

**The role of male territory size and quality in mating and  
reproductive success of Cape and Gurney's Sugarbirds, *Promerops  
cafer* and *Promerops gurneyi***

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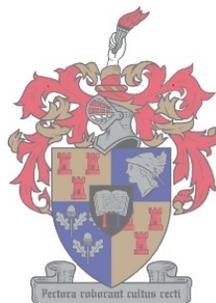
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## **Declaration**

I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

## Abstract

There are two species of sugarbirds, the Cape and Gurney's sugarbirds, and both are endemic to southern Africa. The role of territory size and quality on their mating and reproductive success was determined. Differences in male territory size and quality between Cape and Gurney's sugarbirds reflect the higher *Protea* species diversity and tree density of Cape sugarbird habitat. Both mating (the number of eggs laid by the female of the pair) and reproductive (the number of successful fledglings) success were greater for Cape sugarbirds than for Gurney's sugarbirds, indicating that nectar and arthropod energy availability constrained their mating and reproductive success. No significant differences were found in mating or reproductive success between seasons for Cape sugarbirds.

Many Cape sugarbirds returned annually to their previous breeding territories; non returners may have been predated on or moved elsewhere to improve territory size and quality. Male Cape sugarbird mating and reproductive success were significantly greater for males defending large territories, with greater nectar energy availability. Sugarbird adults feed arthropods to their offspring but arthropod energy availability was abundantly available to Cape sugarbirds and did not influence their mating or reproductive success. Low arthropod energy availability, however, constrained Gurney's sugarbird reproductive success.

Male sugarbirds have elongated tails and a bulge on the sixth primary feathers, but in neither case was ornament length related to mating or reproductive success in either Cape or Gurney's sugarbirds. Tail length and displays of sugarbirds may be important in territory maintenance as male Cape sugarbirds in 1999 and male Gurney's sugarbirds with long tails defended larger mid breeding season territories

than males with short tails. Similarly, male Gurney's sugarbirds with longer primary feather bulges defended larger territories at the end of the breeding season. The reduced sexual dimorphism in wing and tail ornamentation in Gurney's sugarbirds may be a result of low food availability either constraining ornament growth, or reduced territoriality with an associated decline in the importance of ornaments used in territorial displays.

Both Cape and Gurney's sugarbirds spent more time probing inflorescences for nectar than hawking for arthropods. Within each species, there were significant differences in the amount of time spent in some activities at different times during the day - Gurney's sugarbirds spending considerably longer feeding off territory or hidden in trees than Cape sugarbirds. Time spent probing inflorescences for nectar was significantly correlated with nectar volume, concentration and energy availability for Cape sugarbirds. They appear to maximise energy gain by feeding on nectar from bearded *Protea* in the morning and feeding on all *Protea* groups at midday, when nectar energy availability was greatest. In contrast, Gurney's sugarbirds spent the same amount of time feeding throughout the day. Cape sugarbirds fed mostly from bearded *Protea* at mid breeding season, but from spoonbract *Protea* at the end of the breeding season, once bearded *Protea* had finished flowering.

## Uittreksel

Daar is twee spesies suikervoëls, naamlik die Kaapse en Gurney se suikervoël, beide endemies tot suider Afrika. Die rol van territoriumgrootte en kwaliteit op hulle paringsukses en voorplantingsukses is vasgestel. Verskille tussen hierdie twee spesies, wat betref manlike territoriumgrootte- en kwaliteit, reflekteer die hoër *Protea* spesiesdiversiteit en boomdigtheid van die Kaapse suikervoël se habitat. Beide paringsukses (die aantal eiers gelê deur die wyfie van die paar) en voorplantingsukses (die aantal suksesvolle kleintjies) van die Kaapse suikervoël was hoër as dié van Gurney se suikervoël. Dit dui aan dat die beskikbare energie in nektar en Athropoda die parings- en voortplantingsukses van Gurney se suikervoël benadeel. Geen beduidende verskille in parings- of voorplantingsukses is gevind tussen die twee broeiseisoene van die Kaapse suikervoël nie.

Baie Kaapse suikervoëls het jaarliks na hulle vorige broeiterritoria teruggekeer. Die res is moontlik deur roofdiere gevang, of het elders gegaan om hul territoriumgrootte- en kwaliteit te verbeter. Die parings- en voortplantingsukses van manlike Kaapse suikervoëls was beduidend hoër vir mannetjies wat groot territoria, met 'n hoër nektar energie beskikbaarheid, verdedig het. Energie beskikbaarheid in arthropoda het nie parings- en voortplantingsukses van Kaapse suikervoëls beïnvloed nie, aangesien dit volop beskikbaar was. Daarenteen het die lae arthropoda energie beskikbaarheid geblyk om die voortplantingsukses van Gurney se suikervoël te benadeel, aangesien volwasse suikervoëls arthropoda vir hulle kleintjies voer.

Manlike suikervoëls het 'n verlengde stert en 'n knop op die sesde primêre vere, maar in die geval van beide spesies was daar nie 'n verband tussen ornamentlengte en parings- en voortplantingsukses nie. Stertlengte en vertonings van

suikervoëls mag belangrik wees vir territoriumbehoud aangesien manlike Kaapse suikervoëls in 1999 en manlike Gurney's suikervoëls met lang sterte, groter middel broeiseisoenterritoria verdedig het as mannetjies met kort sterte. Eweneens het manlike Gurney se suikervoëls met langer primêre veerknoppe groter territoria verdedig aan die einde van die broeiseisoen. Die verminderde seksuele dimorfisme in vlerk- en stertornamentasie by Gurney se suikervoël, mag die resultaat wees van lae voedselbeskikbaarheid, wat óf ornamentgroei benadeel, óf territorialiteit, met 'n gepaardgaande afname in die belangrikheid van ornamente wat in territoriumvertonings gebruik word.

Beide Kaapse en Gurney se suikervoëls het meer tyd gespandeer om bloeiwyses te ondersoek vir nektar, as om te soek vir arthropoda. Daar was tussen die twee spesies beduidende verskille in die tyd spandeer aan sekere aktiwiteite gedurende verskillende tye van die dag: Gurney se suikervoël het baie meer tyd geneem om buite die territorium te voed of in bome te skuil as die Kaapse suikervoël. Vir laasgenoemde was die tyd gespandeer om bloeiwyses te ondersoek vir nektar beduidend gekorreleerd met nektarvolume- en konsentrasie, sowel as met energie beskikbaarheid. Dit blyk dat hulle energie opbrengs maksimaliseer deur in die oggend op nektar van die bearded *Protea* te voed, en in die middag, wanneer nektar energie beskikbaarheid die hoogste is, op alle *Proteagroepe*. Daarenteen het Gurney se suikervoël ewe lank gevoed reg deur die dag. Kaapse suikervoëls het meestal op die bearded *Protea* gevoed tydens die middel van die broeiseisoen, maar meestal op die spoonbract *Protea* aan die einde van die broeiseisoen, nadat die bearded *Protea* reeds opgehou blom het.

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## Chapter 1: General introduction

### 1.1. Sexual selection

Current signalling theory suggests that receivers pay attention to signals to gain information about the signaller (Grafen 1990a; Evans 1997). Sexual selection is the selection for signals or traits that are solely concerned with increasing reproductive success (Darwin 1871). In mate choice, females assess particular signals to discriminate between different males as potential mates and to estimate the quality of the breeding opportunity (Evans & Hatchwell 1992a; Evans & Hatchwell 1992b; Lifjeld 1994; Moore 1994; Weatherhead & Boag 1995; Evans 1997). If some males have better genes than others, then by choosing good genes the female's offspring are better able to survive, compete and reproduce (Partridge 1980). Females may choose mates according to male territory size and quality (Cronin & Sherman 1976; Alatalo, Lundberg & Glynn 1986; Savalli 1994a), male potential parental care (Trivers 1972; Johnstone, Reynolds & Deutsch. 1996), their dominance (Ryan 1997), their position in a lek (Wiley 1974), past tradition (Greenwood 1980; Krebs & Davies 1993), by copying the choice of others (Ryan 1997; Savalli 1994b), or according to a physical or behavioural characteristics of the male (Catchpole 1980; Andersson 1982; Møller 1988; Evans 1991; Evans 1996).

### 1.2. Ornaments

Male ornaments are widespread in birds. They serve two main signalling functions: (1) advertisement to females for mate choice purposes (inter-sexual selection); and (2)

advertisement to males competing with other males for fertilisations or resources (intra-sexual selection) (Butcher & Rohwer 1989; Evans 1991).

The influence of ornaments on sexual selection has been the subject of many theoretical (Fisher 1930; Grafen 1990a) and field based studies (Andersson 1982; Møller 1988). Ornaments may have evolved from a female preference for male characters (Kirkpatrick 1982; Evans & Hatchwell 1992a; Evans & Hatchwell 1992b; Lifjeld 1994; Moore 1994; Johnstone 1995). For example, Catchpole (1980) found that male European sedge warblers with the most elaborate songs, containing many trills, whistles and buzzes, were the first to acquire mates in the beginning of the breeding season. There are two competing hypotheses to explain mate choice resulting in female preference for elaborate traits related to genetic benefits – Fisher's (runaway) hypothesis and the handicap hypothesis.

### 1.2.1. Fisher's (runaway) hypothesis

Fisher (1930) suggested that male ornaments make males more attractive to females. Females may have initially preferred a particular male trait: males with large ornaments may be better able to survive or, alternatively, the larger ornaments were easier to detect and females had a pre-existing sensory bias to respond to certain trait stimuli (Fisher 1930; Ryan, Fox, Wikzinski & Rand 1990; Birkhead & Møller 1993; Krebs & Davies 1993). As runaway positive feedback between female preference and male ornament size occurred the benefit of attractive sons eventually became the reason for mate choice (Zahavi 1975; Grafen 1990a; Krebs & Davies 1993; Roldan & Gomendio 1999). If ornament size in males is the result of genetic differences, the advantage will be passed on to the female's sons and preference for long tailed mates

in the female's daughters (Fisher 1930; Grafen 1990a; Roldan & Gomendio 1999). When the decrease in survival ability of males counter-balances sexual attractiveness, selection for increasing ornament size will stop (Harvey & Bradbury 1991).

### 1.2.2. Handicap hypothesis

The "handicap" suggests that a cost is necessary for the maintenance of honesty (Zahavi 1977; Krebs & Davies 1993; Johnstone 1995; Roldan & Gomendio 1999). Ornaments are costly to produce and maintain (Trivers 1972; Zahavi 1975; Johnstone 1995; Saino & Møller 1996). As individuals vary in quality, males only express the handicap when in good condition and when environmental resources are available (Grafen 1990a; Johnstone 1995; Saino & Møller 1996; Olsen and Owens 1998; Roldan & Gomendio 1999). For example, increased food availability might increase the size of signals and increased parasite load reduce them (Hamilton & Zuk 1982; Saino & Møller 1996; Sheldon & Verhulst 1996). Therefore elaborate and costly ornaments evolve to reliably reveal individual phenotypic or genotypic quality because of the differential costs of signals (Hamilton & Zuk 1982; Grafen 1990a; Johnstone 1995; Saino & Møller 1996; Roldan & Gomendio 1999). If the ability to survive despite the handicap of an ornament is heritable, then the capability to survive is passed on to offspring (Ryan 1997; Roldan & Gomendio 1999). The handicap principle alone, unaided and uninfluenced by the self-reinforcement of preferences discovered by Fisher, can account for the development of sexual ornaments (Zahavi 1975).

### 1.2.3. The influence of non-genetic benefits on mate choice

Females may choose mates according to direct (non-genetic) benefits which accrue to herself or to her progeny: for example, male territory size and quality may affect the success of breeding attempts of females (Alatalo *et al.* 1986; Partridge & Halliday 1984; Evans 1991). Male resources may be assessed directly, females choosing males defending large or high quality territories, with the female and her offspring benefiting from the resources available, and the male benefiting from higher mating success (Partridge & Halliday 1984; Evans 1991; Savalli 1994b). Ornament development may be constrained by the resources defended by the territorial male which may also be important direct benefits for the female, and may, therefore, provide an indication of the quality of those resources (Partridge & Halliday 1984).

As a result of female choice, males may compete for access to the resources that attract females (Savalli 1994a). If males with large or conspicuous ornaments were better able to defend territories through intrasexual competition, female choice would benefit those males through increased mating success (Evans 1991; Savalli 1994a). By choosing a male with the best resources, females also mate with a superior competitor and may gain genetic benefits without having to choose a male directly (Butcher & Rohwer 1989; Savalli 1994a).

Females may base mate choice on multiple signals – those providing genetic and non-genetic benefits (Savalli 1994a; Ryan 1997). Monogamous mates may be chosen according to resources defended by the male but males chosen for extra-pair copulations (EPCs) may have larger or more conspicuous ornaments (Savalli 1994a; Petrie & Kempnaars 1998). Therefore the signals influencing mate choice are not mutually exclusive but all influence the mating success of males (Harvey & Bradbury

1991).

### 1.3. Sugarbirds

There are two endemic southern African species of sugarbirds (Skead 1963; Skead 1967; Hall & Moreau 1970; Maclean 1993). They are the largest nectarivores in southern Africa. They have a very restricted distribution and show movements in response to the flowering phenology of their food plants, namely certain *Protea*, *Aloe* and other fynbos plant species (Rebelo 1987; Mostert, Siegfried & Louw 1980; de Swardt 1993a; de Swardt 1993b; de Swardt & Louw 1994). The distribution of the two sugarbird species is parapatric - overlapping distributions were last recorded in the Amatole Mountains in 1963 (Skead 1964; de Swardt 1997b; Fraser 1997), despite extensive censusing for the recent atlas project. Cape sugarbirds are common residents in the extreme south-west and southern Cape, whereas Gurney's sugarbirds are found in the Eastern Mpumalanga, Kwazulu-Natal and the Eastern Cape provinces. Gurney's sugarbirds have been described as being rare to locally common, usually occurring solitarily or in pairs, and sometimes in small, loose groups at good food sources (Skead 1963; Skead 1967; Maclean 1993; de Swardt 1997a; Fraser 1997). Their shy and retiring nature makes them less well known than the Cape sugarbirds and they are listed as "meriting careful monitoring" in the South African Red Data Book - Birds as they are found in small numbers and rarely seen (Brooke 1984).

### 1.3.1. Reproduction in sugarbirds

Sugarbirds breed during the peak flowering season of their favoured food plants. Therefore Cape sugarbirds breed during the winter, from March to September, and Gurney's sugarbirds breed during the summer, from September to March (Skead 1967). Sugarbirds may move in response to food availability but return to breeding sites at the beginning of the breeding season (Skead 1963; Skead 1967; Craig & Hulley 1994).

Sugarbirds form monogamous pairs at the beginning of the breeding season (Skead 1967; Seiler & Prys-Jones 1989). Monogamy is a prolonged association between one male and one female resulting in the production and raising of common offspring. Female sugarbirds, however, expend far more energy on the offspring than male sugarbirds as females build the nest, incubate the eggs alone and brood the nestlings with little help from the male (Skead 1967; de Swardt 1992). Although the male occasionally feeds the young, his main contribution to reproduction is the contribution of sperm and defence of the territory and nest (Skead 1967; Seiler & Prys-Jones 1989). Sugarbirds usually lay clutches of two eggs and may rear more than one clutch during the season (Broekhuysen 1963; Skead 1967; Seiler & Prys-Jones 1989).

### 1.3.2. The role of tail ornamentation in mate choice of sugarbirds

Cape sugarbirds show extraordinary sexual dimorphism in tail length: male tail length varies from 100 to 350 mm, whereas female tail length varies from 70 to 130 mm (Skead 1967; Friedman 1952; Seiler and Fraser 1985; Maclean 1993; Sinclair,

Hockey & Tarboton 1997). Gurney's sugarbirds, however, show much less sexual dimorphism in tail length - the ranges in tail length of the two sexes overlaps to a large extent as male tail length varies from 94 to 186 mm and female tail length up to 130 mm (de Swardt 1990). Elongated tails in sugarbirds is very likely to be a sexually selected feature, with that of Gurney's sugarbirds being more constrained by environmental conditions than Cape sugarbirds. Tail length could play an important role in both female choice and male-male competition. As investment in parental care by female sugarbirds is much greater than that by male sugarbirds (Skead 1967), male provisioning potential is unlikely to be an important selection pressure in female mate choice, which could be based on either genetic or non-genetic benefits.

In addition, sugarbirds have a roughly triangular bulge on their sixth primary feathers that can make a "clacking" sound during flight (Seiler & Fraser 1985; de Swardt 1990). These ornaments play a role in male sugarbirds' elaborate tail-whipping and wing "clacking" display flights that are often performed in response to territory intruders or to other male displays (Skead 1967) and may influence the abilities of males to defend territories and attract mates.

#### 1.4. Territoriality

A home range is the area in which an animal lives, exclusive of migrations, emigrations, or unusual erratic wanderings (Brown & Orians 1970). Home range is defined only by the presence of the individual, not by particular behaviour patterns (Brown & Orians 1970). The degree to which a home range overlaps intra-specifically varies between species - in some there is no overlap while in others it may be almost complete (Brown & Orians 1970). Although nonoverlap may be caused by mutual

avoidance, physical barriers or differing habitat preferences, in most cases the causative factor for non-overlap of home ranges is territorial behaviour (Brown & Orians 1970; Pyke, Christy & Major 1996). Territoriality occurs when an animal defends a spatially limited site against another, thus restricting the use of environmental resources to satisfy its own requirements (Wolf 1969; Stiles & Wolf 1970; Gass, Angher & Centa 1976; Hixon, Carpenter & Paton 1983; Beletsky & Orians 1987; Pyke *et al.* 1996; Gordon 1997). Resources may include food, nesting sites, shelter or mates (Armstrong 1996; Evans 1996).

Territories are usually fixed areas that may change slightly over time - territories being regulated to maintain a constant energy supply (Brown 1964; Gass *et al.* 1976; Eberhard & Ewald 1994). Owners may adjust territory size as a direct response to food availability, or as an indirect response through effects of food availability on intrusion pressure (Evans 1991; Eberhard & Ewald 1994). Theoretical analyses predict that territory size should decrease as food availability increases under most but not all conditions (Brown & Orians 1970; Hixon 1982; Evans 1991; Eberhard & Ewald 1994).

### 1.5. Territoriality in nectarivorous birds

Nectarivorous birds are adapted to feeding from nectar-producing inflorescences as they have elongated, often decurved bills and specialised tongues with which they can extract nectar (Skead 1967; Daniels 1987). Although nectar is an important energy source, nectarivorous birds also feed on arthropods (Recher & Abbott 1970; Mostert *et al.* 1980; de Swardt & Louw 1994). Arthropods are not only an energy source but provide proteins, lipids and other nutrients (Skead 1967; Ford & Paton 1976; Mostert

*et al.* 1980; Gass & Montgomerie 1981; Baker & Baker 1986). The population density, localised movements and breeding seasons of nectarivores depend on food availability which is determined by the flowering season of their food plants (Wooller 1982; Rebelo *et al.* 1984; Paton 1985; Rebelo 1987; Dowsett-Lamaire 1989; de Swardt 1991; Craig & Hulley 1994; Eberhard & Ewald 1994; Evans 1996; McFarland 1996).

#### 1.5.1. Economic defendability in nectarivore territoriality

Studies of nectarivores have resulted in seemingly inconsistent relationships among territory size, food availability and intrusion rate (Eberhard & Ewald 1994). Birds can assess territory quality through inflorescence inspection and sampling of nectar over a number of days and this allows them to make adjustments in territory size in response to food availability (Eberhard & Ewald 1994). Defence of inflorescences, from which nectar can be extracted, seems to be an adaptive response to limited food resource availability (Brown 1964; Stiles & Wolf 1970; Gill & Wolf 1975; Frost & Frost 1980). For example, Hawaiian honeycreepers defend territories at some times but not at others (Carpenter 1987). Territorial behaviour disappeared when the increase in food availability resulting from territory defence was inadequate to pay for the cost of defence when resources were scarce (Carpenter & MacMillan 1976; Carpenter 1987). This is the “lower threshold” of food productivity for territoriality - the resource was economically undefendable (Carpenter 1987). Individuals abandoned their territories and may move to other areas where richer food sources are found (Gill & Wolf 1975). Territoriality in honeycreepers, golden-winged and olive (*Nectarinia olivacea*) sunbirds disappeared above another, higher level of food availability, the “upper

threshold” (Gill & Wolf 1975; Carpenter 1987). Territoriality was abandoned because individuals did not gain energetic benefit from the defence of extra inflorescences and the costs of territorial defence due to high intruder rate could not be recoverable (Gill & Wolf 1975; Carpenter 1987). Therefore territory defence occurs only when the energetic gain from territoriality exceeds the costs of defence (Brown 1964).

### 1.5.2. Optimal territory size

Nonmanipulative studies of nectarivorous birds document strong negative correlations between food abundance and territory size (Gass *et al.* 1976; Gill & Wolf 1975). Nectarivores defend territories of a size that maximises energy gain (Carpenter, Paton & Hixon 1983; Hixon *et al.* 1983). Reductions in food abundance increased territory size of rufous hummingbirds (*Selasphorus rufus*) and New Holland honeyeaters (*Phylidonyris novaehollandae*) (Hixon *et al.* 1983; McFarland 1986). Gass (1979) found that rufous hummingbirds with better quality territories, more inflorescences available, foraged more efficiently and had more time for territory defence than individuals with poorer territories. Individuals with poorer territories, however, spent less time in territory defence and more time foraging (Gass *et al.* 1976). These individuals also spent more time foraging away from the territory (Gass *et al.* 1976; Paton 1985; McFarland 1986; Pyke *et al.* 1996). Increases in intrusion rate resulted in a decrease in feeding territory size of black-chinned hummingbirds (*Archilochus alexandri*) and Anna’s hummingbirds (*Calypte anna*) (Norton, Arcese & Ewald 1982; Eberhard & Ewald 1994). Therefore territory size is dependent on food availability and intruder pressure and changes in territory size occur in order to maximise energy gain.

### 1.5.3. The effect of territory size and quality on reproductive success

In many animal species males defend breeding territories containing resources which play a crucial role in the survival of a female's eggs or young (Ryan 1997). Food is a resource which often limits a female's capacity to produce eggs, and consequently territorial male birds need to defend adequate resources for himself, his mate and his offspring during the breeding season. For example, Evans (1996) found that male scarlet-tufted malachite sunbirds (*Nectarinia johnstonii*) with small territories precluded themselves from breeding as their territories were too small to support a male, a female and potential offspring. Males with large territories spent more time defending their territories than males with smaller territories but produced more offspring as females were more likely to lay larger clutches (Evans 1996). Territory size and quality can, therefore, affect reproductive success.

