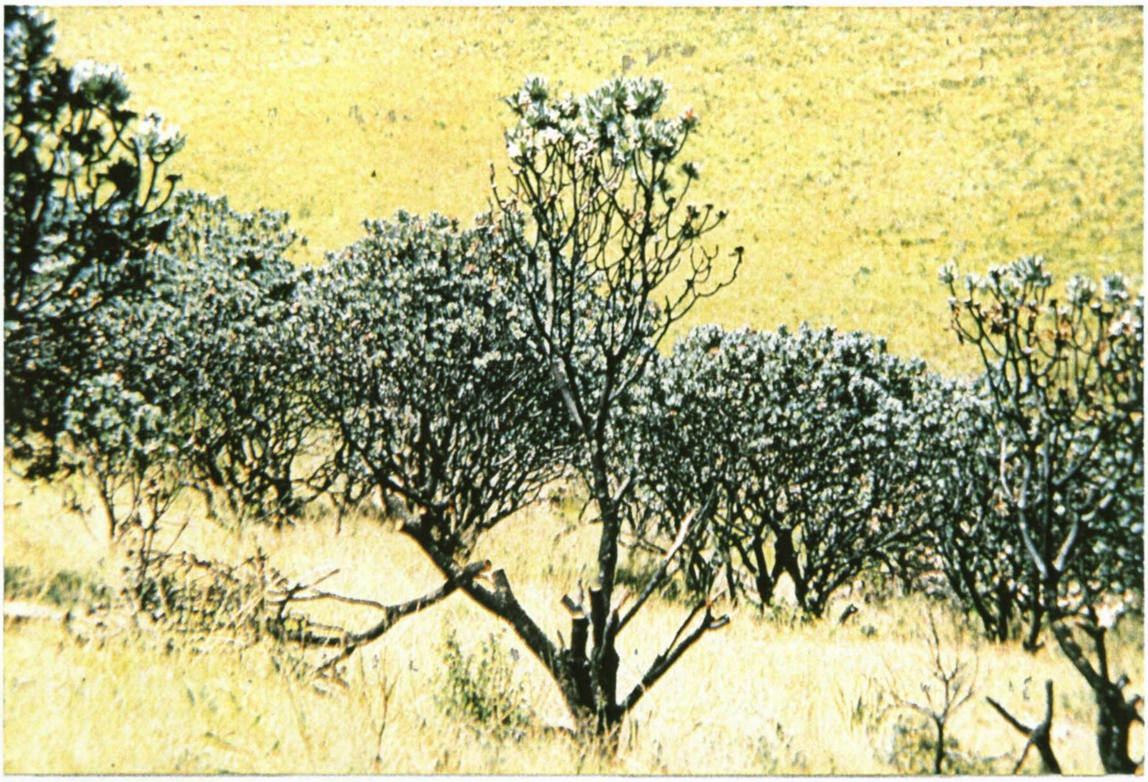


FIGURE 39: *Protea roupelliae* bushes at Honingkloof, Qwaqwa National Park, cut for firewood by local residents near the Park. Only the stumps of some trees are visible where the branches were sawn off.

Historically firewood collection practice was recorded in Lesotho, where Guillarmod (1961) noted the scarcity of *Protea* trees in the southern parts of the country and mentioned that *Protea* populations are declining as the trees are being cut for fuel. These practices were mostly for the benefit of the local chiefs who protect large *P. roupelliae* populations for personal gain use as firewood (Guillarmod, 1968). No evidence is available for the occurrence of Gurney's Sugarbirds in Lesotho along the eastern border (Bonde, 1993; De Swardt, 1997). Skead (1967) considered the interior of Lesotho unsuitable for sugarbirds (as no proteas occur there), and this bird was only recorded in adjacent areas of KwaZulu-Natal. Only *P. caffra* are currently known to occur in Lesotho, but no distribution data are available as during recent times no surveys for *Protea* distribution have been carried out in these areas (Protea Atlas Project, unpubl. data).

10. SUMMARY

Several aspects of the ecology of Gurney's Sugarbird were studied in the Lydenburg area (Mpumalanga) and at Sterkfontein Dam Nature Reserve and Qwaqwa National Park (Free State) during the period April 1980 to June 1998.

The distribution pattern of Gurney's Sugarbird is closely associated with that of *Protea roupelliae* along the Drakensberg escarpment in the Grassland Biome. Nectarivore densities at *Protea* clumps were affected by the size of clumps, flower availability and grasssland fires. Sugarbird densities were higher during winter, spring and early summer when sufficient flowers were available.

Male sugarbirds were significantly larger than females in all body measurements, except tarsus length. Significant correlations were recorded between culmen/total head length and wing/tail length of the two sexes, and between maximum width of the bulged P6/wing length in males. Monthly variations in body mass were recorded in both sexes, and birds were heaviest during the November-March breeding season. Adults with long, fully-grown tail ornaments usually had longer wings, while males had wider bulged P6. Primary moult occurred between November to March, coinciding with the breeding season. Tail moult also occurred during this period and were replaced as soon as their condition worsened.

The sugarbirds have a September-March breeding season, with a peak from November to December in the Lydenburg area. *P. roupelliae* were usually selected for nesting sites, while *P. caffra* was also occasionally used. Nests were completed within five days by the female; mean nest height was 1,85 m. Nests were lined with the brown, fluffy seeds of *P. roupelliae*. Incubation period was 16-17 days, nestling period 21-23 days, and post-nestling period 20-30 days. Breeding success was 41,4%, higher than that of the Cape Sugarbird.