### 1.5.4. Improving territory size and quality

Site fidelity - returning to or remaining in the same breeding territory in subsequent breeding seasons - should be advantageous as the individual has knowledge of food resources, predator habits, hiding places and conspecific neighbours (Beletsky & Orians 1987). Males with small or poor quality territories may, however, attempt to take over a larger or better quality territory. For example, male red-winged blackbirds (*Agelaius phoeniceus*) remained on the same breeding territory if they bred in successive years (Beletsky & Orians 1987). After a season of poor breeding success, territorial individuals moved territories (Beletsky & Orians 1987). Although the male risked failure of take-over or even loss of his former territory, and time and energy

was spent in familiarisation with the new territory, the better quality territory improved reproductive success (Beletsky & Orians 1987). Males may also increase their original territory by annexing parts of adjacent territories, with a resultant increase in reproductive success (Beletsky & Orians 1987).

#### 1.5.5. The role of ornaments in territory ownership competition

Ornaments may be favoured by increased intrasexual selection among males competing for territories. Territory defence does not only include detecting and chasing off intruders but also advertisement. Sound production or extravagant plumage can be used to advertise in territory ownership displays (Peek 1972; Miller & Inouye 1983; Savalli 1994a). For example, male broad-tailed hummingbirds produce a wing whistle, male red-winged blackbirds (*Agelaius phoeniceus*) have red epaulets on their wings and male yellow-shouldered widowbirds (*Euplectes macrourus*) have elongated tails (Peek 1972; Miller & Inouye 1983; Savalli 1994a; 1994b). The removal of these ornaments resulted in a reduction in the males' success in aggressive encounters with other individuals and maintenance of their territories (Peek 1972; Miller & Inouye 1983; Savalli 1994a). Andersson (1982), however, found no relationship between tail length and territory holding capabilities in long-tailed widowbirds (*Euplectes progne*) although males with shorter tails had a higher rate of territory defence and display.

## 1.6. Territoriality in sugarbirds

Breeding male sugarbirds defend large territories. Their territorial behaviour involves singing from perches in the territory, chasing intruders from the territory and advertisement displays (Skead 1967; Steyn 1997). Like rufous hummingbirds (Gass 1979), sugarbird males fly closer to the ground, are quieter and less challenging when intruding into another individual's territory (Skead 1967). Seiler and Prys-Jones (1989) observed the frequency of displays by resident male Cape sugarbirds to increase with an increase of core intrusions by strange males. Both were correlated with the time covering the presumed fertile period of the resident female (Seiler & Prys-Jones 1989). Boundary skirmishes were part of ongoing territory demarcation (Seiler & Prys-Jones 1989).

Sugarbirds coexist with several sunbird species and as in Hawaiian honeycreepers (Stiles & Wolf 1970; Carpenter 1987), inter- and intraspecific competition for resources have been observed (Skead 1967; Seiler & Prys-Jones 1989; Rebelo 1987). Although male sugarbirds actively defend their territories against all other bird species, interspecific territorial exclusion does not occur completely (Skead 1967). Morphological differences in size and shape or behavioural differences (Martin & Thibault 1996) may make ecological segregation resulting from subtle differences in habitat use possible (Skead 1967).

### 1.6.1. Feeding preferences and territory size and quality of sugarbirds

Sugarbirds typically feed by probing *Protea* inflorescences for nectar and arthropods associated with the inflorescences (Skead 1967; Mostert *et al.* 1980; de Swardt &

Louw 1994). The size and quality of male sugarbird territories is, therefore, affected by the number of inflorescences available (Mostert *et al.* 1980; Daniels 1987; de Swardt & Louw 1994). Nectar volume and concentration of the inflorescences varies between the different *Protea* species (Skead 1967; Mostert *et al.* 1980) and different arthropod species may be associated with the different *Protea* species (de Swardt & Louw 1994). Therefore some *Protea* species may be preferred to others if they offer higher quality resources, and improve territory size and quality. Hawking for arthropods may be energetically expensive compared to feeding on nectar (Recher & Abbott 1970). Therefore sugarbirds may feed more extensively on nectar as an energy source whilst obtaining required protein and other nutrients from arthropods.

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**A comparison of territory size and quality in Cape and Gurney's Sugarbirds  
(*Promerops cafer* and *Promerops gurneyi*)**

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Running header: Calf *et al.* – territory size and quality of sugarbirds

## Summary

Territory size and quality were determined for Cape and Gurney's sugarbirds in Helderberg Nature Reserve, Western Cape, and Qwaqwa National Park, eastern Free State respectively. Differences in territory size and quality between the two sugarbird species reflects the higher *Protea* species diversity and tree density of Cape sugarbird habitat in the reserve. Cape sugarbirds returned annually to their previous breeding territories; the territories of non returning males were taken over by new males or annexed into other territories. Non returning males had smaller territories and lower mating and reproductive success in the previous season than returning males, and may have moved elsewhere to improve territory size and quality, or they may have been predated on. No changes in territory size in response to changes in food availability were observed for Cape sugarbirds during the course of the breeding season, or between seasons. Changes in territory size of Gurney's sugarbirds reflect increases in territorial competition and number of inflorescences at mid breeding season. Gurney's sugarbirds had significantly larger territories, with more inflorescences than Cape sugarbirds at mid and at the end of the breeding season, possibly on account of low nectar energy availability from the inflorescences. Cape sugarbird territories contained significantly more arthropod energy than those of Gurney's sugarbirds, again reflecting low food availability from inflorescences. The large territory size and low nectar and arthropod energy availability may constrain mating and reproductive success in Gurney's sugarbirds. Although territory size and quality of Cape sugarbirds in 1998 were not correlated with secondary sex characters measured, male Cape sugarbirds with long tails defended larger mid breeding season territories than males with short tails in 1999. Similarly, male Gurney's sugarbirds with longer tails

defended larger territories in the middle and at the end of the breeding season, and males with longer primary feather bulges defended larger territories at the end of the breeding season. This indicates that tail length and displays of sugarbirds may be important in territory maintenance.

**Keywords:** ornamentation, foraging, intra-sexual selection

## Introduction

Territoriality occurs when an animal defends a spatially limited site against another, thus restricting the use of environmental resources to satisfy its own requirements (Gass, Angehr & Centa 1976; Pyke, Christy & Major 1996). Resources may include food, nesting sites, shelter or mates (Armstrong 1996).

Nectarivorous birds feed mostly on nectar but obtain proteins, lipids and other nutrients from arthropods associated with nectar-producing inflorescences (Recher & Abbott 1970; Ford & Paton 1976; Mostert, Siegfried & Louw 1980; de Swardt & Louw 1994). Therefore food availability is constrained by the flowering season of their chosen food plants (Craig & Hulley 1994).

Territoriality may be advantageous to nectarivores, the degree of territoriality varying in response to changes in inflorescence availability (Carpenter 1987; Armstrong 1991). For example, Anna's Hummingbirds (*Calypte anna*) lower territorial exclusiveness with a decline in energy rewards (Ewald & Carpenter 1978), and Hawaiian honeycreepers abandon territoriality altogether when the energetic costs of territorial defence are too high to derive an energetic benefit from doing so (Carpenter 1987). On the other hand, Craig and Douglas (1986) found that New Zealand bellbirds (*Anthornis melanura*) defended territories when nectar sources were dispersed, but had a fixed dominance hierarchy when nectar sources were concentrated in a single tree.

Territories are usually fixed areas that may change slightly over time - being regulated in order to maximise the energy gain from defended resources (Brown 1964; Gass *et al.* 1976; Carpenter, Paton & Hixon 1983; Hixon, Carpenter & Paton

1983). Therefore territories may change in response to changes in food availability and/or intruder pressure.

Research has focussed on territoriality of nectarivores during non-breeding periods because it is thought that non-breeding territoriality may be explained purely by energy-based economic models (Carpenter 1987; Armstrong 1991). Breeding birds may also adjust their territories in response to energetic changes, but this may be complicated by other factors (Armstrong 1991).

There are two species in the southern African endemic family Promeropidae: Cape sugarbirds (*Promerops cafer*) and Gurney's sugarbirds (*P. gurneyi*) (Skead 1967; Maclean 1993). Breeding males of both species actively defend territories (Skead 1967). For example, male Cape sugarbirds displaced orangebreasted sunbirds (*Nectarinia violacea*) from *Leucospermum conocarpodendron* inflorescences (Wooller 1982) and Gurney's sugarbirds displaced malachite sunbirds (*Nectarinia famosa*) from *Protea* inflorescences (de Swardt 1993). Although male sugarbirds defend territories, complete territorial exclusion does not occur (Skead 1963; Skead 1967; Rebelo, Siegfried & Louw 1984).

Female birds may maintain permanent social pairings to ensure the maintenance of a permanent territory with exclusive use of resources: for example, splendid fairy wrens (*Marurus splendens*) (Brooker & Rowley 1995). Sugarbirds, however, often leave their breeding territories in search of food during summer and return to the same breeding sites each year (Craig & Hulley 1994; Henderson unpublished data) and therefore territory size and quality may play a role in mate choice of sugarbirds and thus affect the breeding success of individuals. Females may base their choice of mate on (1) the abundance of some resource within the male's territory independent of territory area; (2) the territory area independent of resource

density; or (3) the quality of the male himself, in which case territory size and quality are unimportant (Hixon 1987). In practice, it may not be possible to separate these parameters as they can be related to each other.

The size and quality of male sugarbird territories is defined by the area defended and the number of inflorescences available for feeding within that defended area. In many species of birds variation in breeding success has been attributed to differences in territory quality. For example, magpies (*Pica pica*) occupying preferred territories with better resources had a higher breeding success in terms of the proportion of years in which some chicks fledged, and the mean number of young fledged each year, than those in less favoured territories (Goodburn 1990). To improve breeding success, individuals improve territory size and quality by moving to areas with richer resources or increasing existing territories by annexing parts of other territories into their own (Petersen & Best 1987; Goodburn 1990; Pyke *et al.* 1996). Therefore it was predicted that male sugarbirds move or increase the size of their territories to improve energy availability and as a result improve mating (the number of eggs) and reproductive (the number of chicks fledged) success during and between breeding seasons.

The distribution of the two sugarbird species is parapatric - overlapping distributions were last recorded in the Amatole Mountains in 1963 (Skead 1964; de Swardt 1997b; Fraser 1997), despite extensive censusing for the recent atlas project. Cape sugarbirds are common in fynbos vegetation, dominated by members of the Proteacea family, in the extreme south-west and southern Cape. Gurney's are rare to locally common, usually occurring solitarily or in pairs, and sometimes in small, loose groups at good food sources in montane grasslands, again characterised by belts of *Protea* trees, in eastern Mpumalanga, Kwazulu-Natal and the Eastern Cape provinces

(Skead 1963; Skead 1967; Maclean 1993; Sinclair, Hockey & Tarboton 1997; de Swardt 1997; Fraser 1997). As the habitat of the two species differs, it was predicted that there would be differences in territory size and quality between the two species.

Sound production or extravagant plumage can be used to display territory ownership, in addition to being important in mate choice (Peek 1972; Miller & Inouye 1983; Savalli 1994). For example, the removal of wing ornaments of male broad-tailed hummingbirds that produce a wing whistle resulted in a reduction in male success in aggressive encounters with other individuals and their ability to maintain territories (Miller & Inouye 1983). Male sugarbirds have sexual dimorphism in tail length, that in Cape sugarbirds being greater than that in Gurney's sugarbirds (Seiler & Fraser 1985; de Swardt 1990). In addition to their elongated tails, male sugarbirds have almost triangular bulges on their sixth primary feathers which are used in a wing "clacking", tail flicking display flight that occurs in response to other male displays and after intruder chases (Skead 1967). This display flight may be used in advertising for mates, but it also serves as a territorial advertisement to other males (Skead 1967). Therefore it was predicted that males with longer tails and larger sixth primary feather bulges were able to obtain and defend larger, better quality territories due to their more elaborate territorial advertisement.

The aim of this study was to compare the two species of sugarbirds in terms of (1) male territory size and quality; (2) adjustments in territory size in response to changes in energy availability during the breeding season and between seasons; and (3) the importance of male secondary sexual characters in obtaining and holding territories.

## Materials and methods

### Study site

Cape sugarbirds were studied at Helderberg Nature Reserve, Western Cape (34° 03'S to 34° 05'S, 18° 52'E to 18° 53'E) during the breeding season, between March and September of 1998 and 1999. The study site was a small portion of the entire 480 ha reserve, comprising 26 ha on the south-facing slope of the Helderberg Mountain. Despite its small size the site contained 5218 *Protea* trees in the study area. Many of the *Protea* trees had initially been planted in 1974, therefore the *Protea* species composition and tree density in the study site was higher than that found naturally in the Cape.

Gurney's sugarbirds were studied in Qwaqwa National Park (QNP), eastern Free State (28° 24'S to 28° 35'S, 28° 32'E to 28° 49'E), for one breeding season. Observations began in early September 1998 and continued to the end of February 1999. The study area in QNP consisted of 5078 naturally growing *Protea* trees divided into two sites. The first, dominated by *Protea caffra*, was 83 ha in size. The second, dominated by *Protea roupelliae*, was 58 ha in size.

### Identification of individuals

Birds were captured in mist nets, and individuals were banded with aluminium SAFRING leg bands and unique combinations of plastic colour leg bands for identification. The mass of the birds was determined using a Salter balance; wing was measured with a wingrule; tail length with long aluminium ruler; and tarsus, culmen,

head and the sixth primary feather bulge were measured with Digimax callipers. Birds were then released at the site of their capture.

### Mapping of territories

All the *Protea* trees in the study sites were initially tagged using numbered, plastic nursery tags. Different species of *Protea* were identified with the help of Dr. John Rourke of the National Botanical Institute at Kirstenbosch Botanical Gardens. A Trimble TDC1 Global Positioning System (GPS) was then used to map individual trees in Helderberg Nature Reserve, and a Geoexplorer II was used in Qwaqwa National Park. Different GPSs were used as the high density of trees at Helderberg Nature Reserve demanded more accurate mapping of individual trees than required in Qwaqwa National Park, where the trees were widely spaced. The species, number, height and diameter of the each tree were recorded. These data were then downloaded into PATHFINDER, an interface program and corrected using data available on the internet from Telkom and Eskom, before being transferred into a Geographical Information System (GIS), ARCVIEW.

Territorial behaviour was observed for the sugarbirds. Birds within randomly chosen 100m x 100m areas were observed for half an hour at a time. A minimum of three observations were made in each area, and all individuals displaying and singing and all intra- and interspecific interactions were observed during this time. Ownership of trees was assigned according to these observations. Trees were classified as being owned if they were used for displays or were defended from other individuals through aggressive interactions. These data were used to create a territory map in ARCVIEW.

### Inflorescence availability

Once a month the number of inflorescences of 25 trees of each *Protea* species were counted. Inflorescences were divided into four categories: bud, just open, fully open and seed/dead. Seed/dead inflorescences were not counted as they were not used as a food source. The number of buds available was counted to provide an indication of future flower availability but was not used in further analyses. The number of partially and fully open inflorescences available in the study site could then be extrapolated from the average number of inflorescences of each *Protea* species and the number of trees in the study site (van Tets in press). The total number of inflorescences was the sum of the number of partially open and the number of fully open inflorescences available.

### Arthropod energy availability

Once a month six inflorescences of each *Protea* species were collected at random. Arthropods were separated from the inflorescences, dried and weighed to determine biomass (Mostert *et al.* 1980). Arthropod energy availability within individual *Protea* inflorescences was determined using the energy value of arthropods calculated by Golley (1961). Energy availability from arthropods for individual trees of each *Protea* species and then for individual territories were determined through extrapolation (van Tets in press).

## Male breeding success

For each breeding season, nesting success of individual birds was monitored and if individuals showed any signs of nesting behaviour they were observed. New nests were also sought by checking individual trees in the study site. Number of eggs laid and the number of chicks reared successfully by each pair were counted, and chicks were ringed prior to their fledging. The mating success (the number of eggs laid by the female), and the reproductive success (the number of offspring produced) of the males were determined over the six month breeding seasons for Cape and Gurney's sugarbirds.

## Statistical analysis

In cases where means were determined, they were given as  $x \pm SD$ . The data was not normally distributed; therefore nonparametric statistical methods were used (Siegal & Castellan 1988). Comparisons of territory size and quality, wing and tail ornament size and mating and reproductive success between Cape and Gurney's sugarbirds and between individuals within the same species between and within breeding seasons were performed using Mann Whitney U tests, Wilcoxon ranks tests and Friedman ANOVA (Siegal & Castellan 1988). Spearman rank correlations were performed to determine correlates of wing and tail ornament size and territory size and quality (Siegal & Castellan 1988). STATISTICA was used to determine all statistical results (Statsoft, Inc. 1983-1984).

## Results

### Male territory size and quality

Both species of sugarbirds were highly territorial during the breeding season.

Individual territories were mapped for both Cape and Gurney's sugarbirds (Figures 1a to 1d and Figures 2a to 2c respectively).

Territory data for Cape sugarbirds was collected in the middle of the breeding season during 1998 – between May and July (Figure 1a). In 1999 three sets of territory data were collected: one at the beginning (April and May), one in the middle (June and July), and one at the end (August and September) of the breeding season. The entire study site had 5218 trees, of which 3830 (78%) fell within the boundaries of the 11 territorial birds in mid-breeding season 1998, and 4986 (96%) fell within the boundaries of the 10 territorial pairs at mid-breeding season in 1999.

During 1998 Cape sugarbird territory size varied from 207 m<sup>2</sup> of the Pair 7 male to 25880 m<sup>2</sup> of the Pair 1 male, with a mean territory size of 7134 ± 8757 m<sup>2</sup> for the 11 territorial males (Figure 1a; Table 1). In 1999, mid season territory size varied from 3548 m<sup>2</sup> of the Pair 14 male to 20185 m<sup>2</sup> of the Pair 5 male. Mean territory size in 1999 varied during the season from 8024 ± 6078 m<sup>2</sup> in April and May, to 7727 ± 5965 m<sup>2</sup> in June and July, to 9032 ± 6819 m<sup>2</sup> in August and September (n = 10) (Figures 1b to 1d; Table 1).

Three sets of territory data were collected for Gurney's sugarbirds: one at the beginning (September and October), one in the middle (November and December) and one at the end (January and February) of the breeding season. The entire study site contained 5078 trees, 3378 of which were in the site dominated by *Protea caffra*,

and 1699 in the site dominated by *Protea roupelliae*. In the early season 1426 trees (28%), at mid season 3730 trees (73%), and at the end of the season 3703 trees (73%), fell within the boundaries of the territorial birds. Mid breeding season territory size varied from 5506 m<sup>2</sup> of Pair 5 male to 65685 m<sup>2</sup> of Pair 11 male (Figure 2b; Table 2). Mean territory size varied from 27225 ± 40015 m<sup>2</sup> for the four territorial males in September and October, to 73388 ± 130782 m<sup>2</sup> for the 11 territorial males in November and December, to 112124 ± 156033 m<sup>2</sup> for the seven territorial males in January and February (Figures 2a to 2c; Table 2). Territory sizes for both species were thus highly variable, but those for Gurney's sugarbirds were on average far larger than those of Cape sugarbirds.

#### Cape sugarbird adjustments in territory size between breeding seasons

Territory size and position for individuals returning to Helderberg Nature Reserve in 1999 varied slightly from previous territories (Figures 1a and 1c; Tables 1 and 3). Six of the 11 territorial males observed in 1998 returned to the study site in the beginning of the breeding season in 1999. The Pair 5 male did not return to the study site in 1999, but his 1998 mate returned to the same breeding site and mated with the male that had taken over the territory. The Pair 5 male defended a superior territory in 1998 and produced two fledglings, and it was therefore assumed that this male was predated on rather than moved elsewhere to establish a new territory. The new male had been caught and banded in 1998, but had not been able to obtain a territory in the site that year. The males not returning to the study site in 1999 (excluding the Pair 5 male) defended smaller territories in 1998 than the returning males (Mann Whitney U test:  $U = 0$ ,  $p = 0.01$ ,  $n_1 = 6$ ,  $n_2 = 4$ ), but there was no significant difference in the

number of inflorescences ( $U = 3$ ,  $p = 0.06$ ,  $n_1 = 6$ ,  $n_2 = 4$ ) or in arthropod energy availability ( $U = 7$ ,  $p = 0.29$ ,  $n_1 = 6$ ,  $n_2 = 4$ ) (Tables 1 and 3) on their territories. Of the non returning males none successfully reared fledglings in 1998, and they had a significantly lower mating ( $U = 2$ ,  $p = 0.03$ ,  $n_1 = 6$ ,  $n_2 = 4$ ) and reproductive ( $U = 0$ ,  $p = 0.01$ ,  $n_1 = 6$ ,  $n_2 = 4$ ) success than returning males. Only five of the returning birds maintained territory ownership until the end of the breeding season in 1999: the sixth male, (Pair 6), either left the site or was predated on early in the season without reproducing. The territories of those males not returning to the site were taken over by new males or annexed into existing territories by returning males. There was, however, no significant difference in territory size for the five returning territory owners between mid 1998 and mid 1999 breeding seasons (Wilcoxon matched pairs test:  $z = 0.67$ ,  $n = 5$ ,  $p = 0.50$ ). Only one male that returned to the study site paired with his mate from the previous year, while all the rest paired with new females. In one case, a female “divorced” her previous mate in an adjacent territory to pair up with a new territorial male.

There were no significant differences in territory size ( $U = 40$ ,  $p = 0.29$ ,  $n_1 = 10$ ,  $n_2 = 11$ ), number of inflorescences ( $U = 54$ ,  $p = 0.67$ ,  $n_1 = 10$ ,  $n_2 = 11$ ) or arthropod energy availability ( $U = 57$ ,  $p = 0.82$ ,  $n_1 = 10$ ,  $n_2 = 11$ ) at mid breeding season between 1998 and 1999 for all territorial Cape sugarbird males in the study site (Tables 1 and 3).

#### Adjustments in territory size during the course of the breeding season

There were no significant changes in territory size of Cape sugarbirds during the course of their breeding season in 1999 (Friedman ANOVA:  $\chi^2$  ( $n = 10$ ,  $df = 2$ ) =

1.82,  $p < 0.40$ ; Figures 1b to 1d; Table 1). In Gurney's sugarbirds, only two pairs maintained territories throughout the season, so a statistical analysis of change in territory size was not possible. In both these pairs, territory size decreased at mid season when more birds established territories, and increased again at the end when they left the site (Figures 2a to 2c; Table 2). An additional two males defended territories at the beginning of the breeding season, but left when competition increased at mid breeding season. Of a further five pairs which established territories at mid season and maintained them until the end of the season, four remained constant, and only one increased in size (Figures 2a to 2c; Table 2).