Sugarbirds foraged mostly on the nectar of *P. roupelliae*, but during winter they fed on *Aloe arborescens* in nearby suburban areas and on mountain cliffs. Insect orders which predominated in the diet of Gurney's Sugarbird were Coleoptera and Hymenoptera. These insects also comprised the main arthropod fauna in *P. roupelliae* flowers. Bees and ants were recorded in both stomachs of sugarbirds and *Protea* flowers. Sugarbirds foraged on *P. roupelliae* flowers by probing several times into a flower whilst moving clockwise on it. Beetles were taken from flowers and small flying insects hawked from the air.

Movement and survival data for 93 individuals were obtained from 553 captured sugarbirds in the Lydenburg area. Recaptures showed fidelity to mountain sites, local movements between mountain sites, seasonal movements and individuals recaptured at the same suburban localities during winter. Peak in occurrence in suburban areas was from late May until early July, coinciding with the flowering season of *Aloe arborescens*. Sugarbird movements were after the peak flowering periods of *P. roupelliae*, birds leaving burnt *Protea* veld after fires and after seasons characterised by low annual rainfall.

Annual survival in the Lydenburg area was estimated at 80,7%. Life expectancy was 4,6 years. Two individuals were recaptured after periods of 88 months and one after 74 months. Recapture data suggests a longevity of beyond seven years for this species. This longevity data represents the first of its kind for the species.

The conservation of Gurney's Sugarbird and the management of its *Protea roupelliae* habitat is a priority. Uncontrolled fires in grassland with *P. roupelliae* trees, and logging of wood for fuel, have negative influences on bird and protea populations. The recommended fire regime for *P. roupelliae* woodland is during dry winter periods (June/July), rotated biennially, or as late winter-spring fires (August/September). The application of regular block burns or firebreaks in montane grassland will ensure less damage to tree canopies during accidental fires.

11. OPSOMMING

Verskeie aspekte rakende die ekologie van Rooiborssuikervoëls is gedurende die tydperk April 1980 tot Junie 1998 in die Lydenburg-omgewing (Mpumalanga), Sterkfonteindam Natuurreservaat en Qwaqwa Nasionale Park (Vrystaat) bestudeer.

Die suikervoëls se verspreidingspartoon oorvleuel met dié van *Protea roupelliae* in die grasveldbioom langs die Drakensberg-eskarp. Bevolkingsgroottes van suikervoëls en ander nektarvoedende voëlsoorte word beïnvloed deur faktore soos die grootte van bosgroepe, beskikbaarheid van proteas in blom en die effek van grasveldbrande in *Protea*-veld. Bevolkingsdigthede van suikervoëls was hoër gedurende die winter, lente en vroeë somer wanneer volop blomme beskikbaar is.

Suikervoëlmannetjies was betekenisvol groter as wyfies in alle liggaamsmates, behalwe in tarsus-lengte. Beduidende korrelasies het tussen snawel/totale kop-lengtes en vlerk/stert-lengtes tussen beide geslagte en tussen die maksimum breedte van uitranding in die sesde primêre veer (P6) en vlerklengte in mannetjies voorgekom. Maandlikse variasies in liggaamsmassa kom in beide geslagte voor en voëls was die swaarste gedurende die November-Maart broeiseisoen. Volwasse mannetjies met uitgegroeide ornamentele stertvere het ook meestal langer vlerke en breër uidrandings van P6 gehad. Ververing van die primêre vlerkvere vind tussen November-Maart plaas en oorvleuel met die broeiseisoen. Ververing van stertvere vind ook gedurende die tydperk plaas en word vervang sodra hulle verweer raak.

Die broeiseisoen was hoofsaaklik tussen September-Maart, met 'n piek gedurende November-Desember in die Lydenburg omgewing. Voorkeur word aan *Protea roupelliae*-bome as neslokaliteite gegee, alhoewel *P. caffra* ook benut word. Neste word binne vyf dae deur die wyfie gebou en die gemiddelde neshoogte was 1,85 m. Die saadpluime van *P. roupelliae*-blomme word in die neste uitgelê. Die inkubasieperiode is 16-17 dae, nestyd 21-23 dae en na-nesperiode 20-30 dae. Broeisukses is as 41,4% bereken en is hoër as dié van die Kaapse Suikervoël.

Suikervoëls voed hoofsaaklik op nektar van *P. roupelliae*-blomme en gedurende die winter op *Aloe arborescens*-nektar in bergklowe, asook in dorpsgebiede. Insekordes van veral Coleoptera en Hemiptera word deur die suikervoëls benut. Hierdie insekte kom ook in groot getalle in *P. roupelliae*-blomme voor. Bye en miere, wat in blomme voorkom, is ook in die maaginhoude van suikervoëls gevind. Voeding in *Protea*-blomme vind plaas deurdat die snawel herhaaldelik in die blom ingesteek word om nektar te verkry, terwyl die voël kloksgewys om die blom beweeg. Kewers word vanuit blomme opgepik en klein vlieënde insekte word uit die lug gevang.

Seisoenale migrasie- en oorlewingsdata (553 individue gering) is vanaf 93 suikervoëls in die Lydenburg-studiegebied verkry. Hervangstes is hoofsaaklik in dieselfde berglokaliteite verkry, of as bewegings tussen berglokaliteite, seisoenale bewegings en hervangstes gedurende die winter in die dorp. Suikervoëls is tussen laat Mei en vroeg Julie in die dorp waargeneem, wanneer *Aloe arborescens* in blom is. Seisoenale migrasies was ná die piek blomtyd van *P. roupelliae*, voëls wat gebrande *Protea*-veld verlaat en ná seisoene met lae reënval.

Oorlewing van die suikervoël-bevolking in Lydenburg was 80,7%, met 'n berekende lewensverwagting van 4,6 jaar. Twee individue is na periodes van 88 maande en een na 74 maande gevang. Hervangsdata dui daarop dat suikervoëls tot meer as sewe jaar kan leef en is die eerste van dié data vir Rooiborssuikervoëls.

Die bewaring van Rooiborssuikervoëls en die bestuur van hul *Protea roupelliae*-habitat is 'n prioriteit. Onbeheerde vure in grasveld met *P. roupelliae* bome en die versamel van *Protea*-hout het negatiewe invloede op plant- en voëlbevolkings. Die aanbevole brandseisoen vir *P. roupelliae* is gedurende die droë winter (Junie/Julie), op 'n twee jaarlikse rotasie, of as laat winter/lente-brande (Augustus/September). Die toepassing van gereelde blokbrande of voorbrande in berggrasveldgebiede sal dan tydens toevallige brande minder skade aan kroondakke van proteabome veroorsaak.

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13. REFERENCES

ACOCKS, J. P. H. 1988. Veld types of South Africa. *Mem. Bot. Surv. S. Afr.* 57: 1-146.

ALATALO, R. V., HÖGLUND, J. & LUNDBERG, A. 1988. Patterns in variation in tail ornament size in birds. *Biol. J. Linn. Soc.* 34: 363-374.

ALLAN, D. G., HARRISON, J. A., NAVARRO, R. A., VAN WILGEN, B. W. & THOMPSON, M. W. 1997. The impact of commercial afforestation on bird populations in Mpumalanga Provinve, South Africa – insights from bird-atlas data. *Biol. Cons.* 79: 173-186.

AMES, P. L., 1975. The application of syringeal morphology to the classification of the Old World insect eaters (Muscicapidae). *Bonn. Zool. Beitr.* 26: 107-134.

ANDERSSON, M. 1982. Female choice selects for extreme tail length in a widowbird. *Nature* 299: 818-820.

BARNARD, P. 1991. Ornament and body size variation and their measurements in natural populations. *Biol. J. Linn. Soc.* 42: 379-388.

BARNARD, P. 1995. Timing of ornament growth, phenotypic variation, and size dimorphism in two promiscuous African whydahs (Ploceidae: *Vidua*). *Biol. J. Linn. Soc.* 55: 129-141.

BEARD, J. S. 1963. The genus *Protea* in tropical Africa. *Kirkia* 3: 138-206.

BEASLEY, A. J. 1995. The birds of the Chimanimani mountains. *Honeyguide* 41: 1-60.

BOCK, W. J. 1985. Relationships of the sugarbird (*Promerops*; Passeriformes, ? Meliphagidae) *Proc. Intern. Symp. African Vertebr.* 349-374.

BOND, W. J. & SLINGSBY, P. 1985. Seed dispersal by ants in shrublands of the Cape Province and its evolutionary implications. *S. Afr. J. Sci.* 79: 231-233.

BONDE, K. 1993. *The birds of Lesotho.* Pietermaritzburg: Natal University Press.

BREDENKAMP, G., GRANGER, J. E. & VAN ROOYEN, N. 1996. North-eastern mountain grassland. *IN:* LOW, A. B. & REBELO, A. G. (Eds). *Vegetation of South Africa, Lesotho and Swaziland.* Pretoria: Dept. Environmental Affairs & Tourism. pp. 46-47.

BROEKHUYSEN, G. J. 1959. The biology of the Cape Sugarbird *Promerops cafer* (L). *Ostrich suppl.* 3: 180-221.

BROEKHUYSEN, G. J. 1963. The breeding biology of the Orange-breasted Sunbird *Anthobaptes violacea* (Linnaeus). *Ostrich* 34: 187-234.

BROEKHUYSEN, G. J. 1966. The avifauna of the Cape protea-heath macchia habitat in South Africa. *Ostrich suppl.* 6: 323-334.

BURGER, A. E., SIEGFRIED, W. R. & FROST, P. G. H. 1976. Nest site selection of the Cape Sugarbird. *Zool. Afr.* 11: 127-158.

BURNHAM, K. P. , ANDERSON, D. R. , WHITE, G. C. , BROWNIE, C. & POLLOCK, K. H. 1987. Desighn and analysis methods for fish survival experiences based on release-recapture. *American Fisheries Society Monograph No. 5.* Bethesda, Maryland, USA: American Fisheries Society.

CALDER, W.A. & JONES, E. G. 1989. Implications of recapture data for migration of the Rufous Hummingbird (*Selasphorus rufus*) in the Rocky Mountains. *Auk* 106: 488-489.

CAWTHORNE, R. A. & MARCHANT, J. 1980. The effects of the 1978/79 winter on British bird populations. *Bird Study* 27: 163-172.