Cape sugarbirds had more inflorescences ( $\chi^2 (n = 11, df = 5) = 23.06, p < 0.0003$ ) and more arthropod energy available ( $\chi^2 (n = 11, df = 5) = 32.32, p < 0.00001$ ) at the beginning of the breeding season, compared to both the middle and the end. For Gurney's sugarbirds, by contrast, there were more inflorescences ( $\chi^2 (n = 13, df = 5) = 33.36, p < 0.00000$ ) and arthropod energy available ( $\chi^2 (n = 13, df = 5) = 27.98, p < 0.00004$ ) in the middle of the breeding season than at either the beginning or the end.

#### Comparison of Cape and Gurney's sugarbird territory size and quality

The density and species diversity of *Protea* trees varied between the two study sites (Appendix 1). The site at Helderberg Nature Reserve contained 14 different *Protea* species, which were originally planted, and were at a density of 202 trees/ha. The site at QNP contained three different naturally-growing *Protea* species at a density of 36 trees/ha. All comparisons in this paragraph are made between Gurney's sugarbirds and Cape sugarbirds in 1999, when data were collected at three different stages of the

breeding season. There was no significant difference in territory size between Cape sugarbirds and Gurney's sugarbirds early in the breeding season ( $U = 10$ ,  $p = 0.16$ ,  $n_1 = 10$ ,  $n_2 = 4$ ) but Gurney's sugarbird territories were significantly larger than those of Cape sugarbirds at mid breeding season ( $U = 7$ ,  $p = 0.0007$ ,  $n_1 = 10$ ,  $n_2 = 11$ ) and at the end of the breeding season ( $U = 0$ ,  $p = 0.0006$ ,  $n_1 = 10$ ,  $n_2 = 7$ ). Gurney's sugarbirds had significantly more inflorescences on their territories than Cape sugarbirds at early ( $U = 2$ ,  $p = 0.01$ ,  $n_1 = 10$ ,  $n_2 = 4$ ), mid ( $U = 12$ ,  $p = 0.002$ ,  $n_1 = 10$ ,  $n_2 = 11$ ) and end ( $U = 0$ ,  $p = 0.0006$ ,  $n_1 = 10$ ,  $n_2 = 7$ ) breeding season. Cape sugarbird territories contained significantly more energy from arthropods than those of Gurney's sugarbirds at early ( $U = 2$ ,  $p = 0.01$ ,  $n_1 = 10$ ,  $n_2 = 4$ ), mid ( $U = 0$ ,  $p = 0.0002$ ,  $n_1 = 10$ ,  $n_2 = 11$ ) and end ( $U = 0$ ,  $p = 0.006$ ,  $n_1 = 10$ ,  $n_2 = 7$ ) breeding season.

The importance of secondary sexual characteristics in territory size and quality

Mean tail length for Cape sugarbirds was  $308.13 \pm 37.09$  mm ( $n = 8$ ) in 1998, and  $313.19 \pm 20.07$  mm ( $n = 8$ ) in 1999, while the length of the sixth primary feather bulge was  $42.57 \pm 3.41$  mm ( $n = 7$ ) in 1998 and  $38.44 \pm 3.87$  mm ( $n = 7$ ) in 1999. There was no significant difference in tail length ( $U = 25$ ,  $p = 0.46$ ,  $n_1 = 8$ ,  $n_2 = 8$ ) or the length of the sixth primary feather bulge ( $U = 10$ ,  $p = 0.06$ ,  $n_1 = 7$ ,  $n_2 = 7$ ) of Cape sugarbirds between the two seasons. Nor was there any significant difference in tail length (Wilcoxon matched pairs test:  $z = 1.46$ ,  $n = 4$ ,  $p = 0.14$ ) or the length of the sixth primary feather bulge ( $z = 1.60$ ,  $n = 3$ ,  $p = 0.11$ ) for the same individuals between the two seasons.

Neither tail length nor sixth primary feather bulge length in Cape sugarbirds were significantly correlated with number of inflorescences, arthropod energy

availability or territory size in the middle of the breeding season in 1998 (Table 5). By contrast, in 1999, male Cape sugarbirds with long tails defended larger mid breeding season territories (Table 5), and males with longer sixth primary feather bulges defended more inflorescences over the entire breeding season (Spearman rank correlation:  $r_s = 0.89$ ,  $n = 7$ ,  $p = 0.007$ ).

Male Gurney's sugarbirds mean tail length ( $89.6 \pm 8.54$  mm,  $n = 10$ ) was between a third and a quarter of that of Cape sugarbirds, and the mean length of the sixth primary feather bulge length ( $27.7 \pm 5.56$  mm,  $n = 10$ ) was approximately two thirds that of Cape sugarbirds ( $27.7 \pm 5.56$  mm,  $n = 10$ ). These differences are significant both for tail length ( $U = 0$ ,  $p = 0.0004$ ,  $n_1 = 8$ ,  $n_2 = 10$ ) and sixth primary feather bulge ( $U = 4.5$ ,  $p = 0.003$ ,  $n_1 = 7$ ,  $n_2 = 10$ ). Gurney's sugarbird males with longer tails defended larger territories in the middle (Table 5) and at the end ( $r_s = 0.88$ ,  $n = 10$ ,  $p = 0.0007$ ), but not at the beginning ( $r_s = 0.37$ ,  $n = 10$ ,  $p = 0.29$ ) of the breeding season. Males with longer sixth primary feather bulges defended larger territories only at the end of the season ( $r_s = 0.67$ ,  $n = 10$ ,  $p = 0.04$ ), and more inflorescences over the entire breeding season ( $r_s = 0.66$ ,  $n = 10$ ,  $p = 0.04$ ).

#### Male breeding success

Eleven pairs of Cape sugarbirds were observed in 1998 and ten in 1999. In 1998 20 eggs were laid and 16 chicks fledged successfully, whereas in 1999 30 eggs were laid, but only 18 chicks fledged successfully. The low fledgling success in relation to the number of eggs laid in 1999 was due to predation, as six pairs lost their offspring during the season compared to only two pairs in 1998. Neither mating ( $U = 37.5$ ,  $p =$

0.22,  $n_1 = 10$ ,  $n_2 = 11$ ) nor reproductive success ( $U = 49.5$ ,  $p = 0.39$ ,  $n_1 = 10$ ,  $n_2 = 11$ ) differed between the two breeding seasons.

In both 1998 and 1999 more Cape sugarbird eggs were laid and more Cape sugarbird chicks successfully fledged than Gurney's sugarbirds, but in both cases these differences were marginally significant for mating success ( $U = 35$ ,  $p = 0.07$ ,  $n_1 = 11$ ,  $n_2 = 11$ ) and reproductive success ( $U = 35$ ,  $p = 0.07$ ,  $n_1 = 11$ ,  $n_2 = 11$ ) between Cape sugarbirds in 1998 and Gurney's sugarbirds. Cape sugarbirds in 1999, however, had a higher mating success ( $U = 28$ ,  $p = 0.04$ ,  $n_1 = 10$ ,  $n_2 = 11$ ) and reproductive success ( $U = 30.5$ ,  $p = 0.04$ ,  $n_1 = 10$ ,  $n_2 = 11$ ) than Gurney's sugarbirds.

Of the eleven pairs of Gurney's sugarbirds, only four attempted nesting: one pair deserted the nest before laying, and the remaining three pairs laid ten eggs, one female laying six eggs. Of the ten eggs laid, only five chicks fledged successfully. Although the number of inflorescences available on individual territories did not differ between the two sugarbird species, Gurney's sugarbird territories had significantly less arthropod energy available. Arthropod energy availability on Gurney's sugarbirds was correlated with reproductive success ( $r_s = 0.67$ ,  $n = 11$ ,  $p = 0.02$ ) and appears to have constrained breeding.

## Discussion

Sugarbird males are highly territorial during the breeding season, actively defending their territories against intruders and spending much of their time perching conspicuously, often singing (Skead 1967). They are opportunistic feeders, moving in response to the flowering seasons of their chosen food plants (Skead 1967; Craig &

Hulley 1994), and at the end of the breeding season many sugarbirds that had bred at the study sites appeared to leave in search of food.

#### Cape sugarbird adjustments in territory size between breeding seasons

Territory size and quality may influence breeding success of territorial birds, with individuals defending superior territories benefiting from greater breeding success (Peterson & Best 1987; Goodburn 1990). Therefore territorial individuals with small or poor quality territories should, over time, attempt to improve on initial choice by taking over better or larger territories in following breeding seasons or increasing their original territory by annexing parts of adjacent territories (Beletsky & Orians 1987; Petersen & Best 1987). Fifty-four percent of the male Cape sugarbirds observed in 1998, returned to the study site in 1999 and occupied the same territories. Males not returning to the study site, except for one male, had small territories and had not bred successfully the previous year. Non-returning males may have been predated on, or alternatively established territories elsewhere in an attempt to improve territory size and quality and to possibly improve breeding success. Although there were new individuals defending territories in 1999, there were no differences in territory sizes and quality between the two breeding seasons, as new males either set up new territories or took over territories that had previously been occupied by non-returning individuals.

## Adjustments in territory size during the course of the breeding season

Territory size depends largely on the energetic gain from territoriality (Brown 1964). For example, reductions in food availability resulted in increased territory size of rufous hummingbirds (*Selasphorus rufus*) and New Holland honeyeaters (*Phylidonyris novaehollandae*) although time spent in territorial defence by both species did not change following changes in flower density (Hixon *et al.* 1983; McFarland 1986; Eberhard and Ewald 1994). On the other hand, increased costs of defence can influence territory size: an increase in intrusion rate resulted in a decrease in feeding territory size of black-chinned (*Archilochus alexandri*) and Anna's hummingbirds (Norton, Arcese & Ewald 1982; Eberhard & Ewald 1994). Territory size in sugarbirds was expected to change during the breeding season in response to changes in inflorescence and arthropod energy availability, but Cape sugarbird territory sizes remained constant, although there was a gradual decrease in the number of inflorescences available and arthropod energy availability. Only two Gurney's sugarbirds maintained territories over the entire breeding season and their territories were initially large, but with an increase in the number of territorial birds in the site, were reduced at mid breeding season, and then increased again at the end of the breeding season. A peak in the number of inflorescences and arthropod energy availability corresponded with this time of smallest territory size at mid breeding season. This species appears to reduce territory size due to intruder pressure and an increase in the number of inflorescences available for feeding.

## Comparison of Cape and Gurney's sugarbird territory size and quality

The *Protea* trees in the study site at Helderberg Nature Reserve were initially planted as part of a botanical garden, thus resulting in a tree density and species diversity higher than that found naturally in the area. Therefore territory size of Cape sugarbirds at Helderberg Nature Reserve may be unnaturally small, as a consequence of high inflorescence availability throughout the breeding season. The species diversity and tree density at Helderberg Nature Reserve was also considerably greater than that found at QNP. These differences may have contributed to Gurney's sugarbird male territories being so much larger than those of Cape sugarbirds. The lack of significant differences between the two species at the beginning of the breeding season reflects low numbers of individuals, and correspondingly little intraspecific competition in Gurney's sugarbirds. The differences in territory size between Cape and Gurney's sugarbirds at mid and the end of the breeding season reflects food availability. The large number of inflorescences and low arthropod energy availability per territory in QNP compared to Helderberg Nature Reserve probably reflects low nectar availability due to a particularly dry summer at QNP (Calf *et al.* 1999a). Arthropods may be taken by sugarbirds as a source of protein and other nutrients rather than as an energy source, therefore arthropod energy availability may not be as important a factor in territory size determination as the number of inflorescences (Recher & Abbott 1970; Ford & Paton 1976).

## The importance of secondary sexual characteristics in territory size and quality

Current signalling theory suggests that in a wide variety of birds females select mates based on particular morphological signals (Evans 1997). For example, barn swallows (*Hirundo rustica*) and Jackson's widowbirds (*Euplectes jacksoni*) select males on the basis of tail length (Møller 1988; Andersson 1992). In addition, vocal displays are important in most birds, and many hummingbirds have wing sounds that are used in normal territory maintenance (Peek 1972; Miller & Inouye 1983).

Male sugarbird displays involve flicking their long tails, together with wing “clacking” of the sixth primary feather (Skead 1967). Although tail length did not influence mid breeding season territory size in Cape sugarbirds in 1998, both male Cape sugarbirds in 1999 and Gurney's sugarbirds with longer tails defended larger territories at mid breeding season. The size of the sixth primary feather bulges did not influence territory size or quality of Cape or Gurney's sugarbirds at mid breeding season, indicating that tail length, rather than the length of the sixth primary feather bulge, may be more important in territory defence for both species.

The difference in male tail length is the most striking distinguishing feature between the two species, those of Gurney's sugarbirds being much shorter than those of Cape sugarbirds. Evans (1991) found that the size of male scarlet-tufted malachite sunbirds (*Nectarinia johnstoni*) pectoral tufts and tails were influenced by environmental conditions, being smaller when food availability was lower. The lower tree density and lower species diversity of *Protea*, and the associated lower food availability, may have constrained the development of long tails and sixth primary feather bulges in Gurney's sugarbirds. Alternatively, Gurney's sugarbirds may not require long tails for male-male competition for territories, as low food availability

may result in reduced territoriality, and a concomitant reduced requirement for advertisement ornaments for territory defence. Cape sugarbirds generally spent more time in territorial behaviour including display, inter- and intraspecific competition, singing and perching conspicuously on top of trees than Gurney's sugarbirds (Calf, Downs & Cherry 1999).

#### Male mating success

No significant differences in the number of inflorescences available and arthropod energy availability were found, and there were no significant differences in mating or reproductive success of Cape sugarbirds between 1998 and 1999. The difference in the number of eggs laid and the number of chicks successfully fledged, particularly in 1999, was due to predation. Gurney's sugarbird have a higher number of inflorescences per territory than Cape sugarbirds, but nectar energy availability of the inflorescences was too low even to quantify (Calf *et al.* 1999a), and was probably a severe constraint on mating and reproductive success. The high diversity of *Protea* species in the study site in the Cape may have resulted in an extended breeding season due to the overlap of flowering seasons of the different *Protea* species. This may have resulted in a higher mating and reproductive success than would be found in under more natural conditions in the Cape. In addition, Gurney's sugarbird territories have lower energy availability from arthropods, and arthropod energy availability significantly correlated to reproductive success. The combination of larger territory sizes and lower food availability would inevitably lead to Gurney's sugarbirds spending more time moving between inflorescences (Calf *et al.* 1999b) resulting in

this species experiencing far heavier energetic constraints on both mating and reproductive success, as well as the evolution of elongated tails.

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Table 1: Territory size (m<sup>2</sup>) of Cape sugarbirds at Helderberg Nature Reserve in 1998 and 1999. Means are given as  $\bar{x} \pm SD$  (n).

Bird	1998	April and May	June and July	August and
		1999	1999	September 1999
Pair 1	25880	14136	14136	18804
Pair 2	1946	-	-	-
Pair 3	6404	4730	4598	4707
Pair 4	2811	12449	9591	11673
Pair 5	19579	-	-	-
Pair 6	3456	3193	-	-
Pair 7	207	-	-	-
Pair 8	14165	10301	10301	13614
Pair 9	393	-	-	-
Pair 10	2679	4441	3708	4186
Pair 11	951	-	-	-
Pair 12	-	734	4683	5671
Pair 13	-	6524	6524	6665
Pair 14	-	3547	3548	4473
Pair 15	-	20185	20185	20575
Mean	7134 ± 8758 (11)	8024 ± 6078 (10)	7727 ± 5965 (9)	9032 ± 6819 (9)

Table 2: Territory size (m<sup>2</sup>) of Gurney's sugarbirds in Qwaqwa National Park from September 1998 to February 1999. Means are given as  $\bar{x} \pm SD$  (n).

Bird	September and October 1998	November and December 1998	January and February 1999
Pair 1	101548	47848	80055
Pair 2	43386	17356	44858
Pair 3	15901	-	-
Pair 4	2513	-	-
Pair 5	-	5506	-
Pair 6	-	17918	-
Pair 7	-	28791	-
Pair 8	-	32210	-
Pair 9	-	38575	40880
Pair 10	-	54543	54543
Pair 11	-	65685	65685
Pair 12	-	34626	34626
Pair 13	-	464220	464220
Mean	27225 $\pm$ 40015 (4)	73388 $\pm$ 130782 (11)	112124 $\pm$ 156033 (7)

Table 3: Mid breeding season territory size and quality for Cape Sugarbirds. Values are means of June and July 1998 and 1999 (in brackets) except the means for all territorial individuals which are given as  $x \pm SD$  (n) for the indicated years.

Male	Territory size (m <sup>2</sup> )	Number of inflorescences	Arthropod energy availability (kJ)
Pair 1	25880 (14136)	1841 (1430)	7312 (4666)
Pair 2	1946 (-)	696 (-)	3196 (-)
Pair 3	6404 (4598)	1486 (902)	4924 (1748)
Pair 4	2811 (9591)	339 (907)	1303 (9191)
Pair 5	19579 (-)	784 (-)	2352 (-)
Pair 6	3456 (-)	753 (149)	3765 (0)
Pair 7	207 (-)	13 (-)	65 (-)
Pair 8	14165 (10301)	558 (0)	860 (1092)
Pair 9	393 (-)	150 (-)	521 (-)
Pair 10	2679 (3708)	255 (273)	822 (1829)
Pair 11	951 (-)	204 (707)	1131 (1659)
Pair 12	- (4683)	- (414)	- (1576)
Pair 13	- (6524)	- (116)	- (4175)
Pair 14	- (-)	- (0)	- (0)
Pair 15	- (20185)	- (916)	- (2598)
Mean 1998	7134 ± 8757 (11)	644 ± 571 (11)	2387 ± 2228 (11)
Mean 1999	7727 ± 5965 (11)	529 ± 472(11)	2594 ± 2631 (11)

Table 4: Mid breeding season territory size and quality for Gurney's Sugarbirds in Qwaqwa National Park. Values are means of November and December 1998 except the means for all territorial individuals, which are given as  $x \pm SD$  (n).

Male	Territory size (m <sup>2</sup> )	Number of inflorescences	Arthropod energy availability (kJ)
Pair 1	47848	4824	9
Pair 2	17356	0	6
Pair 3	0	0	0
Pair 4	0	0	0
Pair 5	5506	876	0
Pair 6	17918	2112	1
Pair 7	28791	4644	3
Pair 8	32210	3132	6
Pair 9	38575	5384	4
Pair 10	54543	3170	0
Pair 11	65685	3078	0
Pair 12	34626	3971	0
Pair 13	464220	0	0
Pair 14	0	0	0
Mean	73389 $\pm$ 130782 (11)	2835 $\pm$ 1890 (11)	3 $\pm$ 3 (11)

Table 5: Correlations of tail length (n = 8) and sixth primary feather bulge length (n = 7) with number of inflorescences available, arthropod energy availability and territory size for Cape sugarbirds in (a) 1998 and (b) 1999 and for (c) Gurney's sugarbirds at mid breeding season. Significant values ( $p \leq 0.05$ ) are asterisked.

	rs	p
<b>(a) Tail length (n = 8)</b>		
- number of inflorescences available	-0.21	0.61
- arthropod energy availability	-0.52	0.18
- territory size	-0.02	0.96
<b>(a) Sixth primary feather bulge length (n = 7)</b>		
- number of inflorescences available	0.22	0.64
- arthropod energy availability	-0.11	0.82
- territory size	0.31	0.50
<b>(b) Tail length (n = 7)</b>		
- number of inflorescences available	-0.02	0.96
- arthropod energy availability	-0.55	0.16
- territory size	0.79	0.02*
<b>(b) Sixth primary feather bulge length (n = 7)</b>		
- number of inflorescences available	-0.36	0.43
- arthropod energy availability	0.29	0.53
- territory size	-0.04	0.94
<b>(c) Tail length (n = 10)</b>		
- number of inflorescences available	0.27	0.45
- arthropod energy availability	0.06	0.87
- territory size	0.72	0.02*

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(c) Sixth primary feather bulge length (n = 12)

- number of inflorescences available	-0.18	0.61
- arthropod energy availability	0.30	0.40
- territory size	0.40	0.26

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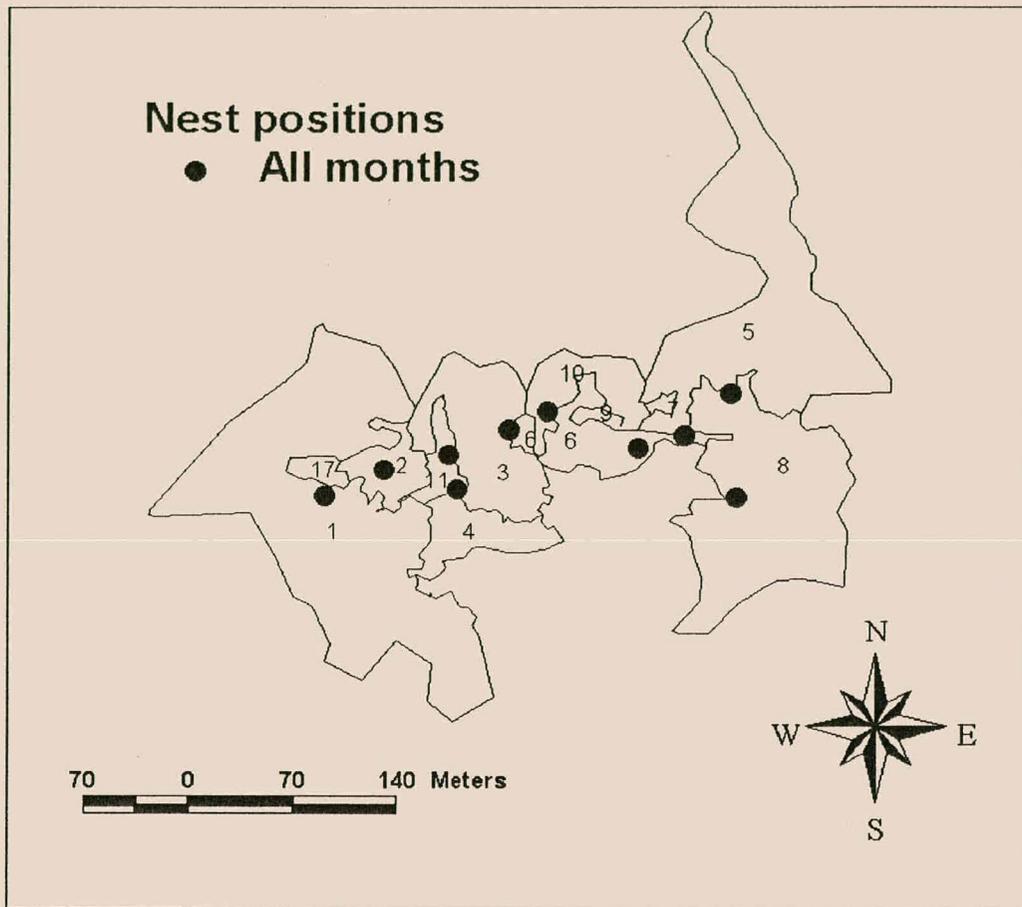
Appendix 1: *Protea* species density and diversity for the two study sites, Helderberg Nature Reserve and Qwaqwa National Park. Helderberg Nature Reserve comprises 14 *Protea* species at a high density whereas Qwaqwa National Park comprises three *Protea* species at a much lower tree density. The *Protea* species are divided into groups classified by Rebelo (1995) and the numbers of trees of each species are given for both study sites in brackets. The last row in the table describes *Protea* tree density (tree/ha).