CLANCEY, P. A. (Ed.). 1980. *S. A. O. S. checklist of southern African birds.* Johannesburg: Southern African Ornithological Society.

CLOBERT, J., LEBRETON, J. D. & ALLAINE, D. 1987. A general approach to survival estimation by recaptures or resightings of marked birds. *Ardea* 75: 133-142.

CLOBERT, J. & LEBRETON, J. D. 1991. Estimation of demographic parameters in bird populations. *IN:* PERRENS, C. M., LEBRETON, J. D. & HIRONS, G. J. M. (Eds). *Bird population studies.* New York: Oxford University Press. pp. 75-104.

COETZEE, J.H. & GILIOMEE, J.H. 1985. Insects in association with the inflorescences of *Protea repens* (Proteaceae). *J. ent. Soc. sth. Afr.* 48: 303-314.

COLLINS, B. G. & GREY, J. 1988. Preferred foraging by honeyeaters in the jarrah forest of western Australia. *Ostrich suppl.* 14: 39-47.

COLLINS, B. G. & PATON, D. C. 1989. Consequences of differences in body mass, wing length, and leg morphology for nectar-feeding birds. *Aust. J. Ecol.* 14: 269 289.

COLLINS, B. G. & REBELO, A. G. 1987. Pollination biology of the Proteaceae in Australia and southern Africa. *Aust. J. Ecol.* 12: 387-421.

CRAIB, C. L. 1977. Gurney's Sugarbird. *W. B. C. Newssheet* 96: 9-10.

CRAIB, C. L. 1981. Gurney's Sugarbird. *W. B. C. Newssheet* 113: 4-7.

CRAIG, A. J. F. K. 1983. Moult in southern African passerine birds: a review. *Ostrich 54:* 220-237.

CRAIG, A. J. F. K. 1989. Tail length and sexual selection in the polygynous Longtailed Widow (*Euplectes progne*): a cautionary tale. *S. Afr. J. Sci.* 85: 523-524.

CRAIG, A. J. F. K. 1996. The annual cycle of wing-moult and breeding in the Wattled Starling *Creatophora cinerea. Ibis* 138: 448-454.

CRAIG, A. J. F. K. & HULLEY, P. E. 1994. Sunbird movements: A review with possible models. *Ostrich* 65: 106-110.

CYRUS, D. P. & ROBSON, N. F. 1980. *Bird atlas of Natal.* Pietermaritzburg: Natal University Press.

DANIELS, C. L. 1987. *The feeding ecology of nectarivorous birds in the Natal Drakensberg.* M.Sc. thesis. Pietermaritzburg: University of Natal.

DEAN, W. R. J. 1978. Life expectancy of the Cape Sparrow. *Ostrich* 49: 16-20.

DEL HOYO, J., ELLIOTT, A. & SARGATAL, J. (Eds). 1992. *Handbook of the birds of the World.* Vol. 1. Barcelona: Lynx Edicions.

DE SWARDT, D. H. 1982. Gurney's Sugarbird. *W. B. C. Newssheet* 118: 11.

DE SWARDT, D.H. 1988. A non-slip device for attaching guy ropes to net poles. *Safring News* 17: 23.

DE SWARDT, D. H. 1989. Some observations on the local movements of Gurney's Sugarbird in the Lydenburg area. *Safring News* 18: 31-32.

DE SWARDT, D. H. 1990a. Birds of the Gustav Klingbiel Nature Reserve and the Sterkspruit area, Lydenburg. *Sthn Birds* 16: 1-67.

DE SWARDT, D. H. 1990b. A new non-slip net attachment and lifting apparatus for erecting mist nets. *Safring News* 19: 45-47.

DE SWARDT, D. H. 1990c. Ageing and sexing: Gurney's Sugarbird. *Safring News* 19: 57-60.

DE SWARDT, D. H. 1991a. The seasonal movements of Gurney's Sugarbird *Promerops gurneyi* in the Lydenburg area, Transvaal. *Ostrich* 62: 40-44.

DE SWARDT, D. H. 1991b. Measurements and moult in the Greater Doublecollared Sunbird. *Safring News* 20: 21-25.

DE SWARDT, D. H. 1992a. Distribution, biometrics and moult in Gurney's Sugarbird *Promerops gurneyi. Ostrich* 63: 13-20.

DE SWARDT, D. H. 1992b. 'n Ongewone Rooiborssuikervoël nes. *The Hornbill* 28: 21-22.

DE SWARDT, D. H. 1993a. The status of Gurney's Sugarbird in the eastern Orange Free State. *Mirafra* 10: 2-3.

DE SWARDT, D. H. 1993b. Factors affecting the densities of nectarivores in *Protea roupelliae* woodland. *Ostrich* 64: 172-177.

DE SWARDT, D. H. 1995. Malachite Sunbird ringing in the Free State. *Safring News* 24: 15-18.

DE SWARDT, D. H. 1997. Gurney's Sugarbird *Promerops gurneyi IN*: HARRISON, J. A., ALLAN, D. G., UNDERHILL, L. G., HERRENMANS, M., TREE, A. J., PARKER, V. & BROWN, C. J. (Eds.).: *The atlas of southern African birds.* Vol 2: Passerines. Johannesburg: Birdlife South Africa. pp. 486-487.

DE SWARDT, D. H. & BOTHMA, N. 1992. Notes on the breeding biology of Gurney's Sugarbird. *Ostrich* 63: 136-137.

DE SWARDT, D. H. & LOUW, S. 1994. The diet and foraging behaviour of Gurney's Sugarbird *Promerops gurneyi*. *Navors. nas. Mus., Bloemfontein* 10: 245-258.

DE SWARDT, D.H. & SCHOEMAN, S. 1997. Sunbird recaptures and seasonal movements at Lydenburg, Mpumalanga Province. *Safring News* 26: 13-15.

DE SWARDT, D. H. & VAN NIEKERK, D. J. 1996. An annotated check list of the birds of Qwaqwa National Park. *Koedoe* 39: 89-106.

DETTMANN, E. B. 1995. Use of the Yolly-Seber model to detect variation in survival, population size and recruitment of Brilded Honeyeaters at Paluma Queensland. *Corella* 19: 61-67.

DOWNS, C. T. & PERRIN, M. R. 1996. Sugar preferences of some southern African nectarivorous birds. *Ibis* 138: 455-459.

DOWSETT, R. J. 1985. Site-fidelity and survival rates of some montane forest birds in Malawi, south-central Africa. *Biotropica* 17: 145-154.

DOWSETT-LEMAIRE, F. 1989. Food plants and the annual cycle in a montane community of sunbirds (*Nectarinia* spp.) in northern Malawi. *Tauraco* 1: 167-185.

EARLé, R. A. 1982. Aspects of the breeding biology and ecology of the Whitebellied Sunbird. *Ostrich* 53: 65-73.

EARLé, R. A. & GROBLER, N. J. 1987. *First atlas of bird distribution in the Orange Free State*. Bloemfontein: National Museum.

EVANS, M. R. & BARNARD, P. 1995. Variable sexual ornaments in Scarlet-tufted Malachite Sunbird (*Nectarinia johnstonii*) on Mount Kenya. *Biol. J. Linn. Soc.* 54: 371-381.

EVANS, M. R. & THOMAS, A. L. R. 1992. The aerodynamic and mechanical effects of elongated tails in the Scarlet-tufted Malachite Sunbird: measuring the cost of a handicap. *Anim. Behav.* 43: 337-347.

EVERARD, D. A., VAN WYK, G. F. & VILJOEN, P. J. 1994. An ecological evaluation of the upper Sabie River catchment, eastern Transvaal. FOR-DEA 705. Division of Forest Science & Technology: CSIR

FAABORG, J. & ARENDT, W. J. 1995. Survival rates of Puerto Rican birds: Are islands really that different? *Auk* 112: 503-507.

FARQUHAR, M. R., LORENZ, M., RAYNER, J. L. & CRAIG, A. J. F. K. 1996. Feather ultrastructure and skeletal morphology as taxonomic characters in African sunbirds (Nectariniidae) and sugarbirds (Promeropidae). *J. Afr. Zool.* 110: 321-331.

FORD, H. A. 1980. Breeding and moult in honeyeaters (Aves: Meliphagidae) near Adelaide, South Australia. *Aust. Wildl. Res.* 7: 453-463.

FORD, H. A. & PATON, D. C. 1976. The value of insects and nectar to honeyeaters. *Emu* 76: 83-84.

FRASER, M. W. 1989. Short-term responses of birds to fire in old Mountain Fynbos. *Ostrich* 60: 172-182.

FRASER, M. W. 1997. Cape Sugarbird *Promerops cafer IN*: HARRISON, J. A., ALLAN, D. G., UNDERHILL, L. G., HERRENMANS, M., TREE, A. J., PARKER, V. & BROWN, C. J. (Eds.).: *The Atlas of southern African Birds.* Vol 2: Passerines. Johannesburg: Birdlife South Africa. pp. 484-485.

FRASER, M. W. & McMAHON, L. 1992. Habitat change by Cape Sugarbirds and Orangebreasted Sunbirds in an apparent response to fire in old Mountain Fynbos. *Safring News* 21: 51-54.

FRASER, M. W., McMAHON, L., UNDERHILL, L. G., UNDERHILL, G. D. & REBELO, A. G. 1989. Nectarivore ringing in the south-western Cape. *Safring News* 18: 3-18.

FRIEDMAN, H. 1952. The Long-tailed Sugarbird of eastern Rhodesia. *J. Wash. Acad. Sci.* 42: 31-32.

FRY, C. H. 1982. *The bee-eaters.* Halfway House: Russel Friedman.

GARGETT, V., GARGETT, E. & DAMANIA, A. 1995. The influence of rainfall on Black Eagle breeding over 31 years in the Matobo Hills, Zimbabwe. *Ostrich* 66: 114-121.

GESS, F. W. 1968. Insects found on proteas. *Journ. Bot. Soc. S. Afr.* 54: 29-33.

GILL, F. B. & WOLF, L. L. 1978. Comparative foraging efficiencies of some montane sunbirds in Kenya. *Condor* 80: 391-400.

GINN, H. B. & MELVILLE, D. S. 1983. *Moult in birds*. Tring: British Trust for Ornithology.

GOUWS, T. 1994. Rariteite en ongewone waarnemings. *Laniarius* 54: 14-16.

GRAHAM, M. F. 1972. A traveller's tale. *Honeyguide* 71: 17-18.

GUILLARMOD, A. J. 1961. The botany of Basutoland. *Journ. Bot. Soc. S. Afr.* 47: 12-14.