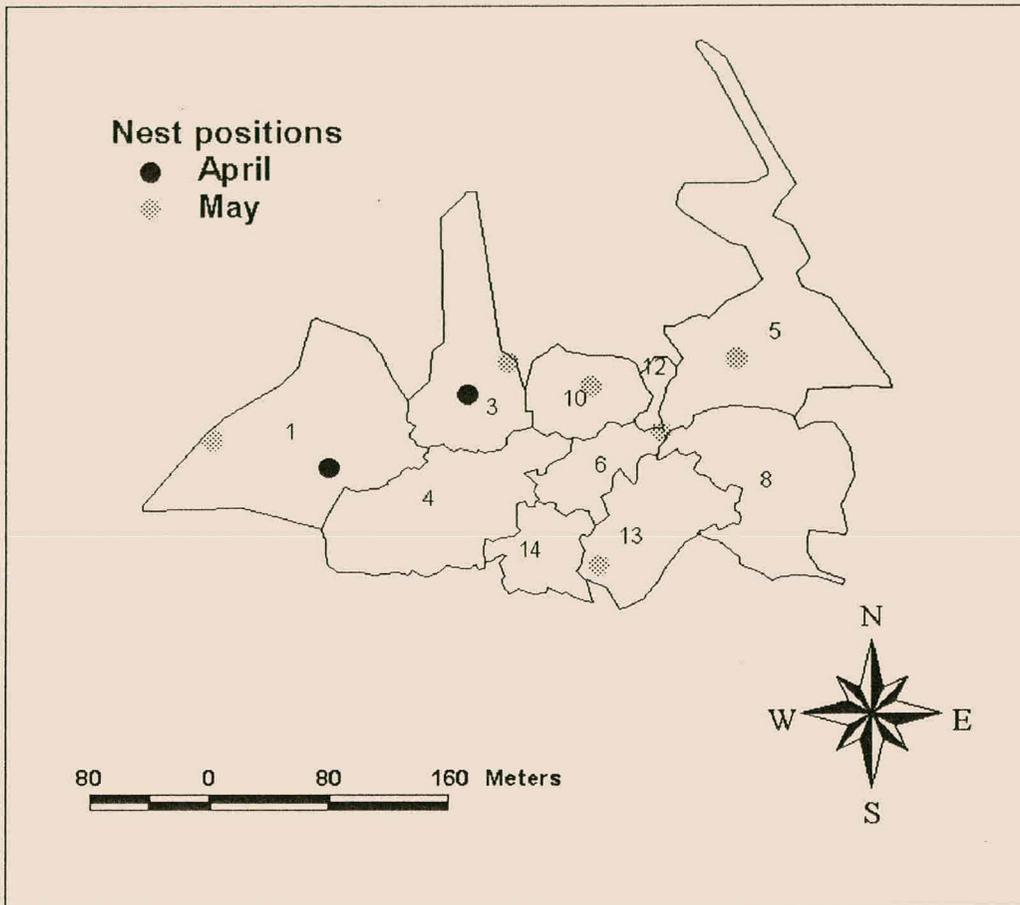
<i>Protea</i> group	Helderberg Nature Reserve	Qwaqwa National Park
Bearded	<i>Protea coronata</i> (19)	
	<i>Protea grandiceps</i> (306)	
	<i>Protea laurifolia</i> (179)	
	<i>Protea lorifolia</i> (1)	
	<i>Protea nerifolia</i> (62)	
Grassland		<i>Protea caffra</i> (3319)
King	<i>Protea cynaroides</i> (38)	
Spoonbract	<i>Protea burchelli</i> (53)	<i>Protea roupelliae</i> (1638)
	<i>Protea compacta</i> (6)	
	<i>Protea longifolia</i> (36)	
	<i>Protea exemia</i> (647)	
True	<i>Protea repens</i> (182)	
White	<i>Protea aurea</i> (1716)	<i>Protea subvestita</i> (121)
	<i>Protea lacticolor</i> (387)	
	<i>Protea mundii</i> (1586)	
Tree density (trees/ha)	202.43	35.84 trees

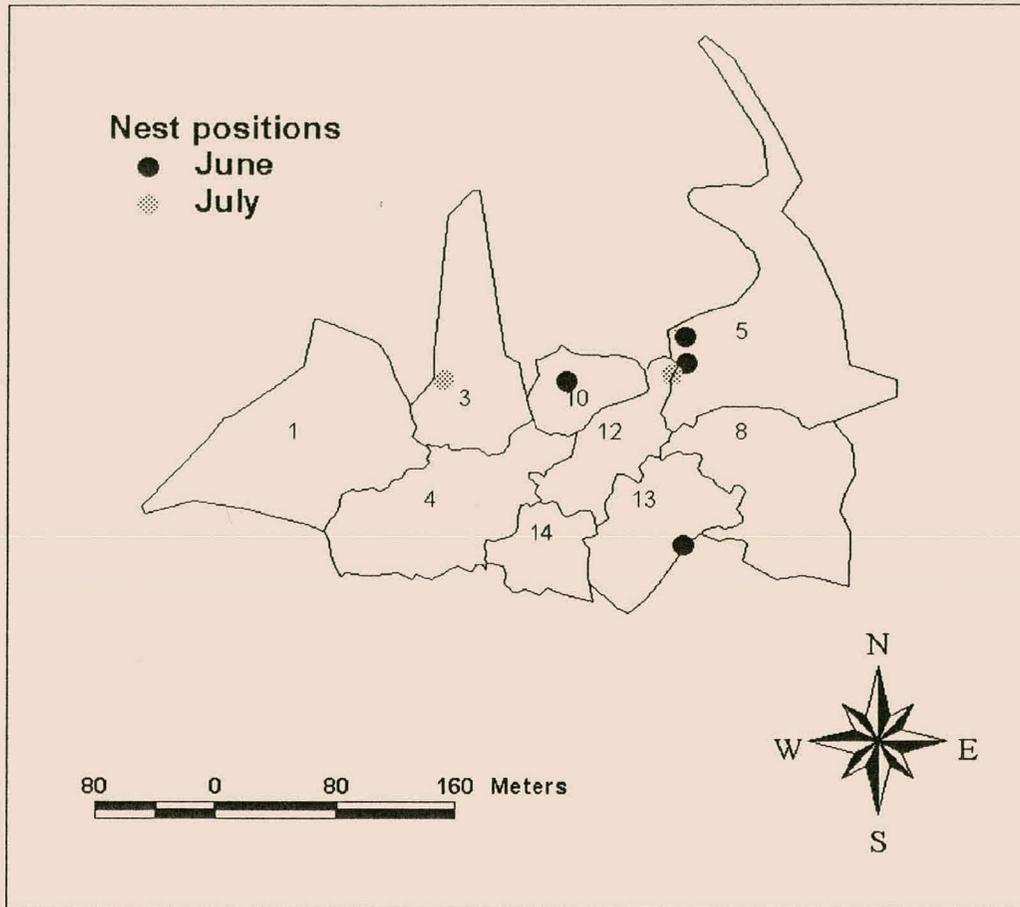
## Figures

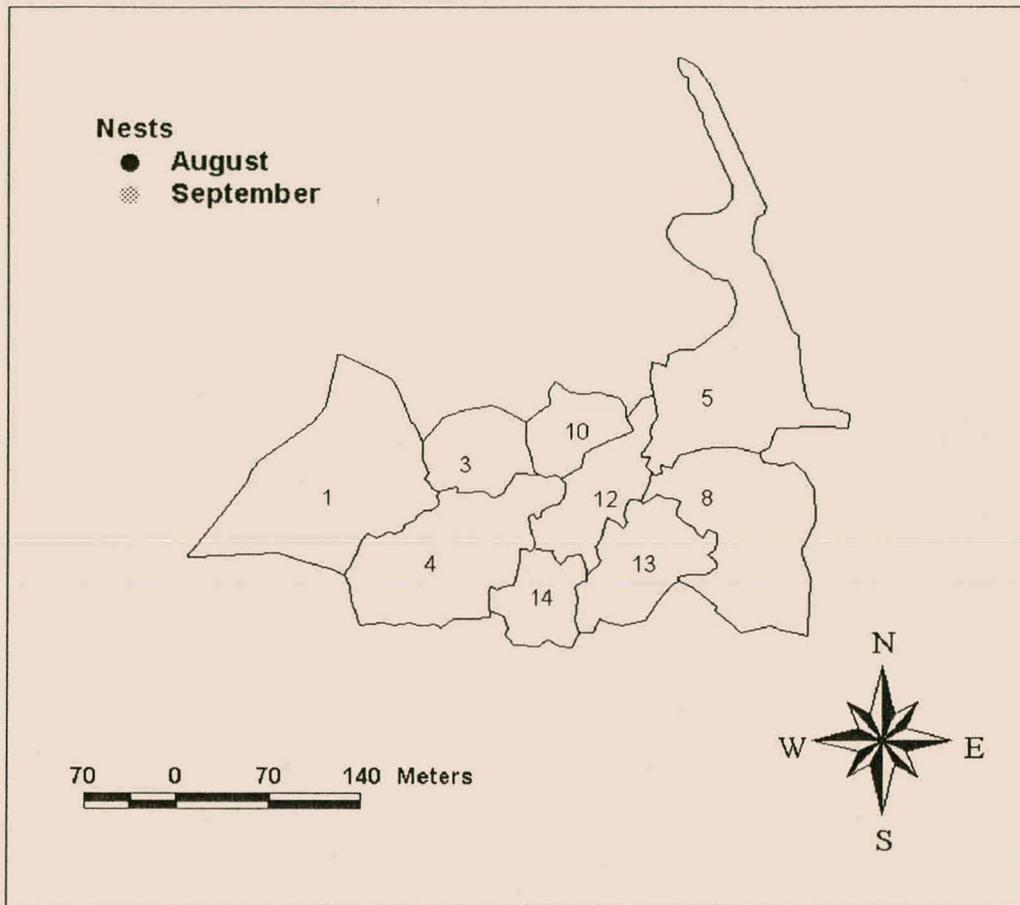
Figure 1: Territory maps for the 11 territorial males in the study site at Helderberg Nature Reserve and the positions of active nests between (a) May and July 1998, (b) April and May 1999, (c) June and July 1999, (d) August and September.

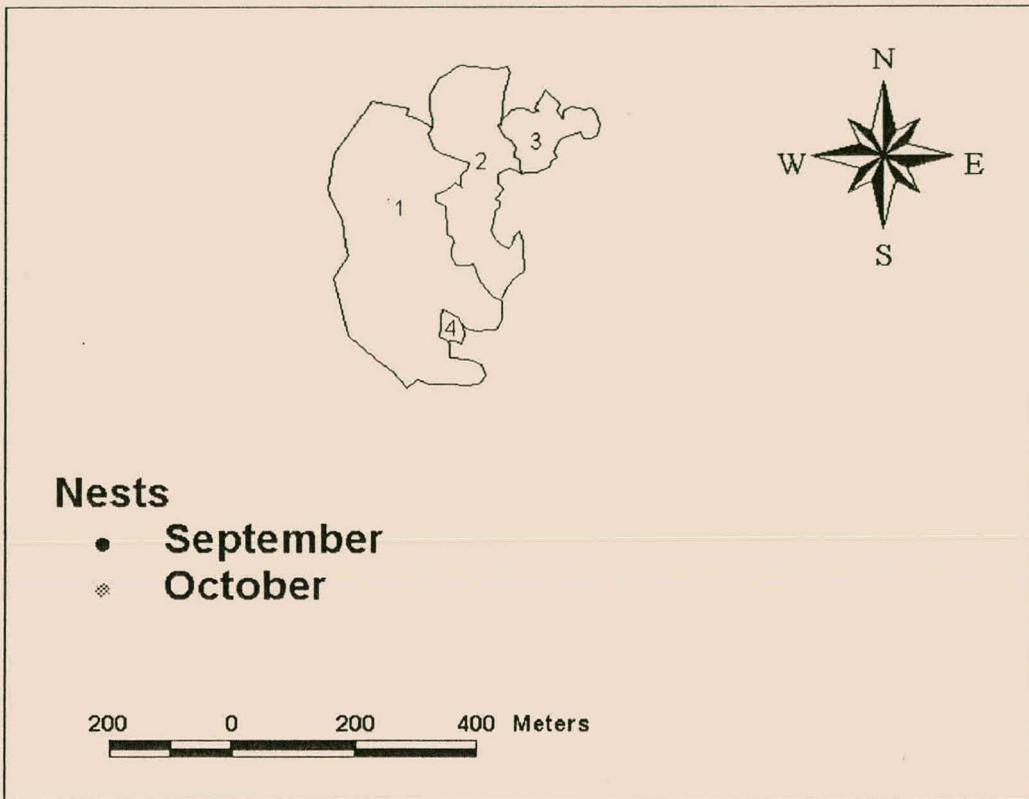
Figure 2: Territory map for the 11 territorial males in the study site at Qwaqwa National Park between (a) September and October 1998, (b) November and December 1998, (c) January and February 1999.

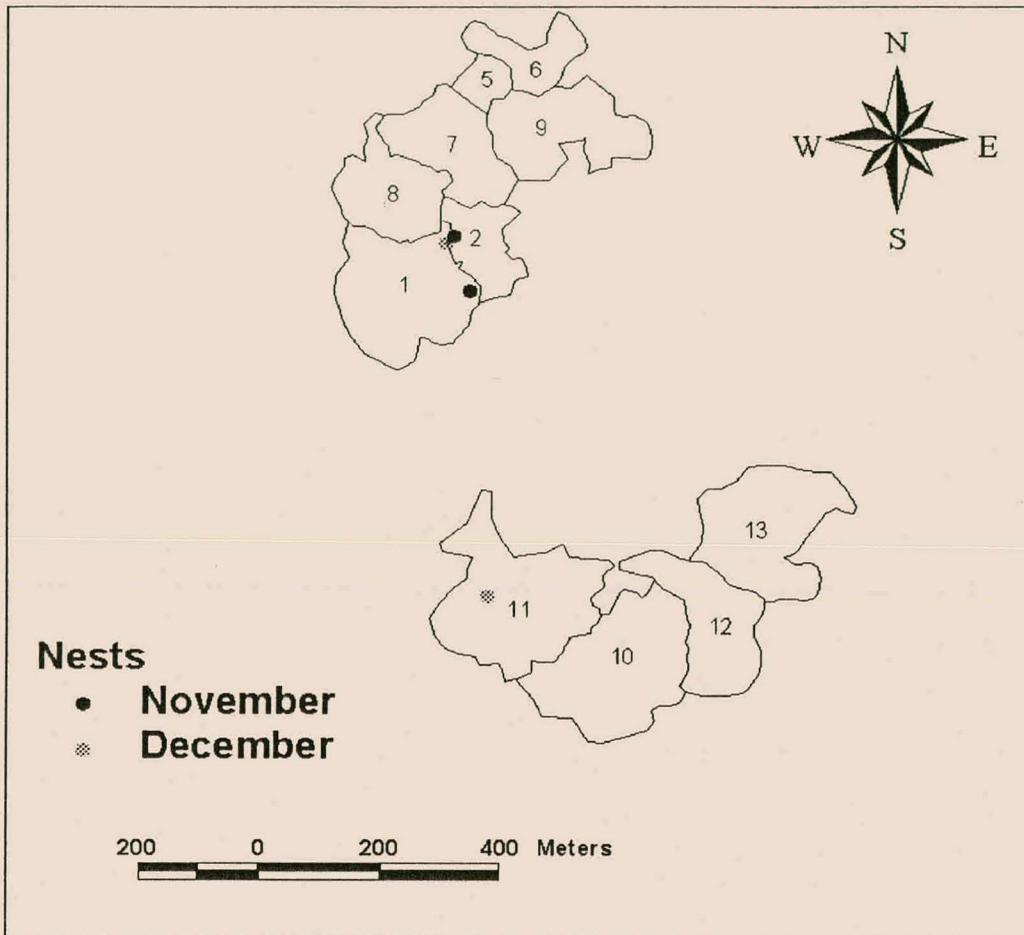


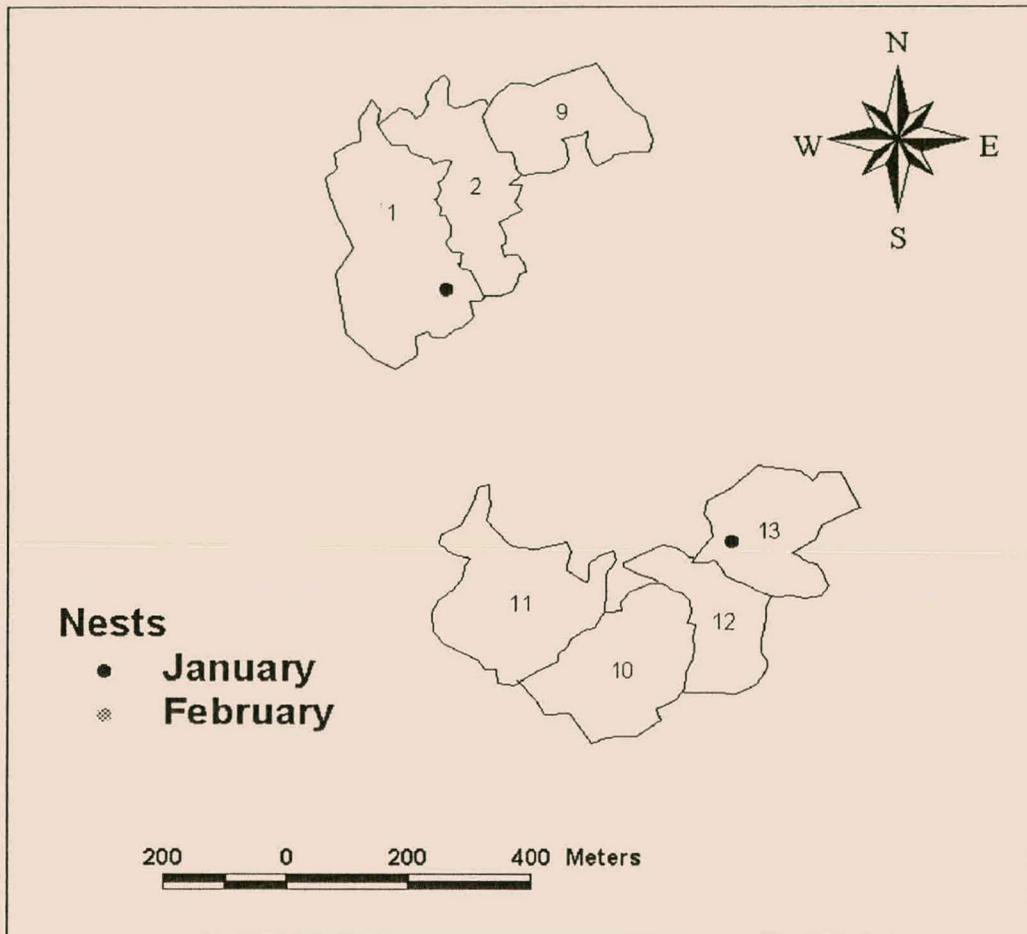












**The role of territory size and quality in mating and reproductive success of Cape sugarbirds (*Promerops cafer*)**

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Running header: Calf *et al.* - Cape sugarbird breeding success

## Summary

Cape sugarbirds are southern African endemics and they feed almost exclusively on the nectar of *Protea* inflorescences. Male sugarbirds are territorial during the breeding season, and territory size and quality, nectar and arthropod energy availability were determined for Cape sugarbirds in Helderberg Nature Reserve, Western Cape. Male sugarbirds defending larger territories had more inflorescences available for feeding and thus, more nectar energy available. Male mating success (number of eggs laid by the female of the pair) and reproductive success (number of successful fledglings) were significantly greater for males defending large territories and territories with greater nectar energy availability. Energy availability from arthropods was much greater than that from nectar, and appears not to constrain mating or reproductive success. Arthropods are energetically expensive to catch, therefore during the breeding season parent sugarbirds may sustain themselves with energy from nectar while feeding their offspring arthropods. The 14 *Protea* species in Helderberg Nature Reserve were divided into five groups: bearded, king, spoonbract, true and white *Protea*. Bearded and true *Protea* nectar energy availability appear not to influence mating or reproductive success: bearded *Protea* were found in all territories and produced the most nectar energy per inflorescence whereas true *Protea* were found in small numbers so their contribution to total nectar energy availability of territories was negligible. The flowering seasons of spoonbract and white *Protea* may have influenced nectar energy availability for adult sugarbirds, thus constraining male mating and reproductive success. Tail and wing ornaments of male Cape sugarbirds were not constrained by energy resources and did not influence intrasexual competition between males for territories, as no relationships were found with

territory size or quality. Intersexual competition for mates was not influenced by tail length or wing ornament size, although females seeking extra-pair copulations may use these secondary sex characters.

**Keywords:** energy, resources, territoriality, ornamentation

## Introduction

Territoriality occurs when an animal defends a spatially limited site against another, thus restricting the use of environmental resources to satisfy its own requirements (Wolf 1969; Stiles & Wolf 1970; Gass, Angehr & Centa 1976; Hixon, Carpenter and Paton 1983; Gordon 1997). Resources may include food, nesting sites, shelter or mates (Burger, Siegfried & Frost 1976; Armstrong 1996; Evans 1996).

Nectarivores feed predominantly on nectar but obtain necessary proteins, lipids and other nutrients from arthropods (Recher & Abbott 1970; Ford & Paton 1976; de Swardt & Louw 1994). Therefore the population density, localised movements and breeding seasons of nectarivores depend on the flowering season of their favoured food plants (Rebelo, Siegfried & Louw 1984; Paton 1985; Rebelo 1987; de Swardt 1991; Maclean 1993; Craig & Hulley 1994; Eberhard & Ewald 1994; McFarland 1996).

Territory defence in nectarivores occurs only when the energetic gain from territoriality exceeds the costs of defence (Brown 1964). Birds can assess territory quality through flower inspection and sampling of nectar over a number of days, and this allows them to make adjustments in territory size in response to food availability and intrusion pressure to maximise energy gain (Carpenter, Paton & Hixon 1983; Hixon *et al.* 1983; Eberhard & Ewald 1994). Territory size and quality may, however, limit mating success (the number of eggs laid by the female of the pair) and reproductive success (the number of successful fledglings) of a male because females prefer mating with males defending larger or better quality territories (Savalli 1994a; Savalli 1994b; Evans 1996). For example, male scarlet-tufted malachite sunbirds (*Nectarinia johnstoni*) with small territories are precluded from breeding if their

territories are too small to support a male, a female and potential offspring (Evans 1996). Male scarlet-tufted malachite sunbirds with large territories spend more time defending their territories than males with smaller territories, but produce more offspring as females are more likely to lay larger clutches (Evans 1996).

There are two endemic southern African species of sugarbirds, of which the Cape sugarbird (*Promerops cafer*) is one (Skead 1963; Skead 1967; Hall & Moreau 1970; Maclean 1993). They are the largest nectarivores in southern Africa, and are restricted in distribution to the south-west and southern Cape, where they are common in fynbos vegetation (Fraser 1997).

Cape sugarbirds breed from March to September, as food availability during winter is greatest (Skead 1967). They form monogamous pairs at the beginning of the breeding season: the females build the nests and incubate the eggs alone, and brood the nestlings with little help from the male (Skead 1967; Seiler & Prys-Jones 1989). Breeding male sugarbirds are highly territorial and defend resources for themselves, their mates and their offspring (Skead 1967; Seiler & Prys-Jones 1989). Therefore territory size and quality of male sugarbirds may determine their mating and reproductive success.

In many species of birds ornamentation is associated with intersexual competition, to attract mates (Andersson 1982; Evans 1991, Petrie, Halliday & Sanders 1991; Johnstone 1995). For example, male peahens (*Pavo cristatus*) have elaborate trains which they display to attract a mate, males with the highest number of "eye-spots" on their trains usually benefiting from more successful copulations (Petrie *et al.* 1991). The handicap hypothesis posits that ornaments are indicators of male quality, and a female benefits from mate choice by her offspring inheriting "good genes" that increase their survival chances (Zahavi 1977; Grafen 1990).

Ornamentation has also been associated with intrasexual competition for resources which may indirectly influence reproductive success: for example, wing ornaments that mechanically produce a wing whistle in male broad-tailed hummingbirds (*Selasphorus platycercus*) are important in the maintenance of courting territories and hence in mating and reproductive success (Miller & Inouye 1983). Cape sugarbirds have sexual dimorphism in tail length: male tail length varies from 100 to 350 mm, whereas female tail length varies from 70 to 130mm (Friedman 1952; Seiler & Fraser 1985). In addition, male Cape sugarbirds have a large bulge on their sixth primary wing feathers (Seiler & Fraser 1985). These ornaments are used in tail-whipping and wing "clacking" advertisement displays performed by territorial males (Skead 1967). Therefore female sugarbirds may assess male ornaments as honest indicators of the breeding opportunity, or ornaments may play a role in intrasexual competition for territories and indirectly influence mating and reproductive success.

The purpose of this study was to determine whether male sugarbirds defending large or high quality territories or males with large or conspicuous ornaments benefit from higher mating and reproductive success. *Protea* species composition of territories may be important in the assessment of territory quality: for example, territories containing large numbers of *Protea* that are preferred food plants would be of higher quality than those without. Therefore *Protea* species composition of territories was related to the mating and reproductive success of male Cape sugarbirds.

## Materials and methods

### Study site

Cape sugarbirds were studied at Helderberg Nature Reserve, Western Cape (34° 03'S to 34° 05'S, 18° 52'E to 18° 53'E) during the breeding season, between March and September 1998. The study site was a small portion of the entire 480 ha reserve, comprising 26 ha on the south-facing slope of the Helderberg Mountain. Despite its small size, the site contained 5218 *Protea* trees.

All the *Protea* trees in the study site were initially tagged using numbered, plastic nursery tags. *Protea* species identifications were confirmed by Dr. John Rourke of the Botanical Institute at Kirstenbosch Botanical Gardens. A Trimble TDC1 Global Positioning System (GPS) was used to map all individually marked trees in Helderberg Nature Reserve. The species, tag number, height and diameter of the each tree were also recorded. This data was then downloaded into PATHFINDER, an interface programme, and the inbuilt satellite error corrected for using data available on the internet from Telcom and Eskom. The data were then transferred into a GIS program, ARCVIEW, for analysis.

### Identification of study individuals

Birds were captured in mist nets, and individuals were banded with aluminium SAFRING leg bands and unique combinations of plastic colour leg bands for identification. The mass of the birds was determined using a Salter balance; wing was measured with a wingrule, tail length with an aluminium ruler; and tarsus, culmen,

head and the sixth primary feather bulge with Digimax callipers, after which the birds were released at the site of their capture.

#### Territory measurement

Territorial occupation was observed for eleven male sugarbirds. Birds within randomly chosen unmarked 100m x 100m areas were observed for half an hour at a time. All birds were observed for a minimum of five observation periods to determine territory boundaries. All individuals displaying and singing, and all intra- and interspecific interactions observed during this time were recorded. "Ownership" was assigned to the earlier identified trees according to these observations. Trees were classified as being "owned" if they were used for displays or were defended from other individuals. This data was used to create a territory map in ARCVIEW, which was then used for analysis.

#### Nectar availability

Once a month over the six month breeding season, over a period of three to five days, standing crop volumes of nectar from ten plants of each *Protea* species were measured from the same inflorescence at three different times throughout the day: at 07h00, 11h30 and 16h00. Nectar was removed from two inflorescences on each plant: one that was partially open and one that was fully open. Two methods were used to determine the volume of nectar available to the birds depending on the *Protea* species concerned. The first involved removal nectar from a central nectar pool and from all the flowers using Pasteur pipettes. The second method involved removal of nectar

from an individual flower in the inflorescence using a 100 $\mu$ l capillary tube (Armstrong & Paton 1990). Total nectar volume for the inflorescence could then be extrapolated, based upon the number of flowers per inflorescence.

The numbers of inflorescences on 25 trees of each *Protea* species were counted monthly over the same period as nectar sampling was performed. Inflorescences were divided into four categories: bud, partially open, fully opened and seed/dead. The seed/dead inflorescences were not counted as this data was not required for nectar availability calculations. The number of buds available was counted to provide an indication of future flower availability but was not used in further analyses. Nectar volume for individual territories was extrapolated, based on nectar volume for a single partially open and fully open inflorescence of each *Protea* species in the site and the number of trees in the site or territory (van Tets in press).

#### Nectar quality and energy

Sugar concentrations of the nectar samples were measured with a temperature-compensated refractometer (Frost & Frost 1980; Collins 1983; Paton 1985). Energy content of the nectar was calculated by converting volumes and concentrations to milligrams of sucrose using tables cited in the "Handbook of Chemistry and Physics 1978-1979" (Bolten, Feinsinger, Baker & Baker 1979; Collins & Briffa 1983; Hixon *et al.* 1983). The number of moles of sucrose was then calculated and converted into energy availability using the conversion that one mole of sucrose provides 5.604J energy (Bolten *et al.* 1979).

Energy availability for a single inflorescence, and the result was then multiplied by the average number of inflorescences per tree to determine tree energy

availability for each *Protea* species (van Tets in press). Values for partially open and fully open inflorescences were added to provide a final energy value for a single tree of each species, and this value was multiplied by the number of trees to obtain a value for the energy availability from nectar for individual territories.

#### Arthropod availability

In addition to nectar, sugarbirds feed on arthropods associated with *Protea*. To determine arthropod availability, once a month six inflorescences of each of the 14 *Protea* species were collected at random from different trees. Arthropods were removed from the inflorescence, dried and weighed to determine biomass (Mostert, Siegfried & Louw 1980). Energy content of insect matter (Golley 1961) was used to determine energy availability from arthropods for individual *Protea* inflorescences (Mostert *et al.* 1980). Energy availability from arthropods for individual trees of each *Protea* species was then extrapolated using the average number of inflorescences on each tree. Extrapolations for partially open and fully open inflorescences were added to provide the final energy value.

#### Male breeding success

Throughout the breeding season, the 11 pairs of birds were monitored and if individuals showed any signs of nesting behaviour they were observed. New nests were also sought by checking individual trees in the study site. The number of eggs laid and the number of chicks reared successfully by each pair were counted, and

chicks were banded prior to their fledging. The reproductive success of males was determined by number of offspring produced over the six month breeding season.

### Statistical analysis

In cases where means were determined, they were given as  $x \pm SD$ . The data was not normally distributed, therefore nonparametric statistical methods were used (Siegal & Castellan 1988). Correlates of mating and reproductive success and territory size and quality were determined using Spearman rank correlations and territory quality differences between pairs were determined using Kruskal-Wallis ANOVA (Siegal & Castellan 1988). Friedman ANOVA and Kendall coefficient of concordance were used to determine the variation in nectar energy availability from the different *Protea* groups within territories (Siegal & Castellan 1988). STATISTICA was used to determine all statistical results (Statsoft, Inc. 1983-1984).

### Results

#### Nectar and arthropod energy availability for the entire study site

Inflorescence counts and nectar and arthropod sampling were performed for all 14 *Protea* species at the study site. Nectar energy content was calculated from nectar volume and concentration measurements for partially and fully open inflorescences for each *Protea* species.

For the entire study site, there was a general decrease in the number of inflorescences available over the breeding season. The total number of inflorescences

available was greatest in April, and lowest in August (Figure 1a). The number of buds was greatest in April and lowest in August (Figure 1b). Partially open inflorescences were most abundant in May and lowest in July, whereas the greatest number of fully open inflorescences was in July, and the lowest in August (Figure 1b). Overall, nectar energy availability was highest in April (55 kJ), but lowest in July (8 kJ) (Figure 1c). Arthropod energy availability showed a similar trend, and was highest in April (360608 kJ) and lowest in August (111 kJ) (Figure 1d). Energy availability from arthropods was much greater than that from nectar and, therefore, total energy availability reflected that of arthropod energy availability to a large extent, being highest in April (360663 kJ) and lowest in August (189 kJ) (Figure 1e).

### Territoriality

Territorial data was collected for 11 males during the breeding season and territories varied in size and quality (Calf, Downs & Cherry 1999; Figure 2). Of the 5218 trees in the study site, 3830 fell within the limits of the 11 territories. Territory size varied from 207 m<sup>2</sup> of the Pair 7 male to 25880 m<sup>2</sup> of the Pair 1 male.

### Male mating and reproductive success

Nine of the eleven territorial males obtained a mate, and eight of the females laid at least a clutch of two eggs. Pair 3 and Pair 6 females had two clutches. The eggs of first clutch of Pair 6 were predated on and those of Pair 11 died from exposure as they were blown from their nest during a bout of particularly bad weather. Pair 3 was the

most successful, fledging four offspring although their territory was not the largest and did not have the most number of inflorescences (Calf *et al.* 1999).

Four different influences on mating and reproductive success were studied: (1) nectar energy availability; (2) arthropod energy availability; (3) total energy availability; and (4) territory size.

Nectar energy availability was significantly correlated with the mating success and reproductive success of male sugarbirds but arthropod energy availability was related to neither (Table 1). There were no significant differences between nectar and arthropod energy availability between pairs that reared two and no fledglings (Kruskal-Wallis ANOVA:  $H = 3.86$ ,  $n = 11$ ,  $p = 0.14$  and  $H = 1.29$ ,  $n = 11$ ,  $p = 0.53$  respectively).

Total energy availability, comprising energy available from both nectar and arthropods, largely reflected arthropod energy availability and was, therefore, not significantly correlated to either mating success or reproductive success (Table 1).

Males that had larger territories had greater mating success and reproductive success (Figure 3a and 3b; Table 1). Territory size was significantly correlated to nectar energy availability, which in turn was significantly correlated to the number of inflorescences available on the territories of male Cape sugarbirds (Table 1). Better reproductive success on larger territories reflects their having more inflorescences, and thus more nectar energy available for feeding (Figures 4a and 4b Table 1).

Territory size did not appear to be related to arthropod energy availability (Figure 4c; Table 1).

The 14 *Protea* species in the study site were divided into five groups according to Rebelo (1995): bearded, king, spoonbract, true and white. As king *Protea* did not flower between March and September 1998 this group was not

included in the analysis. There was no significant difference in the number of trees of each *Protea* type on individual territories (H (9, n = 10) = 9, p = 0.43); in most cases (87%), at least one tree of each *Protea* type was found per territory (Table 2). There was a significant variation in nectar energy availability from the different *Protea* groups within territories during the breeding season (Friedman ANOVA:  $\chi^2$  (n = 11, df = 3) = 17.53, p < 0.0006; Kendall coefficient of concordance: W = 0.53, r = 0.48): bearded *Protea* provided the greatest amount of energy (8.8kJ) and white *Protea* provided the least (0.3kJ). Nectar energy availability for a single inflorescence from a bearded *Protea* was greater than that from all the other *Protea* groups at all times during the day, whereas that from white *Protea* was virtually negligible (Table 3). Only nectar energy availability of spoonbract and white *Protea*, however, was significantly correlated to reproductive and mating success (Table 4). *Protea* species composition on territories may have affected mating and reproductive success. For example, Pair 3, one of the pairs that had a second clutch, had the highest number of spoonbract *Protea* in their territory (Table 2).

Neither tail length nor sixth primary feather bulge length were significantly correlated to the number of inflorescences available, nectar energy availability, arthropod energy availability or territory size; nor were either of these secondary sex characters related to mating success or reproductive success (Table 1).

## Discussion

Cape Sugarbirds breed during the wet season, the period of greatest food availability from *Protea* (Skead 1967). It was expected that the bouts of wet and cold weather would influence the breeding success of Cape sugarbirds. Only one clutch, however,

was lost due to a bout of windy, cold weather. Except for one clutch that was predated on, all the other clutches were successful.

Although there was a large number of *Protea* trees in the study site, including a diversity of species that flowered at asynchronous times of the year, there was a decrease in the availability of inflorescences and associated nectar and arthropods during the breeding season.

The reproductive output of a territory may depend on the resources on that territory (Pyke, Christy & Major 1996). For example, Evans (1997) found that male wrens (*Troglodytes troglodytes*) with large numbers of nests on their territories were more likely to attract females than males with fewer nests, indicating that female wrens used the number of nests on a male's territory as a signal of breeding opportunity. Similarly, female red-winged blackbirds (*Agelaius phoeniceus*) and blackbilled magpies (*Pica pica*) assessed male territory quality in mate choice, and males with territories containing more food benefited from a higher mating and reproductive success respectively (Dhindsa & Boag 1990; Whittingham & Robertson 1994).

As in male scarlet-tufted malachite sunbirds, male Cape sugarbirds defending larger territories had a higher mating and reproductive success than males defending smaller territories (Evans 1991). Sugarbird territory size influenced the number of inflorescences available for feeding, and thus nectar energy availability.

Sugarbirds obtain energy from nectar and arthropods associated with *Protea* inflorescences, and feed their nestlings and fledglings arthropods (Skead 1967), yet only energy availability from nectar appeared to be a significant determinant of mating and reproductive success of Cape sugarbirds. Similarly, the number of inflorescences available on a territory was significantly correlated to nectar energy

availability but not to arthropod energy availability. Arthropod energy availability was far greater than that of nectar and may, therefore, not have constrained mating or reproductive success.

Sugarbirds feed arthropods to their nestlings and fledglings, but hawking for arthropods has been shown to be energetically expensive in other nectarivorous birds (Recher & Abbott 1970; Ford & Paton 1976; Brice 1992), and adult sugarbirds appear to rely primarily on nectar for their own sustenance (Calf personal observations). It was found that the 14 different *Protea* species (divided into five *Protea* groups), at the study site had different nectar concentrations, volumes and production rates, and thus different nectar energy availability. Bearded *Protea* produced the greatest nectar energy per inflorescence of all *Protea* types, and the large quantities of nectar produced by bearded *Protea*, which were found on all territories, could be an important, but not limiting, requirement for successful breeding. In addition, nectar from bearded *Protea* may not be washed out of the inflorescences and are, therefore, important during rainy periods (Nicolson personal communication). Sugarbird territories contained very few true *Protea*, and, therefore this *Protea* type did not provide breeding sugarbirds with significant amounts of nectar. Neither bearded nor true *Protea* energy availability appeared to influence mating or reproductive success, which was correlated only with nectar energy availability from spoonbract and white *Protea* inflorescences. Spoonbract *Protea* flowered throughout the breeding season and may have been an important nectar source for this reason. By contrast, the white *Protea* flowering season ends in the middle of the sugarbird breeding season, there are a large number of white *Protea* trees in the study site and they are the most abundant *Protea* type in several sugarbird male territories; the reduction in their nectar energy as the season progresses may constrain the mating and reproductive success of

sugarbirds. Therefore nectar energy from spoonbract and white *Protea* inflorescences may constrain parent sugarbirds during the raising of offspring.

Ornamentation plays a role in advertisement in both inter- and intrasexual selection (Miller & Inouye 1983; Petrie *et al.* 1991; Johnstone 1995). Evans (1991) found that tail length and the size of pectoral tufts of scarlet-tufted malachite sunbirds increased with an increase in food resources. Ornamentation in the form of tail length and the length of the sixth primary feather bulge did not appear to influence male sugarbird mating or reproductive success at our study site, and neither character appeared to be constrained by nectar resources. Miller and Inouye (1983), by contrast, found that the wing whistle of male broad-tailed hummingbirds (*Selasphorus platycercus*) advertised male presence on a territory, and was important in the maintenance of courting territories and hence affected reproductive success. Territory advertisement rate has been found to be important in several ornamented bird species: for example, male red-winged blackbirds with removed epaulet coloration increase time and energy spent in intrasexual behavioural conflicts to maintain territories (Peek 1972; Miller & Inouye 1983; Beletsky & Orians 1987). Territory maintenance in Cape sugarbirds may, therefore, be influenced by rate of territory advertisement and territory intruder chases rather than the length of male secondary sex characters.

Mating and reproductive success in sugarbirds appear to be based on the quality of resources contained within the male territory, which provide direct benefits to the female and offspring. As ornament length is unrelated to territory size or quality, female sugarbirds appear to choose their mates directly on the basis of territory quality. Although sugarbirds are deemed to be monogamous, multiple paternity has been found in families of socially monogamous bird species (Petrie & Kempnaars 1998), so the possibility remains that females may seek extra-pair

copulations (EPCs) with genetically superior males with larger ornaments (Weatherhead & Boag 1995; Whittingham & Lifjeld 1995; Petrie & Kempenaars 1998).

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Table 1: Spearman rank correlation of mating and reproductive success with (1) nectar energy availability (n = 11); (2) arthropod energy availability (n = 11); (3) total energy availability (n = 11); (4) territory size (n = 11); (5) tail length (n = 8); and (6) sixth primary bulge length (n = 7). Significant values as asterisked ( $p \leq 0.05$ ).

	rs	p
<b>(1) Nectar energy availability</b>		
- mating success	0.68	0.02*
- reproductive success	0.64	0.04*
- number of inflorescences	0.81	0.003*
<b>(2) Arthropod energy availability</b>		
- mating success	0.39	0.24
- reproductive success	0.34	0.30
<b>(3) Total energy availability</b>		
- mating success	0.26	0.44
- reproductive success	0.33	0.33
<b>(4) Territory size</b>		
- mating success	0.62	0.04*
- reproductive success	0.78	0.004*
- nectar energy availability	0.75	0.007*
- arthropod energy availability	0.44	0.18
- total energy availability	0.45	0.17
- number of inflorescences	0.90	0.0002*
<b>(5) Tail length</b>		
- mating success	-0.62	0.10
- reproductive success	-0.59	0.12

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- nectar energy availability	-0.12	0.78
- total energy availability	-0.43	0.29
(6) Sixth primary feather bulge length		
- mating success	-0.27	0.55
- reproductive success	-0.27	0.55
- nectar energy availability	0.27	0.55
- total energy availability	-0.17	0.73

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Table 2: The number of trees of each *Protea* type on the territory of each territorial male.

Pair	Bearded	Spoonbract	King	True	White
1	138	34	4	77	547
2	34	13	5	11	183
3	57	152	6	5	239
4	40	10	1	21	293
5	33	25	0	4	306
6	30	35	1	2	306
7	1	0	0	0	15
8	21	84	17	6	686
9	7	5	0	1	21
10	10	16	0	0	79
11	13	6	1	1	139

Table 3: Total energy availability over the six month breeding season for a single inflorescence from the four *Protea* groups at Helderberg Nature Reserve at three different times during the day (n = 300).