GUILLARMOD, A. J. 1968. Lesotho. *Acta Phytogeographica suecica* 54: 253-256.

HANMER, D. B. 1981. Mensural and moult data of nine species of sunbirds from Mozambique and Malawi. *Ostrich* 52: 156-178.

HANMER, D. B. 1984a. Life expectancy and productivity estimates for three species of bulbul from southern Malawi. *Proc. V. Pan-Afr. Orn. Congr.* pp. 149-161.

HANMER, D. B. 1984b. The Brownthroated Weaver *Ploceus xanthopterus* from Mozambique and Malawi. *Proc. V. Pan-Afr. Orn. Congr.* pp. 121-148.

HARRISON, J. A. 1987. The South African bird atlas project. *S. Afr. J. Sci.* 83: 400-401.

HARRISON, J.A., ALLAN, D. G. & VAN HENSBERGEN, H. J. 1994. Automated habitat annotation of bird species lists - an aid in environmental consultancy. *Ostrich* 65: 316-328.

HARRISON, J. A., ALLAN, D. G., UNDERHILL, L. G., HERRENMANS, M., TREE, A. J., PARKER, V. & BROWN, C. J. 1997. (Eds.).: *The atlas of southern African birds.* (Vol. 1 & 2). Johannesburg: Birdlife South Africa.

HARRISON, J. A. & MARTINEZ, P. 1995. Measurement and mapping of avian diversity in southern Africa: implications for conservation planning. *Ibis* 137: 410-417.

HOLM, E. & MARAIS, E. 1992. *Fruit chafers of southern Africa (Scarabaeidae: Cetoniini).* Hartebeespoort: Ekogilde CC.

IRWIN, M. P. S. 1981. *The birds of Zimbabwe.* Salisbury: Quest.

JACKSON, H. D. 1973. Records of some birds and mammals in the central Chimanimani mountains of Mozambique and Rhodesia. *Durban Mus. Novit.* 9: 291-305.

JOLLY, G. M. 1965. Explicit estimates from capture-recapture data with both dead and immigration – stochastic model. *Biometrika* 52: 225-209.

KEAST, A. 1968. Seasonal movements in the Australian honeyeaters (Meliphagidae) and their ecological significance. *Emu* 67: 159-209.

KRUGER, F. J. & BIGALKE, R. C. 1984. Fire in Fynbos. *IN:* BOOYSEN, P. DE V., TAINTON, N. M. (Eds). *Ecological effects of fire in South African ecosystems.* Berlin: Springer-Verlag. pp. 67-114.

LAWSON, P.C. 1994. Editorial. *The Hornbill* 38: 4-5.

LEBRETON, J. D., BURNHAM, K. P., CLOBERT, J. & ANDERSON, D. R. 1992. Modelling survival and testing biological hypothesis using marked animals: A unified approach with case studies. *Ecol. Monogr.* 62: 67-118.

LE MAITRE, D. C. & MIDGLEY, J. J. 1992. Plant reproductive ecology. *IN*: COWLING, R. M. (Ed.). *The ecology of fynbos*. Cape Town: Oxford University Press. pp. 135-174.

LINDEN, M. & MOLLER, A. P. 1989. Cost of reproduction and covariation of life-history traits in birds. *Trends in Ecology and Evolution.* 4: 367-371.

LLOYD, P. & CRAIG, A. J. F. K. 1989. Morphometrics, moult and taxonomy of the *Nectarinia afra / N. chalybea* complex of southern African double-collared sunbirds. *Ann. Cape Prov. Mus. (Nat. Hist.)* 18: 135-150.

LOW, A. B. & REBELO, A. G. 1996. *Vegetation of South Africa, Lesotho and Swaziland.* Pretoria: Dept. Environmental Affairs & Tourism.

MACLEAN, G. L. 1985. *Roberts' birds of southern Africa.* Cape Town: John Voelcker Bird Book Fund.

MACLEAN, G. L. 1990. *Ornithology for Africa.* Pietermaritzburg: Natal University Press.

MACLEAN, G. L. 1993. *Roberts' birds of southern Africa.* Cape Town: John Voelcker Bird Book Fund.

MANSON, A. J. 1985. Gurney's Sugarbird in the Vumba. *The Honeyguide* 31: 220-221.

MARTIN, R., MARTIN, J. & MARTIN, E. 1988. A comment on the breeding season of Gurney's Sugarbird in Natal. *Bokmakierie* 40: 20.

McLACHLAN, G. R. & LIVERSIDGE, R. 1978. *Roberts' birds of South Africa.* Cape Town: The trustees of the John Voelcker Bird Book Fund..

MENTIS, M. T., MEIKLEJOHN, M. J. & SCOTCHER, J. S. B. 1974. Veld burning in the Giant's Castle Game Reserve, Natal Drakensberg. *Proc. Grassld. Soc. Sth. Afr.* 9: 26-31.

MILLS, G. S., DUNNING, J. B. & BATES, J. M. 1991. The relationship between breeding bird density and vegetation volume. *Wilson Bull.* 103: 468-479.

MOSTERT, D. P., SIEGFRIED, W. R. & LOUW, G. N. 1980. Protea nectar and satellite fauna in relation to the food requirements and pollinating role of the Cape Sugarbird. *S. Afr. J. Sci.* 76: 409-412.