	07h00	11h30	16h00
bearded (kJ)	22.91	22.05	15.22
spoonbract (kJ)	7.81	9.89	4.66
true (kJ)	9.41	15.26	4.15
white (kJ)	0.45	0.58	0.64

Table 4: Spearman rank correlation of the nectar energy availability of four *Protea* types on the mating and reproductive success of Cape sugarbirds. Significant values as asterisked ( $p \leq 0.05$ ).

	rs	p
<b>Mating success</b>		
- bearded	0.46	0.15
-spoonbract	0.73	0.01*
-true	0.18	0.59
-white	0.65	0.03*
<b>Reproductive success</b>		
-bearded	0.43	0.18
-spoonbract	0.74	0.009*
-true	0.37	0.26
-white	0.65	0.03*

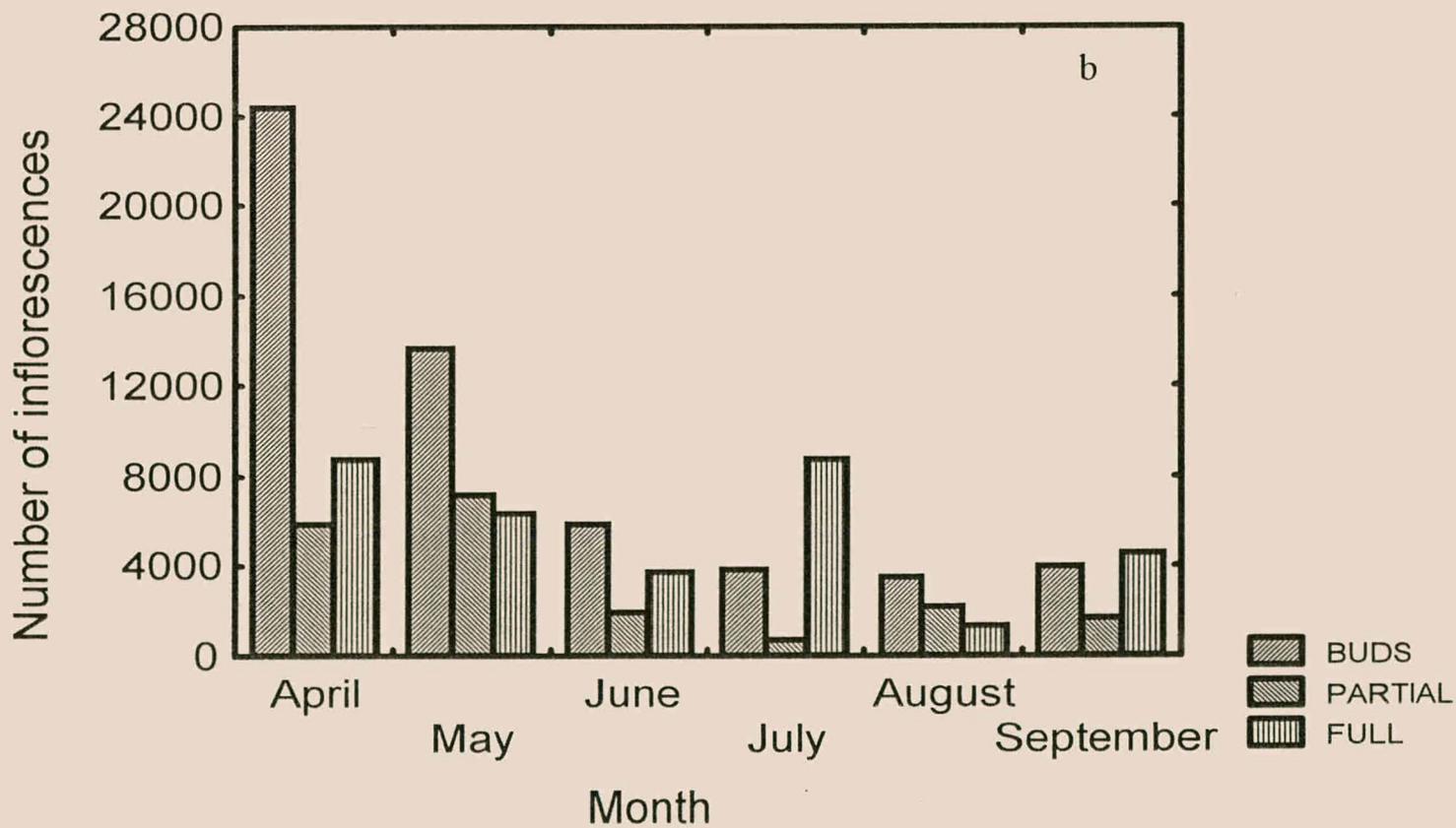
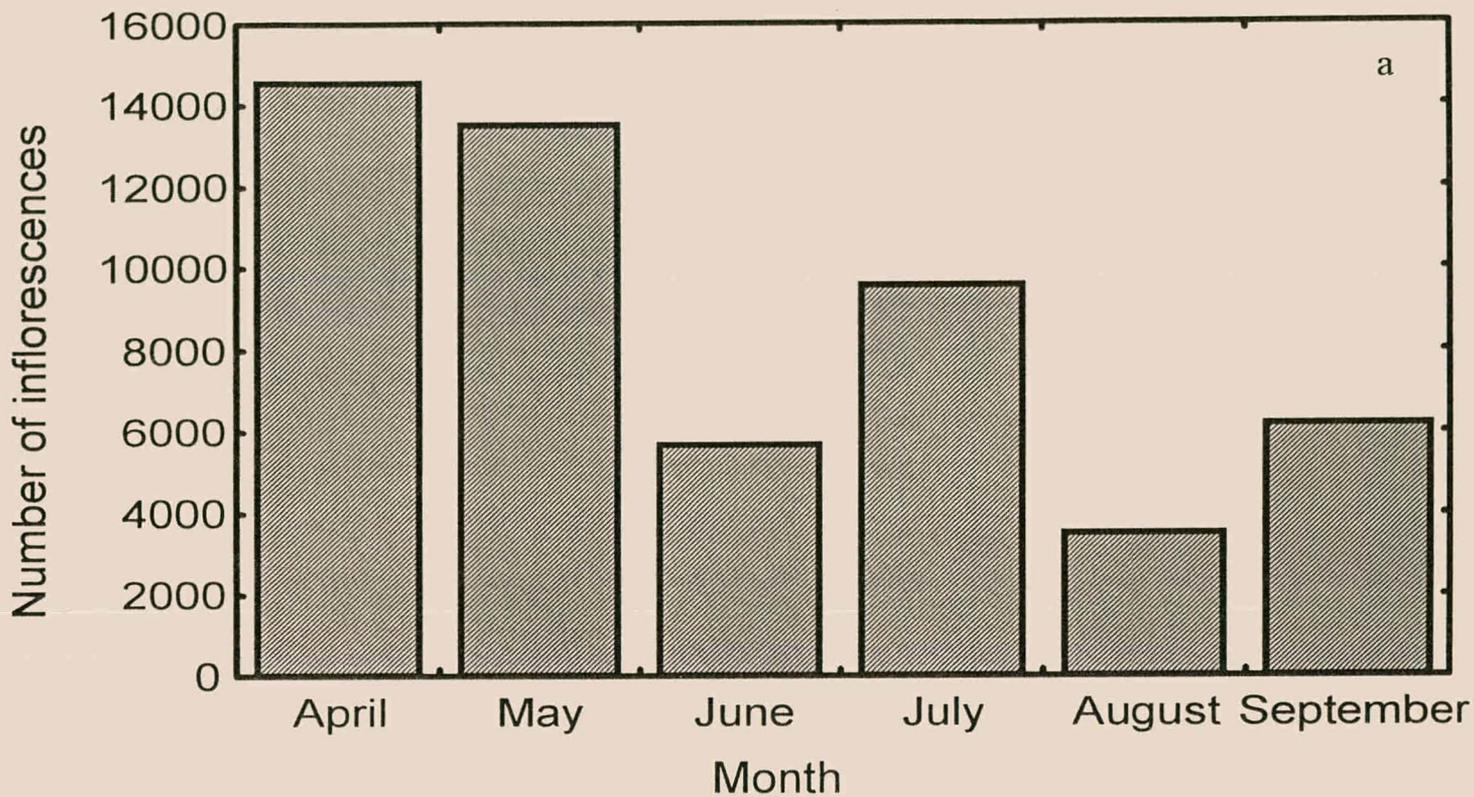
## Figures

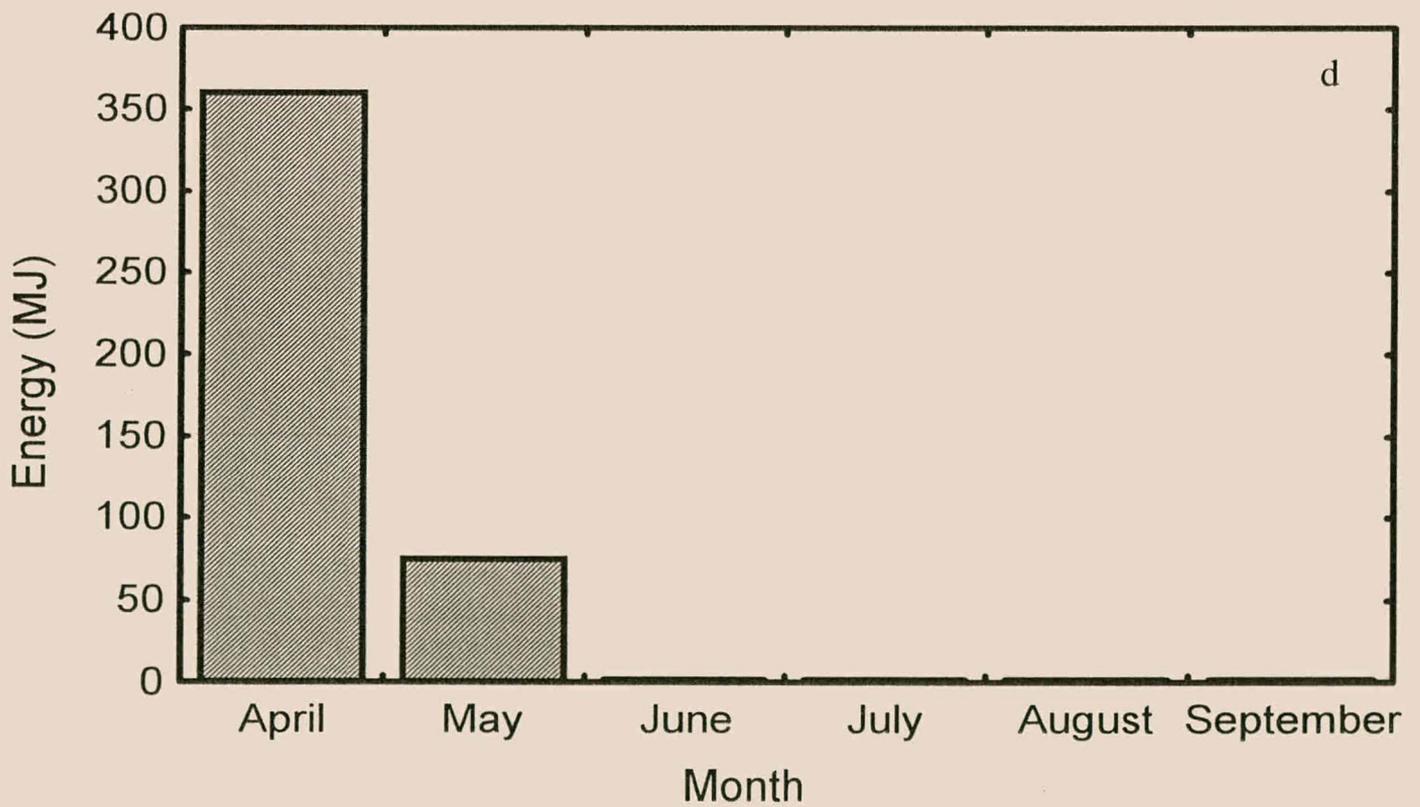
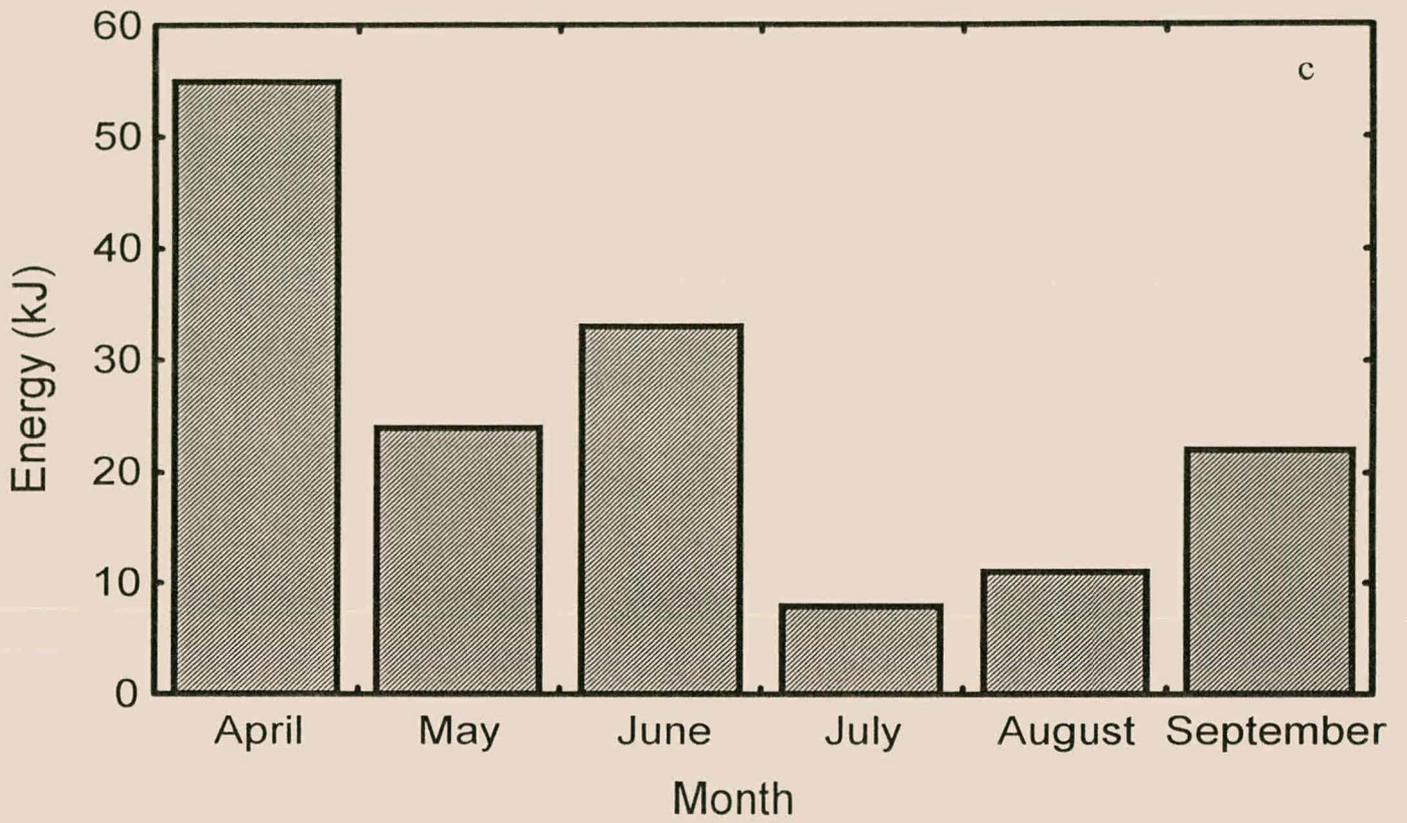
Figure 1: Monthly inflorescence, nectar energy and arthropod energy availability for the entire study site: (a) number of inflorescences available for feeding each month; (b) number of buds, partially open and fully open inflorescences available for feeding each month; (c) nectar energy availability each month; and (d) arthropod energy availability each month.

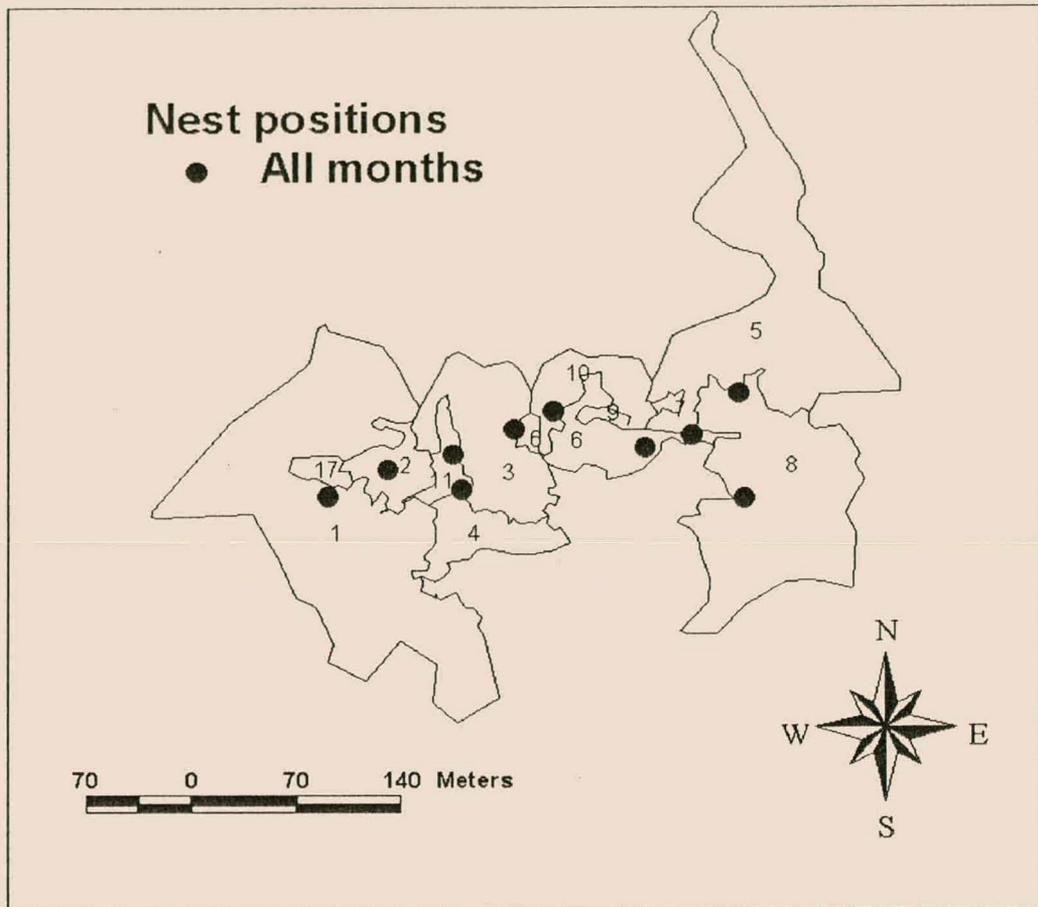
Figure 2: Territory map of the 11 territories and nest positions in the study site.

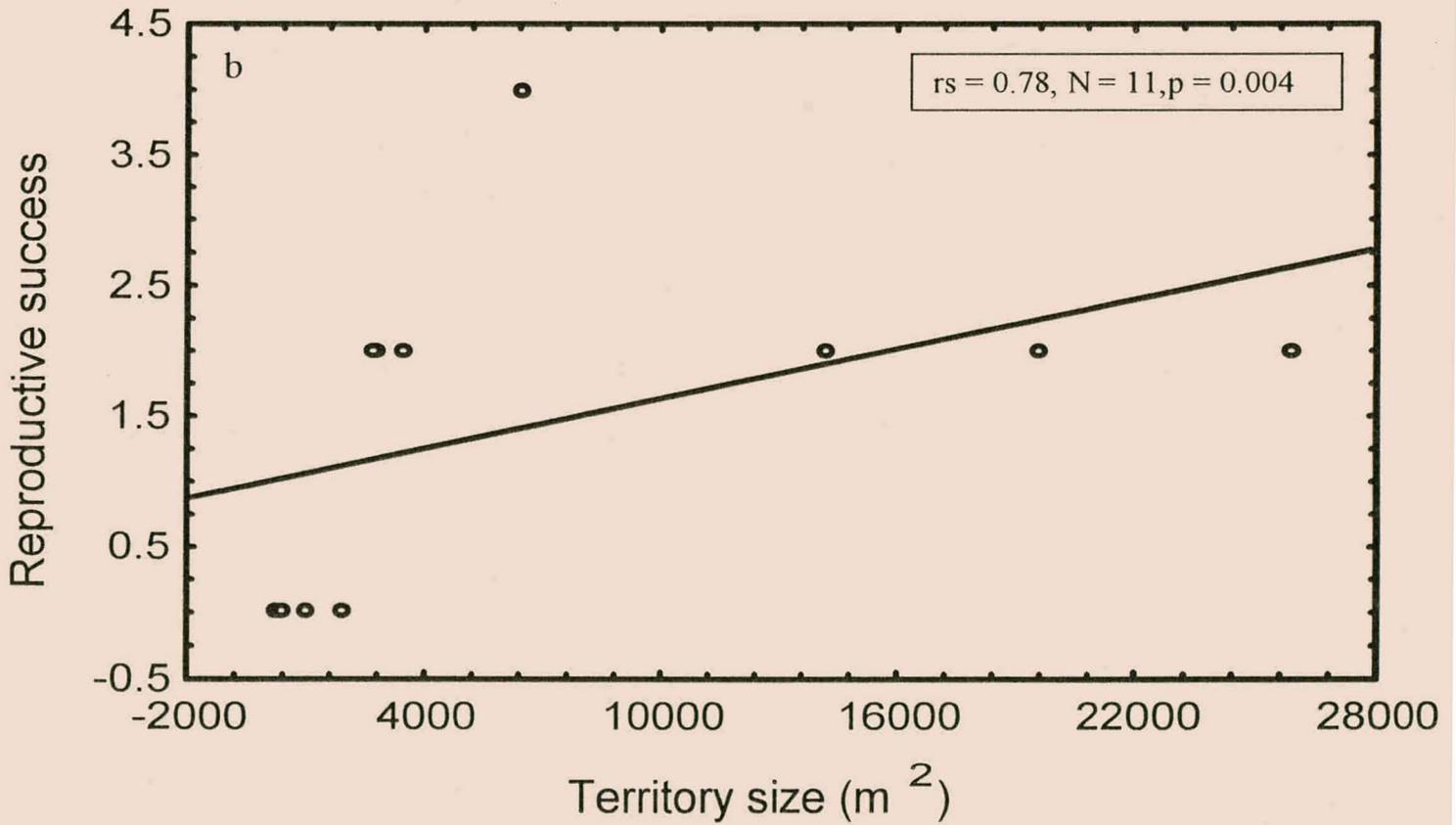
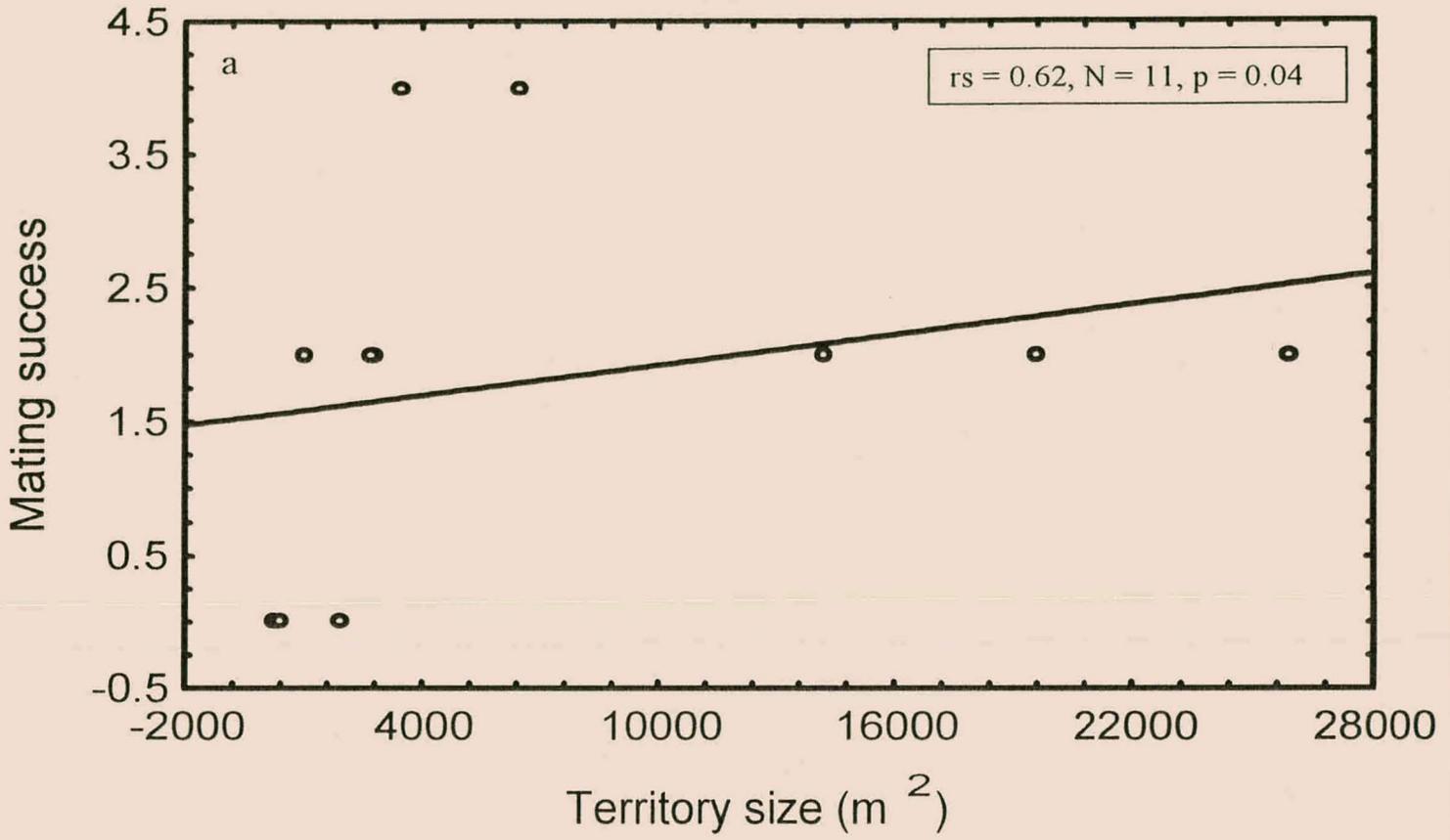
Figure 3: Relationship of territory size with mating and reproductive success: (a) mating success (Spearman rank correlation:  $r_s = 0.62$ ,  $N = 11$ ,  $p = 0.04$ ); and (b) reproductive success (Spearman rank correlation:  $r_s = 0.78$ ,  $N = 11$ ,  $p = 0.004$ ) were significantly correlated with territory size.

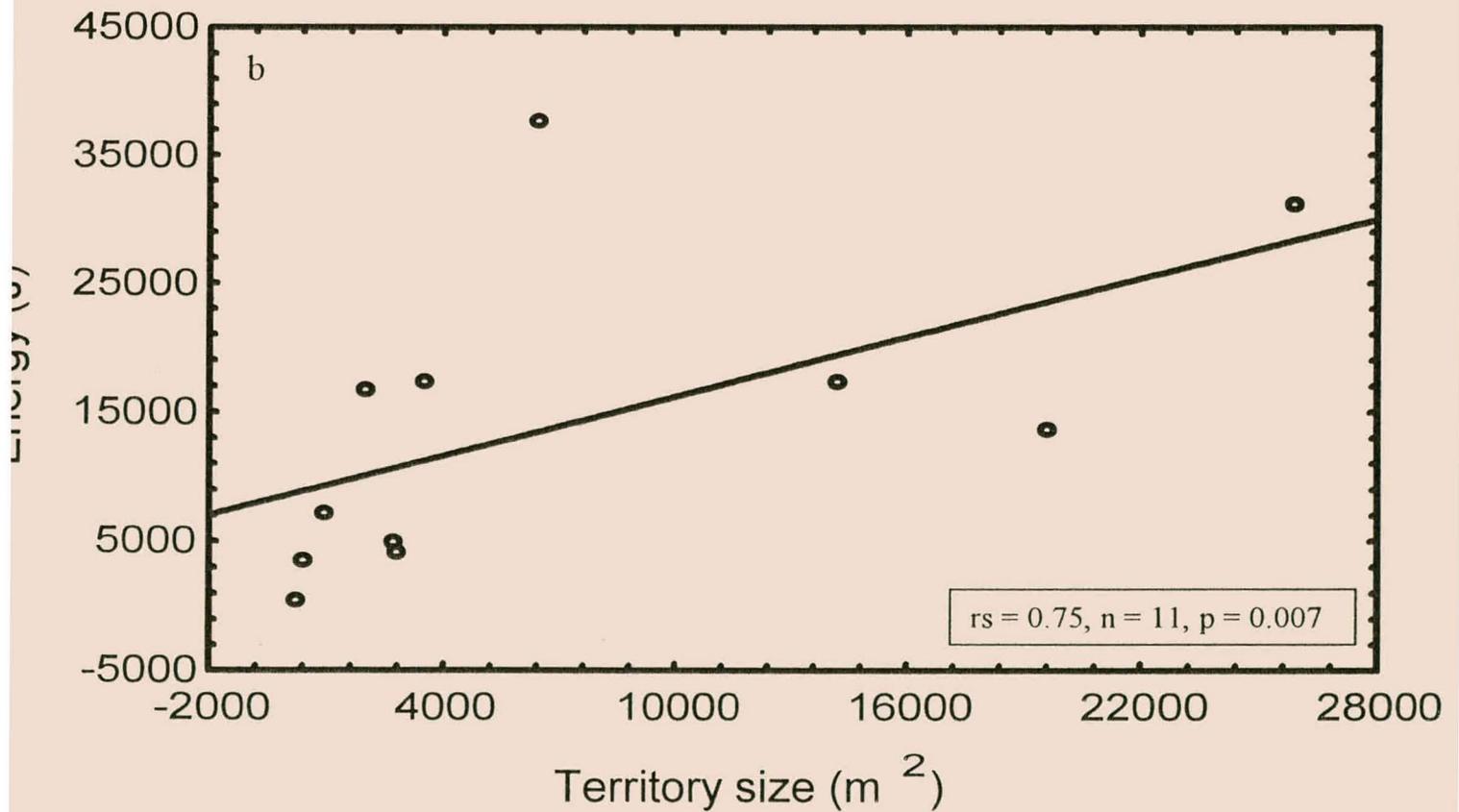
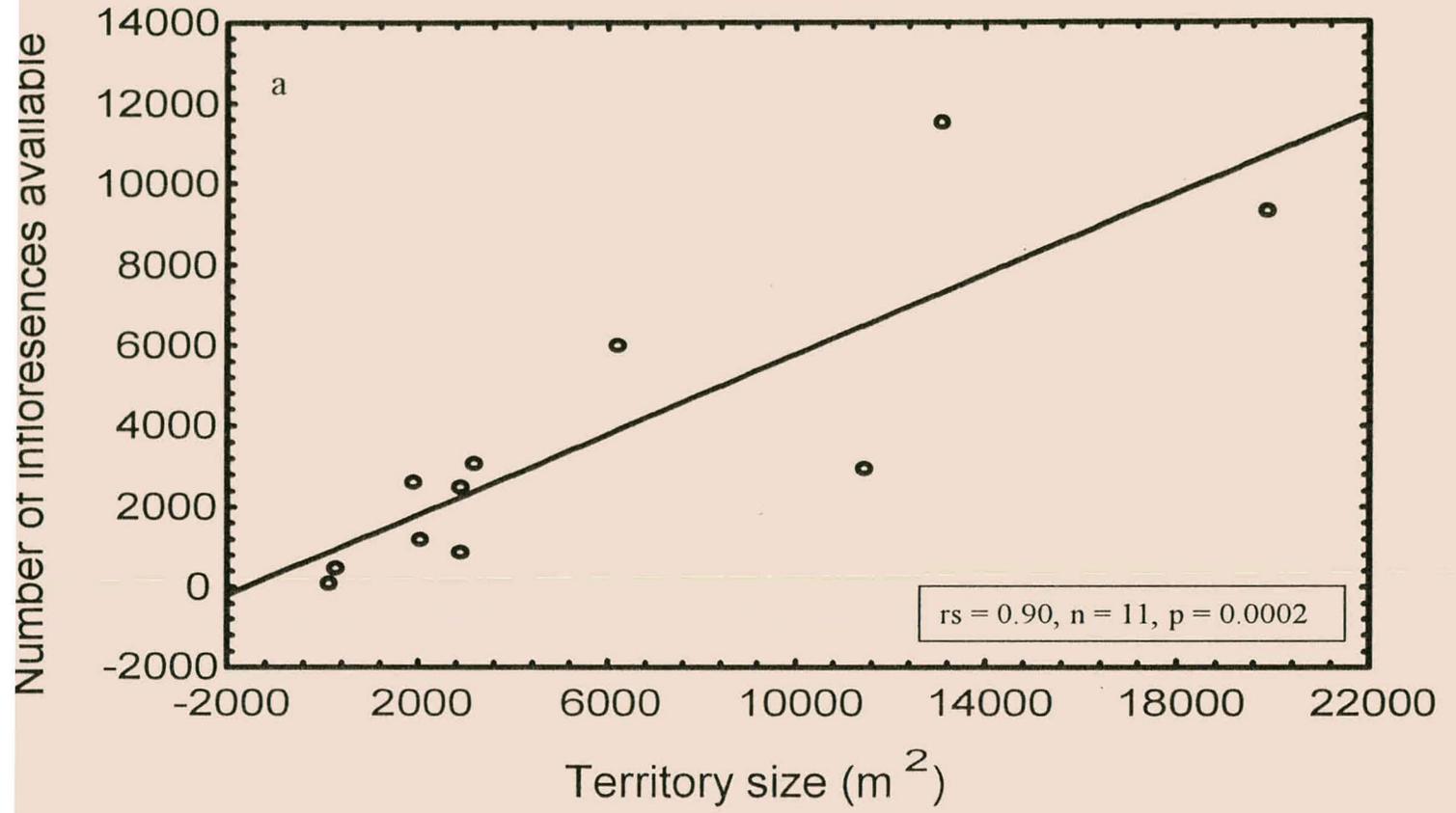
Figure 4: Relationship of territory size with (a) number of inflorescence (Spearman rank correlation:  $r_s = 0.90$ ,  $n = 11$ ,  $p = 0.0002$ ); (b) nectar energy availability (Spearman rank correlation:  $r_s = 0.75$ ,  $n = 11$ ,  $p = 0.007$ ); and (c) arthropod energy availability (Spearman rank correlation:  $r_s = 0.44$ ,  $n = 11$ ,  $p = 0.18$ ) over the six month breeding season.

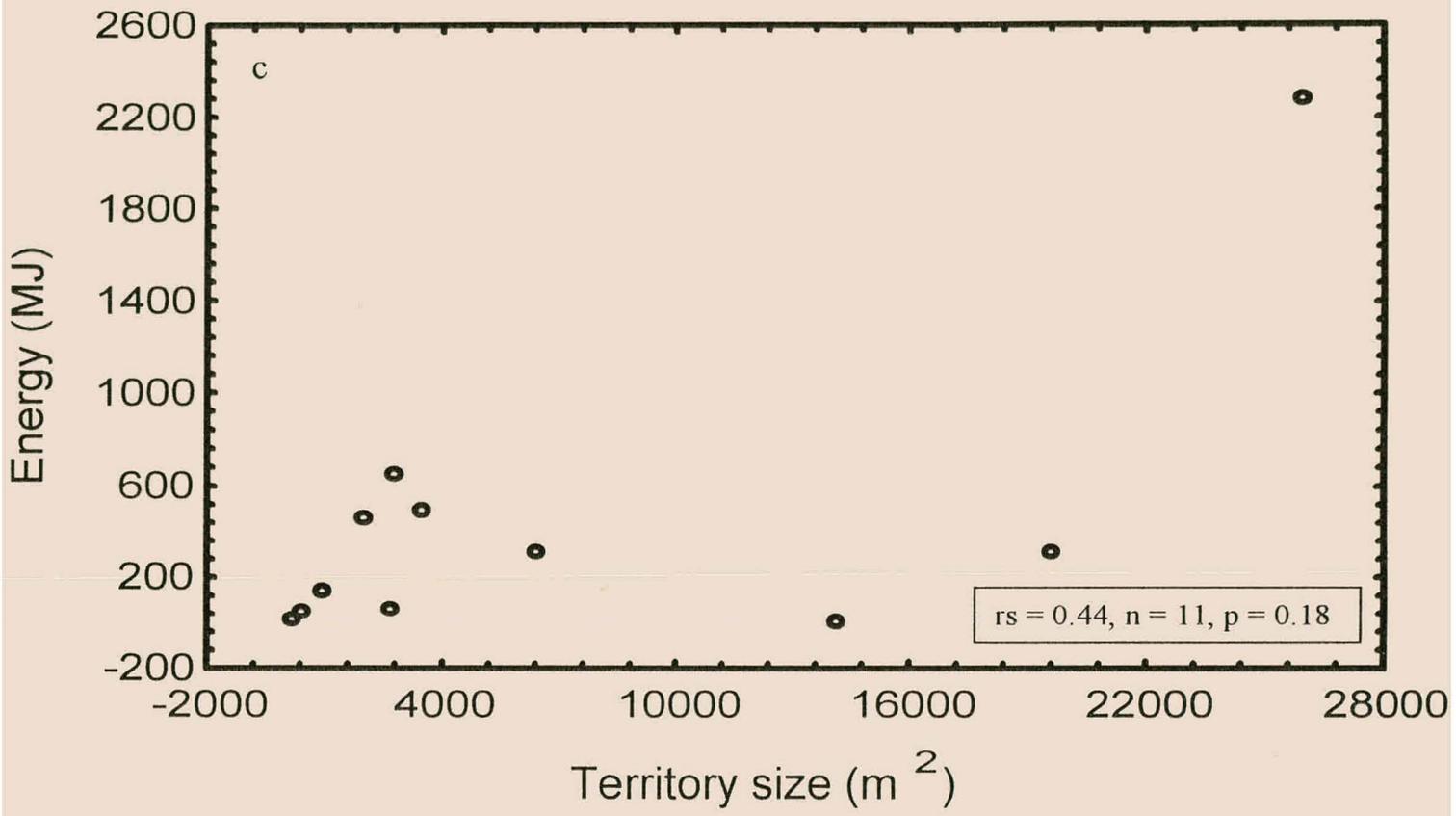












**Territorial and feeding behaviour of male Cape and Gurney's sugarbirds**  
**(*Promerops cafer* and *Promerops gurneyi*)**

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Running header: Calf *et al.* – Cape and Gurney's sugarbird behaviour

## Summary

Territorial and feeding behaviour of Cape and Gurney's sugarbirds in response to food availability were studied at Helderberg Nature Reserve, Western Cape and Qwaqwa National Park, eastern Free State respectively. Differences in habitat in Cape and Gurney's sugarbirds resulted in differences in food availability and hence feeding and territorial behaviour. Both species spent more time feeding on nectar than arthropods, which may be energetically expensive to catch. The different *Protea* species in Helderberg Nature Reserve were divided into five groups, namely: bearded, king, spoonbract, true and white. Cape sugarbirds spent the same amount of time probing inflorescences for nectar in the early morning, when nectar energy from bearded *Protea* nectar was greatest, as at midday, when nectar energy from all *Protea* groups was greatest. This indicates that they replenish energy reserves in the morning, and maximise energy gain by feeding at midday. Gurney's sugarbirds, by contrast, spent less time feeding on nectar in the early morning, and showed little variation in the amount of time spent feeding on nectar throughout the day. Both sugarbird species may spend more time feeding off territory in the afternoon in an attempt to maximise energy gain before the overnight fast, and thus spend more time out of sight. Low nectar energy availability due to lower *Protea* species composition and tree density, is reflected in Gurney's sugarbirds spending more time "lost", feeding off territory, than Cape sugarbirds in the afternoon, and more time flying in the morning and at midday in search of inflorescences from which to feed. Cape sugarbirds spent most of their time in the morning and at midday singing, when nectar energy availability was greatest, but reduced energy expenditure in the afternoon by spending most of their time perching on the tops of trees. Lower nectar energy availability may have

constrained vocal activity in Gurney's sugarbirds, which spent most of their time throughout the day perching silently on the tops of trees. Cape sugarbirds preened more than Gurney's sugarbirds although Gurney's sugarbirds may have preened whilst "lost". The decrease in inflorescence availability during the Cape sugarbird breeding season resulted in a significant decrease in the amount of time spent singing and a significant increase in the amount of time spent perching on the tops of trees at midday during the breeding season. Cape sugarbirds showed a preference for feeding from bearded *Protea* at mid breeding season, but fed mostly on spoonbract *Protea* at the end of the breeding season, once bearded *Protea* had finished flowering.

**Keywords:** foraging, preference, activity, nectar, arthropod

## Introduction

Extensive work has been completed on the energetics and foraging behaviour of avian nectarivores, in particular hummingbirds and honeyeaters (Hainsworth & Wolf 1976; Collins & Morrellini 1979; Armstrong 1991). Time and energy budgets have been established for birds maintained in the laboratory (Hainsworth & Wolf 1976; Collins & Briffa 1983a) and in the field (Wolf & Hainsworth 1978; Frost & Frost 1980; Collins 1983a; Collins 1983b; Collins & Briffa 1983b).

Sugarbirds are the largest of the true nectarivores in southern Africa (Hall & Moreau 1970; Maclean 1993). The two species are geographically separated: Cape sugarbirds (*Promerops cafer*) are found in the extreme south-west and southern Cape, and Gurney's sugarbirds (*Promerops gurneyi*) in the Eastern Mpumalanga, Kwazulu-Natal and the Eastern Cape provinces (Maclean 1993; de Swardt 1997; Fraser 1997). Cape sugarbirds inhabit fynbos habitats (Acocks 1953) with high densities of Proteacea, particularly of the genera *Protea*, *Leucospermum* and *Leucodendron*. Gurney's sugarbirds, by contrast, are found in montane grasslands with low densities of a limited number of *Protea* species.

Collins and Morellini (1979) found that singing honeyeaters (*Meliphaga virescens*) forage for arthropods to a limited extent, but spend most of their time probing inflorescences in search of nectar. As arthropods may be energetically expensive to catch (Recher & Abbott 1970; Ford & Paton 1976), both sugarbird species may feed more extensively on the nectar than the arthropods associated with the inflorescences of certain *Protea* (Mostert, Siegfried & Louw 1980; Rebelo 1987; de Swardt and Louw 1994).

Territoriality occurs when a particular resource can be physically defended and when costs of defence are less than the resultant energy gain (Brown 1964; Gill & Wolf 1975; Carpenter 1987; Hixon, Carpenter & Paton 1983; McFarland 1986). In response to inflorescence availability, hummingbirds adjust territory area and time spent foraging to maximise daily net energy intake (Hixon *et al* 1983). Hummingbirds have also been observed to minimise energy expenditure while defending territories (Gass & Montgomerie 1981): for example, *Eulampis jugularis* hummingbirds advertise their territories by sitting on perches, in addition to other territorial displays (Wolf & Hainsworth 1971). Similarly, territorial behaviour in Anna's hummingbirds (*Calypte anna*) has been observed to decrease as food availability declines (Ewald & Carpenter 1978).

Sugarbirds are also highly territorial during their breeding season (Skead 1967). The two species are found in different habitat types with different densities of *Protea* availability, the density and species diversity of *Protea* in fynbos being much greater than that in montane grassland. Although Cape and Gurney's sugarbirds live in different habitats, the two species have similar feeding and territorial requirements. It was hypothesised that territorial behaviour would change in response to inflorescence availability – sugarbirds spending more time feeding and less time in territory defence when inflorescence availability was low. Therefore it was predicted that due to greater inflorescence availability for Cape sugarbirds, they would spend more time in territory defence than Gurney's sugarbirds. Similarly, we predicted that a seasonal decline in the number of inflorescences available would result in Cape sugarbirds spending less time in territory defence and more time foraging later in the breeding season.

Collins (1983a) noted diurnal variations in energy expenditure and energy intake of the Cape sugarbird in the south-west Cape. Standing crop volumes of nectar in *Mimetes hirtus* inflorescences were significantly reduced by the birds early in the day, when nectar availability was greatest and sugarbirds probed inflorescences most frequently, indicating that sugarbirds may feed when nectar availability is greatest (Collins 1983a). Assuming sugarbirds maximise their total nectar intake and increase their feeding efficiency by feeding when nectar energy availability is greatest, it was predicted that territorial behaviour, in the form of singing and intra- and interspecific competition, would also be greatest when nectar energy availability was greatest (Hainsworth & Wolf 1976).

Different *Protea* species may produce different volumes and concentrations of nectar, and consequently some species may be more important nectar sources than others. Sugarbirds may also show preference in food resources, choosing *Protea* inflorescences containing nectar either in greater volumes or of higher concentration. Since there are numerous *Protea* species, it was predicted that both Cape and Gurney's sugarbirds should have feeding preferences, spending more time feeding on nectar from certain *Protea* species over others.

## Materials and methods

### Study site

Cape sugarbirds were studied at Helderberg Nature Reserve, Western Cape (34° 03'S to 34° 05'S, 18° 52'E to 18° 53'E) during the breeding season, between March and September 1998 and 1999. The study site was a small portion of the entire 480 ha reserve, comprising 26 ha on the south-facing slope of the Helderberg Mountain. Although the site was small in size there were 5218 *Protea* trees. Many of the *Protea* trees had initially been planted in 1974, therefore the *Protea* species composition and tree density in the study site was higher than that found naturally in the Cape.

Gurney's sugarbirds were studied at Qwaqwa National Park (QNP), eastern Free State (28° 24'S to 28° 35'S, 28° 32'E to 28° 49'E) for one breeding season. Observations began in early September 1998 and continued to the end of February 1999. The study area in QNP contained 5078 naturally growing *Protea* trees divided into two sites: the first, dominated by *Protea caffra*, was 83 ha in area and the second, dominated by *Protea roupelliae*, was 58 ha in area.

### Study individuals

Birds were captured in mist nets, and individuals were banded with aluminium SAFRING leg bands and unique combinations of plastic colour leg bands for identification. The mass of the birds was determined using a Salter balance; wing was measured with a wingrule; tail length with a long aluminium ruler; and tarsus,

culmen, head and the sixth primary feather bulge were measured with Digimax callipers. Birds were released at the site of their capture.

### Activity rates

This study focussed on male sugarbird activity, because female activity patterns were influenced by breeding behaviour to a greater degree due to changes in foraging activities in response to incubation or nestling feeding patterns (personal observations by K.M. Calf). Also, male sugarbirds engaged in territorial behaviour, whereas the females were not involved in territorial displays (Skead 1963; 1967).

Comparative observations for Cape and Gurney's sugarbirds were conducted at mid breeding season. A second set of observations was made for Cape sugarbirds at the end of the breeding season, during September, to determine whether there were changes in male activity during the breeding season.