NEVILL, H. 1987. Gurney's Sugarbird breeding in winter. *Bokmakierie* 39: 71-74.

NORRIS, F. G. 1989. Pollination ecology of *Leonotis leonurus*. *Veld & Flora* 75: 7-10.

OATLEY, T. B. 1982. The Starred Robin in Natal, Part 3: Breeding, populations and plumages. *Ostrich* 53: 206-221.

OATLEY, T. B. & BEST, C. C. 1997. Selected recoveries reported to SAFRING: January 1997 – June 1997. *Safring News* 26: 72-80.

OATLEY, T. B. & UNDERHILL, L.G. 1993. Merging recoveries and recaptures to estimate survival probabilities. *IN*: LEBRETON, J-D. & NORTH, P. M. (Eds). *Marked individuals in the study of bird populations.* Switserland: Birkhauser verlag Basel. pp. 77-90.

OLSON, S. L. & AMES, P. L. 1984. *Promerops* as a thrush, and its implications for the evolution of nectarivory in birds. *Ostrich* 55: 213-218.

OSCHADLEUS, D. & FRASER, M. W. 1988. Observations of colour-ringed Cape Sugarbirds at Kirstenbosch. *Safring News* 17: 59-64.

PATON, D. C. 1982a. Moult of New Holland Honeyeaters, *Phylidonyris novahollandiae* (Aves: Meliphagidae) in Victoria. I. Moult of adults. *Aust. Wild. Res.* 9: 331-344.

PATON, D. C. 1982b. Moult of New Holland Honeyeaters, *Phylidonyris novahollandiae* (Aves: Meliphagidae) in Victoria. II. Moult of juveniles. *Aust. Wild. Res.* 9: 345-356.

PATON, D. C. 1982c. The diet of the New Holland Honeyeater, *Phylidonyris novaehollandiae. Aust. J. Ecol.* 7: 279-298.

PATON, D.C. & COLLINS, B.G. 1989. Bills and tongues of nectar feeding birds: A review of morphology, function and performance, with intercontinental comparisons. *Aust. J. Ecol.* 14: 473-506.

PAYNE, R. B. 1990. Natal dispersal, area effects, and effective population size. *J. Field Ornithol.* 61: 396-403.

PEACH, W., DU FEU, C. & McMEEKINGS, J. 1995. Site tenacity and survival rates of Wrens *Troglodytes troglodytes* and Treecreepers *Certhia familiaris* in a Nottinghamshire wood. *Ibis* 137: 497-507.

PRADEL, R. , CLOBERT, J. & LEBRETON, J. D. 1990. Recent developments for the analysis of capture-recapture multiple data sets. *Ring* 13: 193-204.

PRYS-JONES, R. P. & CLARK, D. L. (undated). Species richness, density and biomass of birds in Mountain Fynbos of the Cape of Good Hope Nature Reserve in relation to plant community and burning. Unpubl. report. Cape Town: University of Cape Town.

PYKE, G. H., RECHER, H. F. & O'CONNOR, P. J. 1989. Patterns of residency and movements among honeyeaters in heathland near Sidney. *Emu* 89: 30-39.

PYKE, G. H. 1980. The foraging behaviour of Australian honeyeaters: a review and some camparisons with hummingbirds. *Aust. J. Ecol.* 5: 343-369.

REBELO, A. G. 1987. Bird pollination in the Cape flora. *IN*: REBELO, A. G. (Ed). A preliminary synthesis of pollination biology in the Cape flora. *S. Afr. Nat. Sci. Progr. Rep.* 141:83-108.

REBELO, A. G. 1995. *A fieldguide to the proteas of southern Africa.* Cape Town: Fernwood Press.

REBELO, A. G. & TANSLEY, S. A. 1993. Using rare plant species to identify priority conservation areas in the Cape Floristic Region: the need to standardize for total species richness. *S. Afr. J. Sci.* 89: 156-161.

RECHER, H. F. & ABBOTT, I. J. 1970. The possible ecological significance of hawking by honeyeaters and its relation to nectar feeding. *Emu* 70: 90.

RICHARDSON, D. M. & FRASER, M. W. 1992. The birds of Swartboskloof, Jonkershoek Valley. *Sthn Birds* 17: 1-44.

ROBERTSON, H. G. & ZACHARIADES, C. 1997. Revision of the *Camponotus fulvopilosus* (De Geer) species-group (Hymenoptera: Formicidae). *African Entomology* 5: 1-18.

ROURKE, J. P. 1982. *The proteas of southern Africa.* Cape Town: Purnell.

ROWAN, M. K. 1964. An analysis of the records of a South African ringing station. *Ostrich* 35: 160-187.

ROWLEY, I. & RUSSEL, E. 1991. Demography of passerines in the temperate southern hemisphere. *IN*: PERRINS, C. M., LEBRETON, J. D. & HIRONS, E. J. M. (Eds.). *Bird population studies.* Oxford: Oxford University Press. pp. 22-44.

RUTHERFORD, M. C. & WESTFALL, R. H. 1986. The biomes of southern Africa - an objective categorization. *Mem. Bot. S. Afr.* 54: 1-98.

SEBER, G. A. F. 1965. A note on the multiple-recapture census. *Biometrika* 52: 249-259.

SEATHER, B. E. 1988. Patterns of covariation between life-history traits of European birds. *Nature* 331: 616-617.