Focal studies to determine activity rates for ten male sugarbirds of each species were conducted by scan sampling, in which individuals were observed for 15 minutes and their activity was recorded every 15 seconds during this period. This method assumes that the activity recorded every 15 seconds describes the activity of the focal individual in the 15 seconds preceding recording (Martin & Bateson 1998). Each individual was observed at three different times during the day, beginning at sunrise (07h00 for Cape sugarbirds and 06h30 for Gurney's sugarbirds), as well as at 11h30 and 16h00 for both species. Categories of behaviour modified from Brunton (1988) were used (Table 1), and activity was observed on three different days for each individual. The amount of time spent on each activity during the observation period was determined as follows. The mean time for each activity for each individual from

the three different days was determined and converted to time out of an hour. Time when the focal individual disappeared from sight was referred to as "lost" time. Time per hour for each activity was then converted into time spent in each activity out of an hour excluding "lost" time.

### Feeding and territorial behaviour in response to nectar energy availability

Once a month over the six month breeding season, over a period of three to five days, nectar energy availability was determined three times during the day beginning at sunrise (07h00 for Cape sugarbirds and 06h30 for Gurney's sugarbirds), as well as at 11h30 and 16h00 for both species. Standing crop volumes of nectar from two inflorescences on each plant (one that was partially open and one that was fully open) for ten plants of each *Protea* species were measured. In the study site in the Cape two methods were used to determine the volume of nectar available to the birds depending on the *Protea* species concerned. The first method involved removal of nectar from a central nectar pool and all the flowers using Pasteur pipettes. This method was used for *Protea aurea*, *P. laticolor*, *P. mundii* and *P. repens*. The second method involved removal of nectar from an individual flower in the inflorescence using a 100 µl capillary tube (Armstrong & Paton 1990). Total nectar volume for the inflorescence could then be extrapolated, based upon the number of flowers per inflorescence. This method was used for *P. burchellii*, *P. compacta*, *P. coronata*, *P. eximia*, *P. grandiceps*, *P. laurifolia*, *P. longifolia*, and *P. nerifolia* as these *Protea* did not have a visible nectar pool. In QNP *P. subvestita* did not flower over the sugarbird breeding season but *P. caffra* and *P. roupelliae* were sampled using the second method. Sugar concentrations of the nectar samples were measured with a temperature-compensated

refractometer (Frost & Frost 1980; Collins 1983a; Paton 1985). Nectar energy content was calculated by converting volumes and concentrations to milligrams sucrose using tables cited in the "Handbook of Chemistry and Physics 1978-1979" (Bolten, Feinsinger, Baker & Baker 1979; Collins and Briffa 1983a; Hixon *et al.* 1983). The number of moles of sucrose was then calculated and converted into energy availability using the conversion that one mole of sucrose provides 5.604J energy (Bolten *et al.* 1979).

Activity data was related to time of day and nectar energy availability, in order to determine the time of day when sugarbirds were most active in feeding and territorial behaviour.

### Feeding preferences

The study site at Helderberg Nature Reserve contained 14 different *Protea* species belonging to five different groups: bearded (*P. coronata*, *P. grandiceps*, *P. laurifolia*, *P. lorifolia*, *P. nerifolia*), king (*P. cynaroides*), spoonbract (*P. burchellii*, *P. compacta*, *P. eximia*, *P. longifolia*), true (*P. repens*) and white (*P. aurea*, *P. laticolor*, *P. mundii*) *Protea* (Rebelo 1995). King *Protea* were excluded from analysis as they did not flower during the breeding season. The preferred *Protea* species groups were determined from the amount of time spent feeding on nectar from the inflorescences of the different *Protea* types. Three groups of *Protea* were found in QNP: grassland (*P. caffra*), spoonbract (*P. roupelliae*) and white (*P. subvestita*). As *P. subvestita* did not flower and the two other species were found in two separate sites, the feeding preferences of Gurney's sugarbirds could not be determined.

## Statistical analysis

In cases where means were determined, they were given as  $x \pm SD$ . The data was not normally distributed, therefore nonparametric statistical methods were used (Siegal & Castellan 1988). Comparisons of time spent in different activities between and within sugarbird species and comparisons between the same individuals were performed using Mann Whitney U tests and Wilcoxon ranks tests respectively (Siegal & Castellan 1988). Friedman ANOVA was used to determine differences in behaviour at three different times during the day for all observed individuals. Correlates of feeding behaviour and resource availability were determined using Spearman rank correlations (Siegal & Castellan 1988). STATISTICA was used to determine all statistical results (Statsoft, Inc. 1983-1984).

## Results

### Activity rates

Sugarbirds spent a large percentage of time out of sight, designated as "lost" (Table 2). It was assumed this time was spent either resting in the shelter of trees or feeding off territory. Gurney's sugarbirds spent significantly more time "lost" than Cape sugarbirds in the afternoon (Mann Whitney U test:  $U = 23.5$ ,  $p = 0.05$ ,  $n_1 = 10$ ,  $n_2 = 10$ ) but not in the morning ( $U = 45.5$ ,  $p = -0.34$ ,  $n_1 = 10$ ,  $n_2 = 10$ ) or at midday ( $U = 40.0$ ,  $p = 0.076$ ,  $n_1 = 10$ ,  $n_2 = 10$ ).

The calculation of the amount of time spent on each activity each hour was determined once the amount of "lost" time was removed from the data. Cape

sugarbirds spent 33% of their time singing in the morning (20 min/h), and 40% of their time singing at midday (24min/h). They also spent a large percentage of time perching on the top of *Protea* trees, particularly in the afternoon (43% of their time or 26 min/h) (Figure 1a). Gurney's sugarbirds spent more of their time perching on the top of trees than on other activities at all times during the day: 34% (20 min/h) in the morning; 37% (22 min/h) at midday; and 22% (13 min/h) in the afternoon (Figure 1b). Gurney's sugarbirds spent significantly more time than Cape sugarbirds flying in the morning and at midday but not in the afternoon (Figure 1a and 1b; Table 3). Cape sugarbirds spent significantly more time than Gurney's sugarbirds in preening in the morning and at midday but not in the afternoon (Figure 1a and 1b; Table 3).

#### Probing inflorescences for nectar versus hawking for arthropods

Cape and Gurney's sugarbirds spent significantly more time probing inflorescences for nectar than hawking for arthropods (Wilcoxon matched pairs test:  $z = 3.81$ ,  $n = 30$ ,  $p = 0.0001$ ; and:  $z = 4.29$ ,  $n = 30$ ,  $p = 0.00002$  respectively; Table 3). Gurney's sugarbirds spent significantly more time probing inflorescences for nectar than Cape sugarbirds at midday, but not in the morning or afternoon (Figure 1b; Table 3). No difference was found in time spent hawking for arthropods between the two species (Figure 1a and 1b; Table 3).

## Feeding and territorial behaviour in response to nectar energy availability

Unfortunately nectar volumes in QNP were too low to measure, so observations of behaviour in response to nectar energy availability could be made only for Cape sugarbirds.

Although Cape sugarbirds spent more time feeding in the early morning (10%) and at midday (7%) compared to the afternoon (4%), these differences were not significant (Friedman ANOVA:  $\chi^2$  ( $n = 10$ ,  $df = 2$ ) = 3.2,  $p < 0.20$ ; Figure 1a). A significant correlation was found between time spent probing inflorescences for nectar and nectar volume (Spearman rank correlation:  $r_s = -0.46$ ,  $n = 30$ ,  $p = 0.01$ ), concentration ( $r_s = -0.55$ ,  $n = 30$ ,  $p = 0.002$ ) and energy availability ( $r_s = -0.47$ ,  $n = 30$ ,  $p = 0.01$ ).

There was no significant difference in the amount of time Cape sugarbirds spent in territorial behaviour, namely singing ( $\chi^2$  ( $n = 10$ ,  $df = 2$ ) = 8,  $p < 0.67$ ), in displays ( $\chi^2$  ( $n = 10$ ,  $df = 2$ ) = 2.48,  $p < 0.29$ ) or inter-and intraspecific competition ( $\chi^2$  ( $n = 10$ ,  $df = 2$ ) = 3.5,  $p < 0.17$ ) at different times during the day. Nectar volume, concentration and energy availability did not correlate with the amount of time spent in these behaviours.

## Comparison between mid and end of season activity rates for Cape sugarbirds

There was a significant difference in the amount of time Cape sugarbirds spent on all activities (as opposed to “lost time”) at the end of the breeding season compared to mid season ( $\chi^2$  ( $n = 120$ ,  $df = 2$ ) = 9.50,  $p < 0.009$ , Figure 1a and 1c). They spent most of their time perching on top of trees at all times of the day (42-58%, 25-35 min/h) at

the end of the breeding season (Figure 1c), whereas at mid breeding season Cape sugarbirds spent most of their time in the morning and at midday singing (33-40%, 20-24 min/h). These activities are defined as separate behaviours, but in reality are not mutually exclusive, indicating that the birds were far less vocal at the end of the season.

At the end of the breeding season, the amount of "lost" time was significantly reduced to eight percent in the morning ( $U = 11$ ,  $p = 0.003$ ,  $n_1 = 10$ ,  $n_2 = 10$ ) and at midday ( $U = 24.5$ ,  $p = 0.05$ ,  $n_1 = 10$ ,  $n_2 = 10$ ) but the reduction was not significant in the afternoon ( $U = 47.5$ ,  $p = 0.085$ ,  $n_1 = 10$ ,  $n_2 = 10$ ). Cape sugarbirds spent significantly more time perching and flying at midday at the end of the breeding season than at mid season (Figure 1a and 1c; Table 4).

#### Feeding preferences

Unfortunately feeding preferences could not be determined for Gurney's sugarbirds as the two most common *Protea* species were separated into the two sites in QNP, but mid and end breeding season preferences for Cape sugarbirds were determined.

Mid breeding season Cape sugarbirds fed mostly from bearded *Protea*, (71-78% or 43-47 min/h) (Figure 2a). At the end of the breeding season spoonbract *Protea* were in full flower, white and true *Protea* had finished flowering, and there were a only few bearded *Protea* inflorescences available for feeding (Calf, Downs & Cherry 1999a). Consequently, Cape sugarbirds fed mostly on spoonbract *Protea* - 93% of the time (56 min/h) in the morning and all of the time at midday and in the afternoon (Figure 2b).

## Discussion

A limitation associated with the use of time sampling methods is that unless the sample interval is short relative to the average duration of the behaviour pattern, accurate estimates of the frequency or duration of specific behaviour may be incorrect (Tyler 1979; Martin & Bateson 1998). As the sample interval used in this study was very short (15 seconds), only short flights between bushes may not have been recorded.

Both Cape and Gurney's sugarbirds spent a large amount of time "lost" at mid breeding season, particularly in the afternoon. Gurney's sugarbirds are known to be shyer and are rarer than Cape sugarbirds, and may consequently spend more time out of view (Skead 1963; Skead 1967), although tree density was not high at QNP and they were relatively easy to observe. More likely, Gurney's sugarbirds spent more time "lost" in the afternoon than Cape sugarbirds as they were forced to feed off territory due to low *Protea* nectar availability for territorial individuals. Differences in inflorescence availability related to habitat appear to influence the amount of time spent feeding off territory in the two species.

Energy gained by New Holland honeyeaters (*Phylidonyris novaehollandiae*) from hawking arthropods barely exceeded the energy used in hawking (Ford & Paton 1976; Brice 1992). Sugarbirds spent far more time probing inflorescences, presumably feeding on nectar, than hawking for arthropods, indicating that arthropods may also be energetically expensive to catch in this genus, although as in New Holland honeyeaters and several high montane sunbirds, they may be important in providing protein and other nutrients (Recher & Abbott 1970; Ford & Paton 1976; Wolf and Gill 1986).

Probing inflorescences was observed to be associated with feeding on arthropods in Australian honeyeaters (Collins & Briffa 1983b; Collins 1983a), but sugarbirds have to throw their heads back in order to swallow arthropods while feeding from inflorescences (Skead 1967). This behaviour was not observed and accordingly, feeding on arthropods in inflorescences was regarded as being insignificant or non-existent. Therefore it was assumed that the only arthropods taken were those that were taken while hawking and sugarbirds were only feeding on nectar when probing inflorescences.

As feeding behaviour in nectarivores is limited to daylight hours, sugarbirds may experience an energy deficit during the night as recorded in other nectarivores (Collins & Clow 1978; Collins & Briffa 1983a; Bednekoff & Houston 1994). High rates of nectar ingestion during the first few hours of the day might help offset energy and water imbalances that may have occurred during the night (Collins & Clow 1978; Collins & Morellini 1979; Collins 1981; Collins & Briffa 1983a). The western spinebill (*Acanthorhynchus superciliosus*) and many hummingbird species also have long feeding bouts in the afternoon in an attempt to maximise net energy gain and stabilise evening weights (Collins & Clow 1978). Nectarivores can also alter their nectar intake according to nectar concentration and volume by changing the frequency of feeding bouts (Collins & Clow 1978; Collins & Morrellini 1979; Downs in press).

Collins (1983a) observed that sugarbirds probed *Mimetes hirtus* flowers more often in the early morning when nectar availability was greatest, but we found that Cape sugarbirds spent the same amount of time probing for nectar in the early morning as at midday, but less time during the afternoon. As nectar energy availability was greatest at midday, Cape sugarbirds may feed in the morning to replenish energy deficits and water imbalances experienced at night, but maintain a

high feeding rate at midday to maximise energy gain when nectar energy availability was greatest. The increase in “lost” time in the afternoon may reflect Cape sugarbirds spending more time off territory feeding in an attempt to maximise energy gain before the overnight fast.

Gurney's sugarbirds, by contrast, spent less time feeding on nectar in the early morning and showed little variation in the amount of time spent feeding on nectar throughout the day. This may be a result of low nectar volumes throughout the day, and accordingly there being no significant advantage to feeding earlier in the day. Limited nectar sources appear to result in Gurney's sugarbirds spending more time “lost” than Cape sugarbirds in the afternoon, as they are feeding off territory to maintain a high feeding rate and maximise feeding efficiency before the overnight fast. Gurney's sugarbirds spending more time flying in the morning and at midday than Cape sugarbirds, probably reflects their searching for inflorescences to feed from, in order to replenish energy deficits and water imbalances incurred during the night.

Different activities have different energetic costs (Wolf & Hainsworth 1971; Carpenter & MacMillen 1976). For example, in golden-winged sunbirds one minute of active territorial defence was found to equate energetically to three minutes of foraging or eight minutes of sitting at 25°C (Gill & Wolf 1975). Territoriality should be adaptive only when the defence of a nectar energy source results in an energetic gain.

Collins (1983a) observed the greatest aggression between Cape sugarbirds early in the day, when nectar energy availability was greatest. We found that Cape sugarbird species spent little time in display flights and competitive interactions with other birds, but more display flights and competitive interactions occurred in the early

morning than at midday and in the afternoon. Territory advertisement, by singing at the time of greatest nectar availability, may reduce the amount of nectar removed by territory intruders (Collins 1983a). Male Cape sugarbirds decreased the amount of time they spent in energetically expensive defence by spending less time in aggressive interactions and more time singing or perching on the tops of trees. Cape sugarbirds spent most of their time singing in the morning and at midday, when nectar energy availability was greatest, but in the afternoon spent most of their time perching on the tops of trees. Lower nectar energy availability may have resulted in Gurney's sugarbirds spending most of their time perching on the tops of trees, as this is less expensive than singing (Gill & Wolf 1975). Nectar energy availability from all *Protea* was highest at midday (Calf *et al.* 1999b), therefore if changes in the type of territory defence observed was to change during the season in response to changes in food availability, it was expected to be observed particularly at midday. At the end of the breeding season Cape sugarbirds spent significantly less time singing and significantly more time perching at midday, reflecting a change to less energetically expensive territorial behaviour with a reduction in food availability. It was expected that the costs of territory defence, again due to low inflorescence availability, would have resulted in Gurney's sugarbirds spending less time in intra- and inter-specific competition than Cape sugarbirds but no significant differences were found. Thus it appears that sugarbirds minimise energy loss by changing their type of territory defence through the day, as shown in hummingbirds (Wolf & Hainsworth 1971; Ewald & Carpenter 1978).

Cape sugarbirds spent more time preening than Gurney's sugarbirds in the morning and at midday but Gurney's sugarbirds may have preened during "lost" time.

Cape sugarbirds spent less time "lost" at the end than in the middle of the breeding season, possibly as a result of reduced breeding behaviour. At the end of the breeding season there was no significant difference in the amount of time Cape sugarbirds spent feeding on nectar throughout the day. As territorial behaviour changes in response to territory quality and food availability or quality (Gill & Wolf 1975; Ewald & Carpenter 1978), the decrease in inflorescence availability during the breeding season is reflected in a concomitant decrease in the amount of time spent singing and an increase in the amount of time spent perching on the tops of trees.

Bearded *Protea* nectar energy availability varied significantly throughout the day, and was greatest in the early morning, whereas all the other *Protea* species had greater nectar energy availability at midday (Calf, Downs & Cherry 1999b). Cape sugarbirds showed a preference for feeding from bearded *Protea* at mid breeding season. They spent about the same amount of time feeding in the early morning and at midday, the times of greatest nectar energy availability, thereby maximising their energetic gain. At the end of the breeding season, Cape sugarbirds decreased the amount of time they spent feeding from bearded *Protea* and increased time feeding from spoonbract *Protea*, as the former group had finished flowering.

In summary, sugarbird feeding and territorial behaviour change in response to food availability. When nectar energy availability is greatest, more time is spent feeding within territorial boundaries, and more energetically expensive territorial defence occurs. Due to lower *Protea* species composition and tree density, Gurney's sugarbirds spent more time feeding off territory and less time in energetically expensive territorial defense than Cape sugarbirds. Similarly, with a decrease in inflorescence availability during the breeding season, Cape sugarbirds decrease the amount of intra- and inter-specific competition.

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Table 1: The division of all sugarbird behaviour into categories of somatic and reproductive effort (modified from Brunton 1988).

Category	Behaviour and context
(1) Somatic effort	
Foraging	Feeding on nectar Hawking for arthropods
Lost	Lost time when individual is "hiding" in <i>Protea</i> bushes or feeding off territory
Locomotion	Flight
Maintenance	Feather preening
Communication	This included mates "chatting" with each other while feeding and parents "chirping" to their chicks Interaction with mates
(2) Reproductive effort	
Mating effort	
Mate attraction	Flight display, usually occurring within defended territory
Territory defence	Intra- and interspecific competitive behaviour Singing at the top of a tree. Perching in trees
Parental effort	
Direct care	Incubation, brooding and feeding chicks
Defence	Defence of offspring

Table 2: Percentage time in an hour spent "lost". Cape sugarbird observations started at 07h00 and Gurney's sugarbird at 06h30.

Time of day	Cape sugarbirds	Gurney's sugarbirds
06h30/07h00	32%	39%
11h30	42%	56%
16h30	39%	68%

Table 3: Mean time (min/h) spent by Cape and Gurney's sugarbirds in each activity, and Mann Whitney U values comparing the amount of time spent by both sugarbird species at mid breeding season ( $n_1 = 10$ ,  $n_2 = 10$ ). Significant values as asterisked ( $p \leq 0.05$ ).

Activity	Cape sugarbird	Gurney's sugarbird	U	p
<b>Morning</b>				
probing for nectar	6	8	40	0.45
hawking for arthropods	0	0	30	0.13
perching	17	20	43	0.60
preening	13	3	22	0.03*
singing	20	17	37	0.33
chatting	0	3	32	0.17
display	1	0	40	0.45
flying	2	4	14	0.007*
competition	0	2	28	0.10
interaction with mate	0	0	44	0.65
nesting	0	1	45	0.71
feeding chicks	0	0	50	1.00
<b>Midday</b>				
probing for nectar	4	12	24	0.05*
hawking for arthropods	1	0	32	0.17
perching	15	22	38	0.36
preening	0	0	20	0.02*
singing	24	18	40	0.45

chatting	0	2	30	0.14
display	0	0	41	0.50
flying	0	4	12	0.004*
competition	0	0	30	0.13
interaction with mate	0	0	35	0.26
nesting	0	1	45	0.71
feeding chicks	0	0	50	1.00
Afternoon				
probing for nectar	2	6	41	0.50
hawking for arthropods	1	1	31	0.15
perching	26	13	28	0.10
preening	7	7	42	0.57
singing	17	10	28	0.10
chatting	0	2	39	0.41
display	0	0	41	0.50
flying	1	1	48	0.88
competition	0	1	34	0.24
interaction with mate	0	0	50	1.00
nesting	0	0	50	1.00
feeding chicks	0	0	50	1.00

Table 4: Mean time (min/h) spent by Cape sugarbirds on each activity, and Mann Whitney U values comparing the amount of time spent by Cape sugarbirds at mid and the end of the breeding season in 1999 ( $n_1 = 10$ ,  $n_2 = 10$ ). Significant values as asterisked ( $p \leq 0.05$ ).

Activity	Mid breeding season	End breeding season	U	p
<b>Morning</b>				
probing for nectar	6	13	28	0.10
hawking for arthropods	0	1	35	0.26
perching	17	25	30	0.13
preening	13	8	39	0.40
singing	20	10	27	0.08
chatting	0	0	39	0.42
display	1	0	34	0.22
flying	2	2	49	0.94
competition	0	1	26	0.07
interaction with mate	0	0	49	0.97
nesting	0	0	50	1.00
feeding chicks	0	0	50	1.00
<b>Midday</b>				
probing for nectar	4	5	45	0.71
hawking for arthropods	1	0	37	0.33
perching	15	35	3	0.0004*
preening	10	10	44.5	0.68

singing	24	8	15	0.008*
chatting	0	0	45	0.71
display	0	0	47	0.85
flying	0	1	24	0.05*
competition	0	0	30	0.13
interaction with mate	0	0	50	1.00
nesting	0	0	50	1.00
feeding chicks	0	0	50	1.00
Afternoon				
probing for nectar	2	4	36.5	0.31
hawking for arthropods	1	0	30	0.13
perching	26	29	41	0.50
preening	7	5	49.5	0.97
singing	17	13	32	0.17
chatting	0	0	35	0.26
display	0	0	49	0.94
flying	1	1	47	0.82
competition	0	1	43	0.57
interaction with mate	0	0	50	1.00
nesting	0	0	50	1.00
feeding chicks	0	0	50	1.00

## Figures

Figure 1: Time (min/h) spent probing for nectar, hawking for arthropods, perching on top of trees, preening, flying, singing and in intra- and interspecific competition for (a) Cape sugarbirds at mid season; (b) Gurney's sugarbirds at mid season; and (c) Cape sugarbirds at the end of the season in the morning (06h30/07h00), midday (11h30) and in the afternoon (16h30). Error bars are mean +/- standard deviation.

Figure 2: Time (min/h) spent feeding on the inflorescences of different *Protea* types by Cape sugarbirds: (a) at mid season and (b) at the end of the season in the morning (07h00), midday (11h30) and afternoon (16h30). Error bars are mean +/- standard deviation.