SEILER, H. W. & FRASER, M. W. 1985. Ageing and sexing guide: Cape Sugarbird *Promerops cafer. Safring News* 14: 91-92.

SEILER, H. W. & REBELO, A. G. 1987. A sexual difference in the Cape Sugarbird 's role as a pollinator of *Protea lepidocarpodendron* ? *Ostrich* 58: 43-45.

SIBLEY, C. G. & AHLQUIST, J. E. 1974. The relationships of the African sugarbirds (*Promerops*). *Ostrich* 45: 22-30.

SIBLEY, C. G. & AHLQUIST, J. E. 1990. *Phylogeny and classification of birds*. London: Yale University Press.

SIEGFRIED, W. R. 1983. Trophic structure of some communities of fynbos birds. *S. Afr. J. Bot.* 49: 1-43.

SIEGFRIED, W. R. 1985. Red data books. Bibles for protectionists, aunt Sallies for conservationists. *IN:* MUNDY, P. J. (Ed.). *Proceedings of an international symposium on 'The Extinction Alternative'.* Johannesburg: Endangered Wildlife Trust.

SKEAD, C. J. 1964. Sugarbirds in the Amatole mountains, King William's Town, Cape Province. *Ostrich* 35: 236.

SKEAD, C. J. 1967. *The sunbirds of southern Africa.* Cape Town: Balkema.

SKEAD, C. J. 1987. *Historical mammal incidence in the Cape Province.* The eastern half of the Cape Province, including the Ciskei, Transkei and East Griqualand. Vol.1. Cape Town: CPA Printers. pp. 888-891.

SKEAD, D. M. 1963. Gurney's Sugarbird *Promerops gurneyi* Verreaux, in the Natal Drakensberg. *Ostrich* 34: 160-164.

SOKAL, R. R. & ROHLF, F. J. 1981. *Biometry.* 2nd Ed. San Francisco: W. H. Freeman.

STEYN, P. 1973. A nest of Gurney's Sugarbird. *Honeyguide* 77: 28-31.

TARBOTON, W. R., KEMP, M. I. & KEMP, A. C. 1987. *Birds of the Transvaal.* Pretoria: Transvaal Museum.

TEMELES, E. J. & ROBERTS, W. M. 1993. Effect of sexual dimorphism in bill length on foraging behaviour: an experimental analysis of hummingbirds. *Oecologia* 94: 87-94.

UNDERHILL, L. G. 1994. Identification, ageing and sexing guides published in *Safring News*, 1972-1993. *Safring News* 23: 49-52.

VAN WILGEN, B. W., EVERSON, C. S. & TROLLOPE, W. S. W. 1990. Fire management in South Africa: Some examples of current objectives, practices and problems. *IN*: GOLDHAMMER, J. G. (Ed.). *Fire in tropical biota.* Berlin: Springer-verlag. pp. 179-215.

VERNON, C. J. 1971. A day in the Chimanimani mountains. *Honeyguide* 68: 23-24.

WARKENTIN, I. G. & JAMES, P. C. 1990. Dispersal terminology: Changing definition in midflight? *Condor* 92: 802-803.

WEBB, J. 1996a. Breeding of Gurney's Sugarbird *Promerops gurneyi*, in Chimanimani Mountains. *On Safari* 14: 15.

WEBB, J. 1996b. Winter breeding of sugarbirds. *On Safari* 15: 12.

WHITEHEAD, V. B., GILIOMEE, J. H. & REBELO, A. G.1987. Insect pollination in the Cape flora. *IN*: REBELO, A. G. (Ed). A preliminary synthesis of pollination biology in the Cape flora. *S. Afr. Nat. Sci. Progr. Rep.* 141: 52-82.

WINTERBOTTOM, J. M. 1962. Breeding season of Long-tailed Sugarbird. *Ostrich* 33:77-79.

WINQUIST, T. & LEMON, R. E. 1994. Sexual selection and exaggerated male tail lengths in birds. *Amer. Naturalist* 143: 95-116.

WOLF, L. L. 1970. The impact on seasonal flowering on the biology of some tropical hummingbirds. *Condor* 72: 1-14.

WOOLLER, R. D. 1982. Feeding interactions between sunbirds and sugarbirds. *Ostrich* 53: 114-115.

WRIGHT, M. G. 1994. Seed production by *Protea laurifolia* (Proteaceae) after insect versus insect and bird pollination: a quality difference? *S. Afr. J. Sci.* 90: 199.

WRIGHT, M. G., VISSER, D., COETZEE, J. H. & GILIOMEE, J. H. 1991. Insect and bird pollination of *Protea* species in the western Cape: further data. *S. Afr. J. Sci.* 87: 214-215.

YOM-TOV, Y., McCLEERY, R. & OATLEY, T. B. 1994. The survival rates of some African passerines. *Ostrich* 65: 329-332.

YOM-TOV, Y. MCCLEERY, R. & PURCHASE, D. 1992. The survival rate of Australian passerines. *Ibis* 134: 374-379.

ZAR, J. H. 1984. *Biostatical analysis*. London: Prentice Hall.

ZIETSMAN, P. C., VAN WYK, A. E. & BOTHA, F. C. 1989. Vegetation and reproductive phenology of *Ziziphus mucronata* subsp. *mucronata* (Rhamnaceae). *S. Afr. J. Bot.* 55:564-573.